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Quo Vadis, Behavioural Biology?

Past, Present, and Future of an Evolving Science

Andreas Wessel, Randolf Menzel, and Günter Tembrock† (Eds.)

Deutsche Akademie der Naturforscher Leopoldina –
Nationale Akademie der Wissenschaften, Halle (Saale) 2013

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Quo Vadis, Behavioural Biology? Past, Present, and Future of an Evolving Science

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April 30 to May 4, 2009

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With 139 Figures and 2 Tables

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Cover:
The three foxes represent fundamentally different aspects of behaviour. The first fox stands for motivation and orientation towards a goal at a distance. The second fox signifies activation of a motor pattern with identification of the spatial position of the goal. The third fox marks the end of the sequence with consummatory acts, such as killing and eating.

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Inhalt

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Foreword

On September 1st, 1948, the first behavioural biological research institution in Germany was founded by Günter TEMBROCK at the Berlin University with the support of the German Academy of Sciences Berlin. On the occasion of the 60th anniversary of the foundation of the "Research Institution of Animal Psychology" (*Forschungsstätte für Tierpsychologie*) 32 invited speakers from 9 countries and about 400 attendees participated at the "Berlin Behavioural Biology Symposium" from April 30th to May 4th, 2009 at the Humboldt University Berlin to exchange views about "Past, Present, and Future of an Evolving Science".

The discipline of behavioural biology in Germany has developed into multiple directions with manifold approaches since its foundation as *Tierpsychologie* (animal psychology) at the beginning of the last century. It has been and still is involved in many ways in conceptual and methodological developments in biology experiencing a high degree of differentiation. Subdisciplines such as ethology, behavioural ecology, sociobiology, experimental psychology, human ethology, biosemiotics, evolutionary psychology and many more have not only developed their own ways to interact with other disciplines, but have occasionally even claimed to represent the entire field of behavioural biology exclusively while being subjected to strong integrative efforts within the field at the same time.

Berlin, as one of the founding centres of ethology and modern behavioural biology, with several research groups at each of the city's universities, seems a good place to discuss the past, present and future of the discipline in an international forum. One of the "fathers of ethology", Oskar HEINROTH, worked at the Berlin Zoological Garden, Erwin STRESEMANN, together with HEINROTH, the mentor of Konrad LORENZ, was acting from the Museum of Natural History of the Berlin University, and Günter TEMBROCK founded his research institution for behavioural biology at its Zoological Institute.

Embedded in this historical frame, the international symposium was organized jointly by the Humboldt University and the Leopoldina aiming at discussing and possibly further developing current topics and concepts of behavioural biology. The assessment of the current situation of behavioural biology by renowned representatives of the field served as a starting point, and was challenged, extended and continued by outstanding younger scientists. In order to achieve these goals an innovative concept was devised which proved very successful and was well received by the participants. 16 scientists were invited by the organizers as *Distinguished Senior Lecturers*. Speakers were not only chosen based on ground-breaking research results, but particularly if they had made a major conceptual and interdisciplinary contribution that has considerably influenced and shaped the entire field of behavioural sciences. The *Distinguished Senior Lecturers* were asked to invite an outstanding younger scientist of their choice as an *Invited Co-Lecturer*; both lecturers presented and discussed their topic together (see also Diesner and Wessel 2010).

Fig. 1 Some of the speakers who gathered on the balcony before the Humboldt University Senate hall. From left to right: I. Pepperberg, W. Schiefenhövel, B. Hassenstein, A. Zahavi, P. Klopfer, T. Riede, R. Gadagkar, K. Okanoya, B. Ronacher, G. Tembrock, K. Kotrschal, D. Cheney, R. Menzel, B. Brembs, J. Fischer, C. Lehmann, S. Savage-Rumbaugh. (Photo by T. Diesner)

This generation-spanning meeting of some of the field's leading figures who co-founded the discipline, and the scientists currently conducting the bulk of experimental research allowed for developing a unified perspective of the field incorporating current thinking. The teams were composed as follows:

Distinguished Senior Lecturer:		*Invited Co-Lecturer:*
Patrick Bateson (UK)	—	James P. Curley (US)
Dorothy L. Cheney (US)	—	Julia Fischer (DE)
Raghavendra Gadagkar (IN)	—	Anindita Bhadra (IN)
Bernhard Hassenstein ML (DE)	—	Bernhard Ronacher ML (DE)
Peter H. Klopfer (US)	—	Peter Kappeler (DE)
Hans Kummer ML (CH)	—	Klaus Zuberbühler (UK)

David Macdonald (UK) — Tom Moorhouse (UK)
Peter R. Marler (US) — Kazuo Okanoya (JP)
Randolf Menzel ML (DE) — Björn Brembs (DE)
Irene M. Pepperberg (US) — Adena Schachner (US)
Sue Savage-Rumbaugh (US) — William M. Fields (US)
Wulf Schiefenhövel (DE) — Christian Lehmann (DE)
Wolfgang Schleidt (AT) — Kurt Kotrschal (AT)
Günter Tembrock ML (DE) — Tobias Riede (US)
Elisabetta Visalberghi (IT) — Elsa Addessi (IT)
Amotz Zahavi (IL) — Arnon Dattner (IL)

Thanks to the generous financial support of the *Deutsche Forschungsgemeinschaft* (DFG, German Research Council) and the Humboldt-Universitäts-Gesellschaft the attendance of the symposium was free, consequently reflected in the exceedingly high share of young participants.

Twenty-two speakers provided contributions to this book illuminating the breadth and depth of the topic. Additionally, Bernd Heinrich followed our invitation to contribute a paper. In their entirety the papers give an exciting and forward-looking perspective into the set of issues to which Hans Kummer dedicated himself quite explicitly: Where are our questions coming from?

We resisted the temptation to arrange the chapters according to somewhat contrived criteria, such as taxa dealt with or methods used, but instead let them follow Günter Tembrock's keynote lecture in the same order the authors had presented their papers at the symposium.

The symposium was co-organized by the *Darwin-Gesellschaft zu Berlin, Deutsche Zoologische Gesellschaft, Ethologische Gesellschaft, Gesellschaft für Anthropologie, Gesellschaft für Humanontogenetik, Gesellschaft Naturforschender Freunde zu Berlin, Humboldt-Universitäts-Gesellschaft, Museum für Naturkunde Berlin, Urania Berlin, Zoologischer Garten* and *Tierpark Berlin*.

The Organizing Committee comprised Christoph Markschies (Patron, Humboldt-Universität zu Berlin, President), Jutta Schnitzer-Ungefug (Deutsche Akademie der Naturforscher Leopoldina), Günter Tembrock (Honorary Chair, Humboldt-Universität zu Berlin), as well as Thomas Diesner (Gesellschaft für Humanontogenetik), Joachim Erber (Technische Universität Berlin), Julia Fischer (Deutsches Primatenzentrum Göttingen), Reinhold Leinfelder (Museum für Naturkunde Berlin), Randolf Menzel (Freie Universität Berlin), Bernhard Ronacher (Humboldt-Universität zu Berlin), Andreas Wessel (Darwin-Gesellschaft zu Berlin), Karl-Friedrich Wessel (Humboldt-Universität zu Berlin), and Bernhard Blaszkiewitz (Zoologischer Garten und Tierpark Berlin).

Many thanks for supporting the organization go to Thomas Richter, Eva-Maria Kolb and Ines Martina Bartsch-Huth of the Humboldt University. The symposium could only be implemented so successfully and smoothly because of the untiring commitment of Björn Stelbrink, Thomas Diesner, Sylvia Wendland-Tembrock, Siegfried Jablonski, Fritz Kleinhempel, Jörg Schulz, and Sophia Seidel. Björn deserves special gratitude for his assistance during the entire planning and preparation of the symposium. The junior editor (AW) thanks the Museum of Natural History and especially Hannelore Hoch and Thomas von Rintelen for the provision of working space during the editing of the present book.

Fig. 2 The senior editors in an intense discussion during the Berlin Behavioural Biology Symposium at Humboldt University, May 2nd, 2009 (Photo by J. Schulz).

On January 26th, 2011, Günter Tembrock died in his 93rd year. Even in the winter term 2009/10 he lectured at "his" university about the "fundamental issues of biology" and took an interest in his work until last, thus, his contribution for the present volume became an important legacy (for an obituary see Wessel 2011). In order to maintain and continue Tembrock's achievements, in September 2011, Sylvia Wendland-Tembrock established the Günter Tembrock Foundation at the Humboldt University. The foundation supports the setup of a Günter Tembrock Archive as a vital workplace for integrative life sciences. Furthermore, the Humboldt University and the Tembrock Foundation brought an annual Günter Tembrock Lecture into being, the first of which was given on June 7th, 2011, by Pat Bateson (2012) and which was continued on the same day last year (Günter's birthday) by Peter H. Klopfer (2012).

Tembrock's legacy comprises an exceptional body of work which will undoubtedly be built upon.

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an der Humboldt-Universität zu Berlin

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Address of Welcome

Theodor Hiepe ML (Berlin)

Dear Mr. Vice-President Nagel, dear Prof. Menzel, dear Prof. Tembrock,
dear Dr. Wessel,
dear Academy Members,
Ladies and Gentlemen,

On behalf of the president of the German Academy of Sciences Leopoldina, Prof. Volker ter Meulen, I would like to welcome you to the international symposium "From *Tierpsychologie* to Behavioural Biology".

This highly relevant topic fits the 1st principle ("To Explore Nature to the Benefit of the Human Being") of our academy – continuous existed since 1652 and now, for almost a year, also being a national academy.

The behaviour of organisms, especially of humans, has been on the agenda of the Leopoldina for more than 300 years. Extraordinary scientific characters of this academy dedicated themselves to this issue. I will name only a few: Johann Leonhard Frisch (1666–1743; member of Leopoldina [L] since 1725), Carl von Linnè (1707–1778; L 1736), Carl Asmund Rudolphi (1771–1832; L 1818), Johann Wolfgang von Goethe (1749–1832; L 1818), Alfred Brehm (1829–1884; L 1849), Rudolph Leuckart (1822–1898; L 1853), Ernst Haeckel (1834–1919; L 1863), Oskar Heinroth (1871–1945; L 1936) and Konrad Lorenz (1903–1989; L 1956), Erwin Stresemann (1889–1972; L 1954), Ernst Mayr (1904–2005; L 1970), Heinrich Dathe (1910–1991; L 1974), Randolf Menzel (*1940; L 1996) and Günter Tembrock (1918–2011; L 1965).

The constant search for knowledge of the behaviour of humans and animals is easy to comprehend, since behaviour constitutes an element of life! The continuous quest for new findings in the field of behaviour requires synoptic, transdisciplinary research. One of our academy members, Prof. Günter Tembrock, is one of the leading figures in the field of comparative ethology. I was fortunate enough to experience Günter Tembrock's work at first hand, ever since my appointment to the chair of parasitology of the Humboldt University (in 1960).

As a parasitologist I classify the essence of parasitism to represent co-existence in life. Albeit, so far we have not ventured to learn more about this life-form by means of behavioural research.

During the last few decades, the results of fundamental research in the fields of natural sciences, life sciences, genetics, and gene technology have laid a solid groundwork to furthering the advancement of behavioural research. May this symposium, a cooperation between the Humboldt University and the Academy of Sciences Leopoldina, serve as a platform for comprehensive research in the field of behavioural sciences – according to the 2^{nd} principle of the Leopoldina: "Nunquam otiosus".

I hope this meeting will provide you with plenty of new insights into the topic and I wish you all a pleasant stay in Berlin.

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Ethology in Space and Time – Berlin in the Light

Andreas WESSEL (Berlin)

With 9 Figures

Abstract

Nothing in science makes sense except in the light of history, and ethology does have a rather complex one. In this introductory lecture I will shortly explore the roots and the growth of behavioural biology focusing on developments in Berlin up to the foundation of the first German ethological research institution by G. TEMBROCK in 1948.

Zusammenfassung

Nichts in der Wissenschaft ergibt einen Sinn, außer im Licht der Geschichte. In diesem einleitenden Vortrag beleuchte ich kurz die Wurzeln und das Wachsen der Verhaltensbiologie mit besonderer Berücksichtigung der Entwicklungen in Berlin bis zur Gründung der ersten ethologischen Forschungseinrichtung in Deutschland 1948 durch G. TEMBROCK.

1. Introduction

The title of our symposium “From *Tierpsychologie* to Behavioural Biology – Past, Present, and Future of an Evolving Science” does not contain the word “ethology”, which might be considered suspicious. Nevertheless, the term “ethology” in particular, its origin and development, are intimately connected with Berlin. On the one hand, the local history of science in Berlin highlights the enormous complexity of the development of behavioural biology including the latter’s vulnerability to political and ideological influences. On the other hand, work done in Berlin has initiated and driven developments that have influenced the entire discipline. I will also attempt to review the specific motive of our symposium, the 60th anniversary of the first research facility for behavioural biology in Germany, within its historical context. This short historical sketch aims at providing both a basis for the following lecture by Günter TEMBROCK (1918–2011, Fig. 1) on the change of concepts of behavioural biology at this university as well as some suggestions for the attempts to probe into the future of our discipline during the next few days.

Fig. 1 Günter Tembrock, 1951. (Museum für Naturkunde Berlin, Historische Bild- und Schriftgutsammlungen [MfN, HBSB] / Bestand ZI /Signatur B I/37)

I am occasionally tempted to depict behavioural biology as a tree. We have a mighty albeit short trunk bearing the label 'ethology', which is supported by numerous widely branched and deep roots from apparently disparate fields such as physiology, ecology, taxonomy, phylogenetics, functional morphology and anatomy, as well as psychology and philosophy; from the trunk arise branches of different strength and shape, which form a somewhat ruffled crown that seems undecided on its direction of growth. Looking a bit more closely at the trunk, we will find that beneath the bark a bundle of very diverse and barely connected strands is hidden. These strands influence each other in a highly complicated fashion and are about as frequently attracted by as they seem to repel each other.

The development of a discipline is linked to the development of research institutions and of course also to the actions of individuals operating at these institutions. Personal peculiarities of character and social ties of researchers concerned can hardly be overestimated in this context. Science is basically a social endeavour and each history of science must also reflect sociology of science at a significant level, if it is aiming at approaching some level of truth.

Before turning to the "Laboratory Berlin" and discussing some elements and factors of its development, I would just like to remind you that one of the deepest roots of modern behavioural biology can also be traced to Germany. In 1760, Hermann Samuel Reimarus (1694–1768) published his *Allgemeine Betrachtungen über die Triebe der Thiere* (*General*

Considerations about the Drives of Animals) in Hamburg, which represents an early milestone in the study of instinctive behaviour in animals and was published in a new edition in 1982 with a foreword by Ernst MAYR (1904–2005).

2. The Roots in Berlin

In Berlin, the *Gesellschaft naturforschender Freunde zu Berlin* (The Berlin Naturalists Society) was founded in 1773, which could call almost all persons important in behavioural biology in Berlin their members; among others, seminal papers by Oskar HEINROTH (1871–1945) were published in the proceedings of their meetings.[1] Though, the most important and ultimately consequential event was the foundation of Berlin University almost exactly 200 years ago (1810). From the start, the zoological museum was part of the university and moved as *Museum für Naturkunde* (Museum of Natural History) into its own purpose-built building in 1889. Today, the world's fifth-largest natural history museum, it has recently (2009) become an independent foundation associated with the university. In 1844, the director of the museum, Hinrich LICHTENSTEIN (1780–1857, Fig. 2), founded the zoological garden, which,

Fig. 2 Hinrich LICHTENSTEIN, lithography by L. BUCHHORN, 1823. (MfN, HBSB / GNF / PM XI, 9)

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[1] See e. g. HEINROTH 1930.

based on the example set by London's zoo, he devised primarily as an institution for "scientific observations and studies" of living animals in order to complement museum studies. This aim, which rather represented a perspective, could only be fully realized 50 years later by HEINROTH. In 1869, the popular zoologist Alfred BREHM (1829–1884) opened the first aquarium in Berlin, just a few hundred meters from here (*Unter den Linden 68*) in the centre, which was predominantly devoted to public education. At the university, the zoological institute was founded in 1884 by Franz Eilhard SCHULZE (1840–1921), which subsequently harboured several eminent ethologists and physiologists. Not least, Günter TEMBROCK founded his research centre at the institute, and I will come back later to this in more detail. After BREHM's aquarium was shut down in 1910, a new aquarium was devised at the zoological garden and opened in 1913 by Oskar HEINROTH, who also remained its director until his death in 1945. In 1936, a politically already rather difficult time, the *Deutsche Gesellschaft für Tierpsychologie* (German Society for Animal Psychology) devoted to the "study of the soul of animals and the practical interpretation of results in animal psychology", was founded in Berlin. Since 1937 the *Zeitschrift für Tierpsychologie* had been published by the society's first president, the veterinarian Carl KRONACHER (1871–1938), together with Otto KOEHLER (1889–1974) and Konrad LORENZ (1903–1989). Today, the journal (re-named *Ethology* in 1986) is the official organ of the *Ethologische Gesellschaft*.

After the political and administrative division of Berlin during the post-war period, though before the erection of the Berlin Wall, a separate zoological garden, *Tierpark Friedrichsfelde*, was founded in 1955 in the eastern part of the city by Heinrich DATHE (1910–1991). From its very start it was also intended to serve research in behavioural biology. In the west of Berlin the *Freie Universität Berlin* was founded with the specific aim of serving as a counter-part to the Humboldt University, and given chairs of behavioural biology and neurobiology in 1976. By the way, all of the still existing institutions mentioned so far are co-organizers of this symposium.

3. On the Way to Ethology

Before I mention some relevant persons in more detail, please allow me to dwell a bit on the term ethology: the word was first used by Isidore GEOFFROY SAINT-HILAIRE (1805–1861) in 1854, who used it to denote "the study of relationships of organisms organized in the family and the society, in the aggregation and the community".[2] Until about 1900 the term had then been used synonymously with the term ecology introduced into biology by Ernst HAECKEL (1834–1919). Starting from about the mid-19th century, psychologists and physiologists independently developed an interest in animal behaviour. The resulting fields called animal psychology or comparative psychology, and sensory or neurophysiology, respectively, stimulated each other and were occasionally also merged as psycho-physiology. Only from 1900 onwards, the term ethology was employed in a more narrow sense for the comparative study of inherited or instinctive behaviour, albeit in Germany still more than 50 years parallel with the term animal psychology.

Berlin took its first important role in linking psychology and physiology as the place of Wilhelm WUNDT'S (1832–1920) study, who got acquainted in 1855/56 with the "New

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[2] GEOFFROY SAINT-HILAIRE 1854, p. 285.

Physiology" of Johannes Müller (1801–1858) and also established contact with Emil du Bois-Reymond (1818–1896). In 1874, Wundt published his *Grundzüge der physiologischen Psychologie* (Outlines of physiological psychology), and in 1879, he founded the world's first institute of psychology in Leipzig. In his *Lectures on the Soul of Man and Animals* (1st ed. 1863) he formulated as a principle for animal psychology: "from Human to animal soul, not vice versa, is the only possible direction of comparative psychology".[3]

Since the 1880s both the more comparative-psychological and ecological as well as the physiological branch of studies on animal behaviour have been represented at the university. Karl August Möbius (1825–1908, Fig. 3), director of the zoological museum since 1887, gives one of the world's first lectures on animal psychology *Über das Seelenleben der Tiere* (On the expression of the soul in animals) and the archive of the museum also contains the manuscript of a book planned on this topic.[4] His most important student, Friedrich Dahl (1856–1929, Fig. 4), had been the curator of spiders at the museum since 1898; in 1901, he already used ethology in a more narrow sense and later on published a definition of ethology as "the part of zoology which is dealing with the deliberate movements of animals".[5]

Fig. 3 Karl Möbius, June 1875. (MfN, HBSB / ZM / B I/272)

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[3] Wundt 1911, p. 18.

[4] See Tembrock 2002.

[5] Dahl 1922, p. 2.

Fig. 4 Friedrich Dahl (MfN, HBSB / ZM / B I/1892)

At the zoological institute of the university under Karl Heider (1856–1935) a rather more physiologically inclined branch of animal psychology became established which is associated with the names of Alfred Kühn (1885–1968), Wolfgang von Buddenbrock (1884–1964) and Konrad Herter (1891–1980, Fig. 5). Whereas Kühn and Buddenbrock had been in Berlin for only about two years, Herter was a member of the university from 1921 until 1951, before he switched to West Berlin's *Freie Universität* in 1952. Herter was the first after Möbius to give lectures on "Animal psychology" and was given a chair of "Comparative physiology of sensory organs and animal psychology" in 1926. Karl Heider's successor as director of the institute, Richard Hesse (1868–1944), was particularly interested in specific physiological studies on organism-environment-interaction and became the co-founder of ecophysiology. He supervised the Ph.D. theses of Hansjochem Autrum (1907–2003) and Erich von Holst (1908–1962) on topics in neurophysiology and sensory physiology, respectively. Subsequently, both became assistant professors (*Wissenschaftliche Assistenten*) at the institute.

At about the same time Wolfgang Köhler (1887–1967) pursued a more comparative-psychological approach to behavioural research. He studied in Berlin under Max Planck (1858–1947) and Carl Stumpf (1848–1936), and obtained his Ph.D. on psycho-acoustics under Stumpf in 1909. Between 1914 and 1920 he conducted studies on apes at Teneriffa on behalf of the Berlin Academy of Sciences, and in 1925 he published his seminal study

Fig. 5 Konrad Herter, September 1966. (MfN, HBSB / ZI/ B I/33)

on *The Mentality of Apes* (first German edition in 1917). He was the head of the psychological institute of Berlin University from 1922 until 1935 and became the founder of Gestalt psychology.

4. The Central Figures of Ethology in Berlin

Let's turn to the central figure of ethology in Berlin Oskar Heinroth (Fig. 6). He was born in 1871 and studied at this university from 1896 onwards. Early on, he was seeking contact to the zoological garden, where he had been holding a tenured position since 1904 and started working on the observation and breeding of birds. In 1910, Heinroth was co-organizer of the International Congress of Ornithology in Berlin, where he gave his famous talk *Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden* (Contributions to the biology, particulary ethology and psychology of anatids), which was published a year later in the Conference Proceedings and may retrospectively be regarded as one of the founding documents of ethology (Heinroth 1911). Heinroth already started to record bird songs in nature in the 1920s together with Ludwig Koch (1881–1974). In 1935, they jointly published the first „sounding textbook" *Gefiederte Meistersänger* (Plumaged master singers) with gramophone records.

Fig. 6 Oskar Heinroth, May 1900. (MfN, HBSB / ZM / Orn. 12,8)

Before proceeding to the “Berlin big bang” of ethology it must be mentioned that since 1921 the ornithologist Erwin Stresemann (1889–1972, Fig. 7) had been working first as an assistant, later as curator, at the zoological museum. From 1922 onwards he was also editor of the *Journal für Ornithologie*, and in this position he published seminal ethological studies, such as in 1927, the first paper by Konrad Lorenz. Together with Heinroth, with whom he had been corresponding since 1930, Stresemann became an important mentor for Lorenz.[6]

Retrospectively, one of the most important events for the development of ethology surely was the meeting of Konrad Lorenz and Erich von Holst on February 17th, 1936, in Berlin following a talk by Lorenz, which laid the foundation for a life-long collaboration. Incidentally, Niko Tinbergen (1907–1988) and Lorenz also met for the first time in that year in Leiden. The founding of the German Society for Animal Psychology in the same year has already been mentioned earlier.

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[6] See also Tembrock 1991.

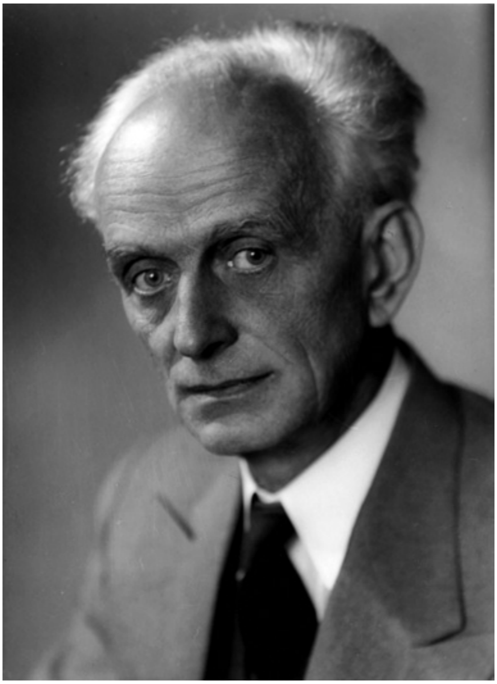

Fig. 7 Erwin STRESEMANN, 1955. (MfN, HBSB / ZM / B I/2206)

In 1937, Günter TEMBROCK started his studies at this university, where he has been continuously working for 73 years.[7] In 1935, still being a pupil, TEMBROCK already visited Oskar HEINROTH and also attended the presentation of the "*tönenden Lehrbuchs*" (sounding textbook) at the Museum of Natural History.[8] Since that time a close contact had been kept with regular visits and discussions within the framework of the *Gesellschaft naturforschender Freunde,* of which TEMBROCK became a member in 1942, in the same year as Katharina HEINROTH (1897–1989, Fig. 8), by the way. TEMBROCK also initiated the evacuation of the important collection of bird eggs from the aquarium, which had been already damaged by bombs, to the museum, where it survived the war. While TEMBROCK's academic teacher at the zoological institute, Konrad HERTER, also worked on problems of animal psychology as I mentioned above, TEMBROCK himself considers the influence of HEINROTH on him as much more important, likewise the early works by LORENZ, which were heavily and critically debated among the students.

HEINROTH and LORENZ represent in several respects two opposite extremes, which equally contributed to shaping TEMBROCK's way of thinking. HEINROTH took a rather critical attitude towards any theorizing and consistently rejected any systematic basis of ethological theory. According to TEMBROCK a typical dictum was: "*Es geht so oder auch ganz anders*" ("It works this way or very differently"); in contrast, Lorenz rather stated: "*Es ist so, und nicht anders!*" ("This is the way it is and not otherwise").

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[7] See WESSEL 2010, 2011.

[8] See TEMBROCK 2001.

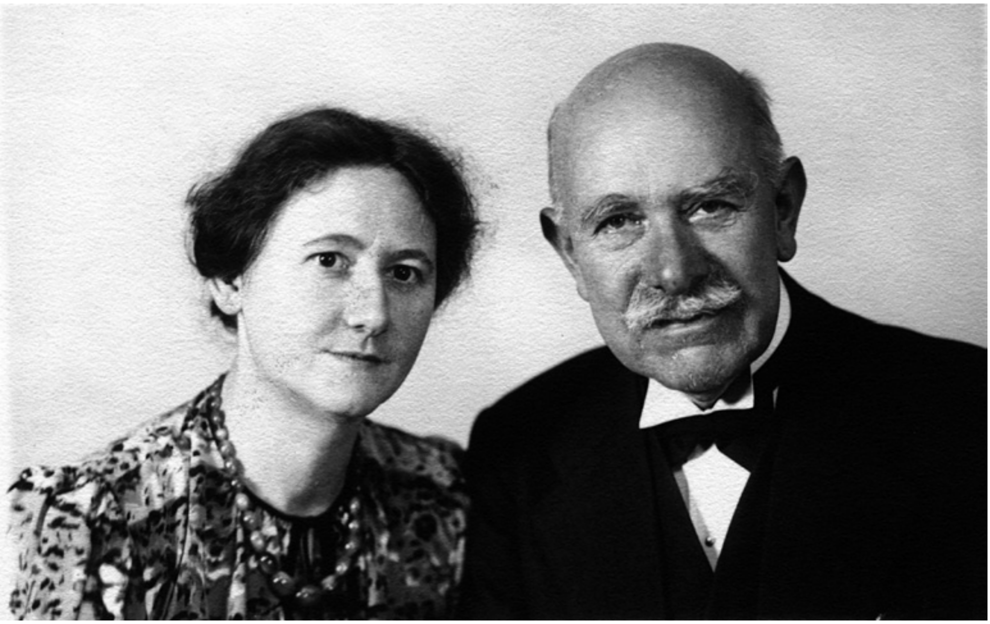

Fig. 8 Katharina Heinroth with Oskar Heinroth, 13th December 1940. (MfN, HBSB / ZM / B II/342)

After the war in 1947, Günter Tembrock (Fig. 9) started studying the last chimpanzee surviving the war at the Berlin Zoo, named Susi, and in 1948, he was able to obtain his first fox, thanks to the mediation of Katharina Heinroth. During the following decades he always attempted to combine observations in the natural environment with experiments, adhering to the maxim of Lorenz that deep ethological insights may only be gained from the experience of the animal lover and keeper. In December 1947, Tembrock addressed the Berlin Academy of Sciences with a "memorandum for the foundation of an institute of animal psychology". In February, the proposal was approved (initially without a definite scheme for funding it) and on September 1st, 1948, the *Forschungsstätte für Tierpsychologie* (Research center for animal psychology) at the zoological institute started its work as the first facility of its kind in Germany. In 1951, Tembrock began his bioacoustic studies, and today, the Berlin archive of animal sounds at the Museum of Natural History has become one of the largest collections in the world.

Tembrock's research plan is remarkably complex from the very beginning and significantly exceeds the scope of Lorenz's ethology. Tembrock attempts an integration or synthesis of function, evolution, mechanism, and individual development, while the concept of information becomes increasingly more important. Aims are an "objective definition of terms" and "exact observations". In this context, Tembrock also argues for a "new animal psychology", which should be based on physiology. In 1957, Tembrock participated in the International Ethological Conference at Freiburg, and also 1959, at Cambridge, due to Otto Koehler's invitation – after having had a serious scientific confrontation with him earlier on, though. Then, this promising start of an independent approach within the international community is abruptly severed. As Peter H. Klopfer states in his book *Politics and People in Ethology*: "Tembrock was isolated in East Berlin when the wall cut off the DDR from

Fig. 9 Heinrich Dathe, on the right, and Günter Tembrock in an intense discussion at Erwin Stresemann's 80th birthday, 1st December 1969. (MfN, HBSB / ZM / B II/411)

the rest of the world. His failure to make concessions to the ruling powers prevented his work from attracting the attention it deserved. He was not allowed to travel, and his correspondence was limited. Had he lived in West Berlin, Tembrock might well have been celebrated as one of the founders of bioacoustics and behavioral ecology."[9]

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[9] Klopfer 1999, p. 104.

There is almost nothing left to add. Particularly the dogmatization of Pawlow's doctrine and the politically motivated Lyssenkoism almost killed behavioural biology in the GDR. The institution could only be navigated safely through the ever changing political white water through cooperations with other institutions, commissions for applied research projects, and enormous private (also financial) engagement. Despite these difficulties over the decades, more than 100 Ph.D. theses were submitted, more than 10,000 students attended Tembrock's lectures, more than 500 publications appeared and several of the 37 published books were printed both in East and Western Germany and became standard texts.[10] Following his retirement in 1983, his own TV show (*Professor Tembrocks Rendezvous mit Tieren*, 1984–1991) made him a TV star in East Germany. I hope you are now as curious as I am myself about Günter Tembrock's own account on "60 years of behavioural concepts at the Humboldt University Berlin" (Tembrock 2012, this volume).

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[10] See Wessel 2004, 2008.

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Change of Concepts of Behaviour over the Last 60 Years at Humboldt University Berlin

Günter Tembrock ML (†)

With 18 Figures and 2 Boxes

Abstract

On September 1st, 1948, the institute of ethology or behavioural sciences was founded as *Forschungsstätte für Tierpsychologie* at Humboldt University Berlin. One of the first research subjects was Susi, the only chimpanzee surviving the war at the Zoo Berlin which resulted in my first book with an ethological approach *Grundzüge der Schimpansen-Psychologie* (*Outlines of Chimpanzee Psychology*). Basic concepts about communication and the development of behaviour emerged from the synthesis of evolutionary theory, systems theory, biocybernetics, and theory of self-organization, but also the development of computer technology had a decisive influence. Thus, a clear distinction from former animal psychology led to classical ethological themes defining "the concept of behaviour as organismic interaction with the environment on the basis of an exchange of information ensuring individual, ecological and inclusive fitness".

Some selected aspects will be addressed: Acoustic biocommunication was not seen as an isolated incidence of sound utterances, but as an interaction between sender and receiver, defined as *affine,* i.e. attractive, distance reducing and *diffugous,* i.e. aversive, distance enhancing sounds, whereas ambivalent *intermediary* signals stabilize the distance. It was part of the research on the behaviour of foxes, that led to a substantial increase of the *Tierstimmenarchiv* (Archive of Animal Sounds) and to the formation of *bioacoustics*. The *Three-Vector-Model of Behaviour* was developed as a framework for studying behaviour. Other specific concepts of behaviour as for example chronobiology and the *Theory of Strata* with four 'strata (layers)' emerged: evolutionary, biogenetic, tradigenetic and ratiogenetic potential. In the 1980's the research concept *Humans as Bio-psycho-social Units* incorporating various aspects into the basis of human behaviour was developed in close cooperation with endocrinologists, developmental psychologists and philosophers.

Zusammenfassung

Am 1. September 1948 konnte die *Forschungsstätte für Tierpsychologie* am Zoologischen Institut der Humboldt-Universität zu Berlin begründet werden. Dieses Vorhaben war bereits auf den Weg gebracht, da zuvor mein Kontakt mit der den Krieg überlebenden Schimpansin Susi im Zoo Berlin, verbunden mit Verhaltensbeobachtungen und einigen Versuchen, dazu führte, dass dann 1949 ein Buch unter dem Titel *Grundzüge der Schimpansen-Psychologie* erschien. Grundfragen der Kommunikation und der Entwicklung des Verhaltens ergaben sich aus der Synthese von Evolutionstheorie, Systemtheorie, Biokybernetik und der Theorie von der Selbstorganisation, aber auch die Entwicklung der Computertechnologie hatte einen entscheidenden Einfluss. Somit führte eine klare Unterscheidung von der früheren Tierpsychologie zu klassischen ethologischen Themen und der Definition: „Verhalten ist organismische Interaktion mit der Umwelt auf der Grundlage eines Informationswechsels im Dienst der individuellen, ökologischen und inklusiven Fitness."

Einige ausgewählte Aspekte werden erörtert: Der wissenschaftliche Ansatz ging grundsätzlich davon aus, dass die akustische Biokommunikation nicht eine isolierte Erscheinung von Lautäußerungen darstellt, sondern eine Interaktion zwischen Sender und Empfänger, die, wenn als *affin* definiert, d. h. attraktiv, zu einer Distanzverringerung führt, als *diffug,* d. h. bei aversiven Lauten zu einer Distanzvergrößerung, wogegen ambivalente Signale, *intermediäre*, für die Aufrechterhaltung innerhalb eines bestimmten Abstandes sorgen. Unsere Forschung über das Verhalten des Fuchses sorgte für eine beträchtliche Erweiterung des *Tierstimmenarchivs* und die Einrichtung der Bioakustik. Das *Drei-Vektoren-Modell des Verhaltens* wurde als Rahmenkonzept zum Studium des Verhaltens entwickelt. Andere spezielle Verhaltenskonzepte wie z. B. die Chronobiologie und die Schichtlehre entstanden: evolutionsgenetisches, biogenetisches, tradigenetisches und ratiogenetisches Potenzial. In den 1980er Jahren wurde in enger Kooperation mit Endokrinologen, Entwicklungspsychologen und Philosophen das Forschungskonzept *Biopsychosoziale Einheit Mensch* entwickelt, das verschiedene Aspekte als Grundlage menschlichen Verhaltens integrierte.

In the year 2009 Charles Darwin (1809–1882) became the focus of life sciences since it was he who had created a new view of the world. He also inspired George Romanes (1848–1894) to describe behaviour in his sense. His representation is determined by the following questions: “The Criterion of Mind; The Structure And Function of Nerve-Tissue; The Physical Basis of Mind; The Root-Principles of Mind; Conciousness; Sensation; Pleasures And Pains, Memory, And Association of Ideas; Perception; Imagination; Instinct; Origin And Development of Instincts”, all to be pursued in detail (Romanes 1883). Regarding the central topic of ‘instinct’ Darwin (1883) also provided his contribution, orientated as always on examples.

Against this background my scientific life has been developed and maintained. Already as a school boy I kept arthropods, particularly myriapods and coleoptera in adequate conditions and spent many hours in nature to watch animals. Animal sounds also attracted my special attention. I reflected on evolution, kinship of animal and wo/man as well as the nature of the sexes. Hence, it became obvious that I should follow certain crucial points during my studies just like during school-time. After my Ph.D. thesis on a beetle (*Carabus ullrichi*) and the evolution of sub-species (1941, see Tembrock 1942, 1944/2004), I turned to behaviour in 1948. At that time there were no concepts within the university curricula in Germany and Konrad Lorenz (1903–1989) who was a professor in Königsberg returned from war imprisonment only in 1948. Thus, my proposal for the establishment of a respective research group at the Berlin University (1946–1949, then Humboldt University Berlin) was substantiated as sub-department of animal behaviour (*Forschungsstätte für Tierpsychologie*) with the support of the German Academy of Sciences. Two scientists and two technical assistants were envisaged. This was realized on September 1st, 1948 (see also Box 1). The following crucial aims were formulated: 1. analysis of principles of animal behaviour, 2. analysis of endogenous psychological processes, 3. investigation of innate behaviour patterns, 4. investigation of learned behaviour (particularly associations, learning capacity, memory, insight behaviour and abstraction), 5. analysis of instinct actions and their releasors (releasing mechanisms) (see also Box 2).

The concept is clearly autonomous which was also a reaction to the ideologically influenced concepts prevailing in Germany until 1945. At that time Konrad Lorenz’ essay on *Innate forms of possible experience* was discussed critically (Lorenz 1943). Over 12 years of dominating ideology had left its mark and only slowly – beginning in 1949 – new concepts and questions emerged. Our way started 1948 after having made observations of and some experiments with the only surviving female chimpanzee of the

Box 1
Letter to Konrad Lorenz, 1949

In order to avoid portraying those times only in retrospect it may be permitted to cite a letter to Konrad LORENZ dated August 25th, 1949 in extracts:

"Our venture roots in my chimpanzee studies. They show me that the research needs to be broadened to achieve appreciable successes. Hence, I contacted the relevant authorities, especially the university [...] and the academy of sciences met my plans with much understanding thus enabling me in the autumn of last year to bring the 'Research Station for Animal Psychology' ('*Forschungsstätte für Tierpsychologie*') into being. I believe in filling a current gap, and particularly hope to interest the young generation yet again for animal psychology to a greater extent and to offer appropriate research opportunities. Thus, already two Ph.D. students are operating here, one on squirrels and the other on mice (behavioural analysis, displacement activities and others). Furthermore, I could gain two assistants: Ms. Dr. Kettner who graduated on colour vision of fishes with Prof. Herter and Mr. Dr. Ohm who specializes on cichlids. Next, I considered it crucial to establish card files of references incorporating all relevant papers which has already progressed quite a bit. A file of photographs is in the making (an indispensable tool of animal psychology), accordingly, a film archive is planned. Understandably, the library increases slowest as unfortunately, the flow from outward sources is indeed very sparse. At the very beginning, coincidence led a fox to us so that we found our first research animal without knowing that Dr. Seitz had already collected much more extensive material. Happily, our projects seem to complement each other well so that we – lacking appropriate outdoor facilities – can carry out behavioural studies only marginally (and under very artificial keeping conditions in rooms)... Thus, we work primarily experimentally with issues of gestalt psychology and association problems have particular priority inspired by a paper of W. Köhler (which I cite in my paper enclosed). Furthermore, we examined colour vision of foxes which appears to be close to that of dogs. Six foxes live with us at the moment. Some golden hamsters, one Siberian hobby, a Little owl and a magpie as well as squirrels and diverse cichlids complement our little zoo. I don't know whether you know our zoological institute here in Berlin, where we have four rooms at our disposal; naturally, one can't accommodate much here. However, with the vegetable gardening decreasing I begin to reserve our garden hoping to be able to install there some outdoor enclosures. Moreover, I consider working in the zoo with complaisance of Ms. Dr. Heinroth thus expanding the base step by step, since only comparative and once again comparative studies can further our cause. In seminars and colloquia we try to clarify terms and to stimulate the young generation. Thus, I hope to succeed with our modest means to contribute a bit to our science which needs above all good observers and experimenters who also understand really getting into contact and building up a relationship with the animal."

Zoo Berlin (Fig. 1) leading to a book with the title *Outlines of Chimpanzee Psychology* (TEMBROCK 1949a). This presentation shows elements characterizing the start of behavioural biology in connection with the concept of the sub-department of animal behaviour founded in 1948 at Humboldt University having been pursued for now over 60 years. One may detect an 'evolution' leading now to global concepts which maintain a holosphere as a synthesis of biosphere and noosphere linked with viable and sustainable behaviour.

Box 2

Schedule of work documented for the first years of the Sub-Department of Animal Psychology at the Zoological Institute of the Humboldt University Berlin (founded September 1st, 1948; funded by the German Academy of Sciences).

Schedule of Work 1948/49

1. Basic research
   - Field studies
   - Studies under captive conditions
   - Experimental research: field, zoological garden, laboratory

   Topics and questions:
   - Physiological basis of animal behaviour
   - Analysis of endogenous (psychological) processes
   - Ontogeny of innate behaviour
   - Acquired types of behaviour
   - Analysis of innate behaviour, fixed action patterns, and releasing mechanisms

2. Establishment of methods for the application of results of basic research for keeping and breeding of animals

Schedule of Work 1950

1. Experimental research of red foxes
2. Observation on releasing mechanisms of various species
3. Investigation on reproductive behaviour in cichlids
4. Installation of a central literature index
5. Establishment of a film and slide collection
6. Installation of a subject-catalogue (for a dictionary)

Schedule of Work for 1951

1. Installation of a literature and figure catalogue
2. Comparative-psychological studies on canids
3. Studies on reproductive behaviour in cichlids
4. Continuation of the studies on the behaviour of chimpanzee “Susi”
5. 2 PhD students work on guinea pigs, rats, and mice
6. Installation of the working library

Public work in the media (magazines, radio, including West-Berlin) and public lectures.

Our research station began critically debating ‘animal psychology’ against the background of *Chimpanzee Psychology* applying the argument that insights can only be won by including the evolutionary process as already requested by the concept of research of 1948 (see Box 2). Thus, I can assume that this started the long way to be talked about here. The next step is marked again by a book that appeared in 1956 allowing for portraying these unu-

Fig. 1 First visit of the author to chimpanzee Susi on May 13, 1947, at the Berlin Zoo (from Tembrock 1949a).

sual 60 years very precisely and not glossed over (Tembrock 1956).[1] The second book is called *Animal Psychology* (Fig. 2), an essentially inappropriate title, but stipulated by the publisher. It should be named "Behavioural Biology". The 48 figures, nevertheless, refer to behavioural patterns, orientation and special issues of behaviour. For the understanding of behaviour, concepts had priority such as for current instinct actions, terms coined by William H. Thorpe (1902–1986, Thorpe 1951) and Robert A. Hinde (1954a, 1954b), the SAP – 'specific action potential'. The ethological term 'drive' is differentiated here into the instinct actions and appetitive behaviour proceeding into a consummatory action as formulated by Robert Hinde (1953).

Now, the new quality of labelling behaviour should be mentioned which replaced the former psychological way of describing behaviour with the one of 1956. Part of it includes the theory of strata (theory of layers), developed as early as in 1949 (Tembrock 1949b), which later on is underlying many representations as 'encapsis' represented by a 'bowl model' whereas the fields are made smaller and put one on top of the other (see Fig. 3). Within this context subject-related terms also appeared in my work. It becomes apparent

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[1] The 'evolution' of the different books by Günter Tembrock is illustrated in a supplementary Figure provided by the editors (Fig. S1).

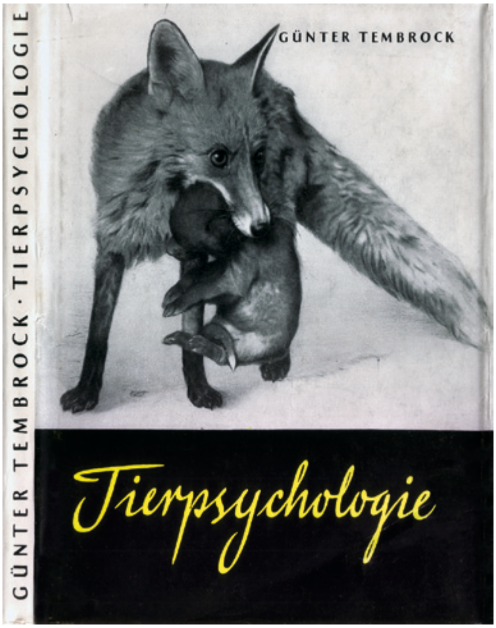


Fig. 2 Cover of the author's first book (1956) on animal psychology. The vixen carries a 23-day-old puppy in rigour (*Tragestarre*). (Photo by the author)

in the chapter "The behaviour of animals". The first figure shows a vixen (*Vulpes vulpes*) in a room displaying species-specific behaviour which in natural surroundings normally leads to burying remaining morsels of meat. Since here this was not possible two species-specific elements of behaviour ensued on the window-sill in the corner where pawing and thrusting were executed completely without functionally leading to any success (Fig. 4). Later on, we filmed this in the outdoor enclosure: After the highest ranking male fox had dug the hole the meat was removed by another fox. After hesitating briefly the male fox continued, closed the pit, covered it with soil and patted it with the tip of his muzzle. Such species-specific behaviour was measured and documented in 'ethograms' (or 'catalogues of actions'). These catalogues of actions were summarized and assigned to 'functional circles' (*Funktionskreise*), e. g. as 'behaviour caused by metabolism'. Behavioural biology is depicted by the following chapters: behaviour and sociology, behaviour and experience, pre-linguistic accomplishments, play, territory, animal and wo/man, psychoneuroses and stereotypes. Furthermore, ontogeny, research methods as well as neurobiology, sensory perception and vocal utterances were addressed. This array also represents our research concepts at that time. Up to 1958, 13 theses including 2 habilitations (post-doctoral qualifications) were completed within the framework of our research.

At that time acoustics gained in importance since from 1951 onwards we had a tape recorder at our disposal. The funds were justified by our proposals to include acoustic behaviour into our investigations and to establish an archive of animal sounds based on the level of tape recorder technique. In 1959, I published the first text book on animal sounds (Tembrock 1959, Fig. 5). Its complete title was: *Animal Sounds. An Introduction to Bioacous-*

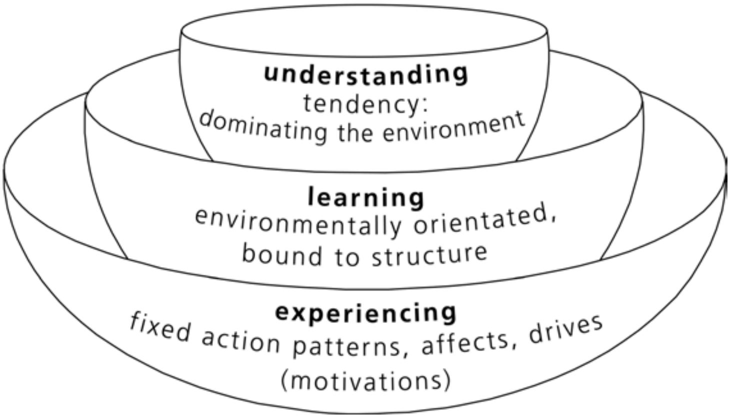


Fig. 3 Theory of Strata (Theory of Layers). The strata or layers form a hierarchical-encaptic system (encapsis). Encapsis means 'nesting' and we chose a 'bowl model' where each 'bowl' depicts a sphere which encompasses all smaller ones completely. This illustration states that for each embedded 'bowl' the properties or regularities, respectively, of the bigger bowls still apply. These properties, however, are now embedded in different framework conditions leading to a new quality.

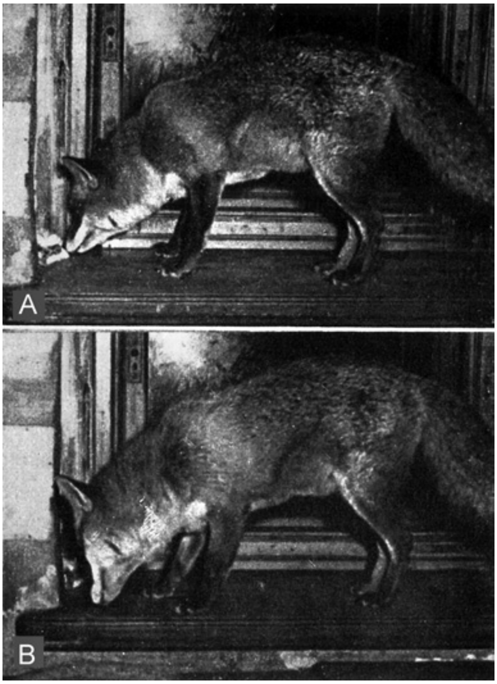


Fig. 4 A vixen of the red fox 'hiding meat'. The operation is performed completely despite of no apparent success: (*A*) shows butting with the muzzle, (*B*) shoving, but without soil as she would do under natural conditions. (Photo by the author)

Fig. 5 (*A*) Covers of the first (1959), and (*B*) the third (1982) edition of the text book on bioacoustics.

tics. The scientific approach fundamentally postulated that ‘bioacoustics’ contained producing of *and* listening to sounds whereas the international approach of ‘biological acoustics’ principally related to the ‘voice of an animal’.

The concept of my presentation reflects the then scientific approach of our research indicated by our questions: relations between tones, complex sounds (clang) and noises, listening to and producing sounds, properties of species-specific sounds of animals, interior factors, sound and meaning, innate and acquired aspects of sound production, ontogeny and phylogeny, animal sounds and human speech, applied bioacoustics and methods. It becomes apparent that behavioural biology is the basis of this way of thinking. Thus, I probably offered the first introduction to bioacoustics as a lecture at a university (since 1963). Here, further new avenues were taken (from an international point of view): they are also combined with a first-time professional sound film for the university centre (Educational film: Tembrock 1958). The topic referred to comparative investigations on canids with regard to kinship as well as to the ontogeny of sound production of the red fox. At the International Conference of Ethology in 1957 I showed a film on the fighting behaviour of the red fox which triggered a lively debate by Konrad Lorenz. At that time we were internationally in the fore-run considering these issues, but we were systematically hampered by the university authorities concerned, combined with the cut of all financial support so that we could not keep the lead. Nevertheless, sound recordings were continued so that nowadays we belong to the three most comprehensive animal sound archives (see internet: www. tierstimmenarchiv.de). The construction of the Wall in 1961 resulted in the loss of our last permanent position (Dietrich Ohm, 1924–2004), and he had to resettle at the Free University in Western Berlin where he engaged in particular in the gender-change of certain fish species.

Despite all the difficulties during that phase I continued my work. In 1961, the next book was published, the newly conceptualized ethology text book in German (Tembrock 1961). Its title read as follows: *Behavioural Science. An Introduction to Animal-Ethology*. It contains 114 figures which graphically illustrate species-specific, functionally-based and other issues. Additionally, it incorporates numerous figures from the literature. The main chapters deal with general ethology, systematic ethology, and experimental behavioural research. An odd era depicting the GDR: the text book was published, but the author of this discipline should not operate any longer. Just having been appointed a professor I was officially not allowed to supervise Ph. D. students which in fact I did unofficially.

In 1959, the vacant chair was filled with a nuclear biologist as the authorities were aiming at removing behavioural sciences from biology. However, I was appointed assistant director of the institute. The new director of the institute (Kurt Erdmann, 1907–1980) was meant to establish nuclear biology instead, but failed to do so. This period of the '60 years' encompasses the era of the zoological institute from 1959 to 1968 and the 'Third University-Reform' (*3. Hochschulreform,* i. e., reform of the higher education system) which led to the dissolution of the zoological institute as it was incorporated into biology. During my term as deputy director (1952–1959) there were two externally funded projects: the behaviour of guide dogs for the blind as well as behavioural concepts for deep-sea fishery. At the same time I initiated a cooperation in neurophysiology (which already existed in Berlin) in alliance with Hans Drischel (1915–1980, University of Leipzig). In connection with the concepts developed until 1959 my field of research within the zoological institute was summarized into three sections under the notion of 'behavioural sciences':

(*1.*) Communication, from insects to primates (with focus on bioacoustics).
(*2.*) Neuroethology.
(*3.*) Selective questions: reinforcing effects in schools of fish; behaviour of schools of fish under time-dependent stimuli; motor activity of golden hamsters under high voltage (externally funded projects, model for humans).

These activities and behavioural research led to us being assigned by the Ministry of Science and Technology to the 'Main Research Area Cybernetics' (biocybernetics), in the Central Working Group 'Human and Animal Physiology'. Under these given premises I could take on in 1968/69 the directorship of the former zoological institute together with the professorship as 'Department of Behavioural Sciences' to which I added unofficially 'zoology' in parentheses since we had to look after this field as a basic education, too (including medical students). Thus, during my term of service the behavioural way had been secured as the only one in the whole GDR. Despite certain SED (party)-functionaries – known to me – who caused many problems I was able to develop the scientific concept according to my own sense. The dynamics of my scientific development have manifested themselves in continuing the preparation of the overviews the last one having been presented in 1961. For the next book again animal psychology was requested as a title: *Principles of Animal Psychology* (Tembrock 1963). To deal critically with this term a 'history' is placed in front and the ‘psychological’ was discussed separately. I can refer to still being persecuted by it. Instinct and experience are logically intertwined. The concept is coupled with the following aspects: the term of instinct, the physiological base of instinctive behaviour, the performances of receptors, central coordinations, obligatory learning, the problem of plasticity, subjective phenomena, genetic bases, orientation in space and time, pre-linguistic performances. The new way of thinking becomes apparent, resulting in the principal separation of ‘facultative learning’ and ‘obligatory’ behaviour. In 1968, my book titled *Outlines of Behavioural Sciences* is published (Tembrock 1968), coining a permanent term which the university chose as a title for the ‘zoological institute’ during the Third University-Reform.

Thus, the chapters chosen here also show the ‘evolution’ of behavioural sciences: ‘the behaviour’, ‘motivations’, ‘releasors and releasing mechanisms’, ‘regulatory principles’ (here biocybernetics), ‘adaptation of behaviour’, ‘evolution and behaviour’. This concept suggests to bring into focus major relationships which form a hierarchical-encaptic system: the ‘world’ of humans (noosphere) presupposes the biosphere (the ‘life’) originated billions of years ago and this in turn the geosphere linked with the rules of the solar system which shows properties called self-organization (Fig. 6, see also Fig. 15). Thus, at an early stage defining ‘life’ became the request. The origin was and is the attempt to proceed from two elementary aspects:

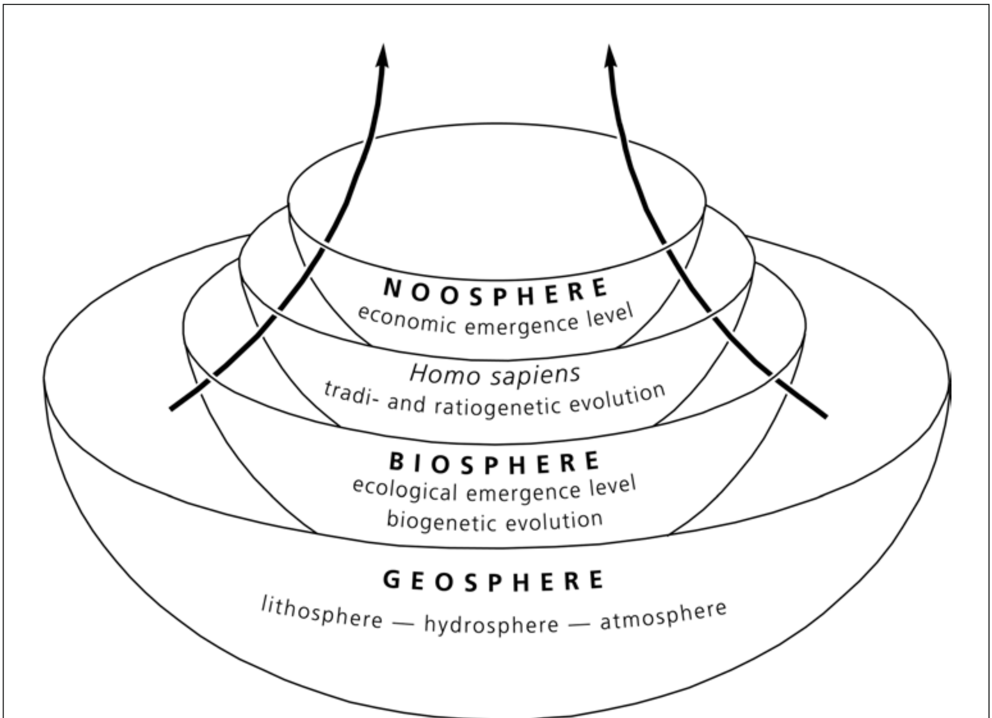


Fig. 6 Levels of emergence in the process of self-organization

(*1*.) Living beings are individuals (organisms);

(*2*.) Living beings are constituted of three basic characteristics that represent a functional unit: information exchange, metamorphosis and metabolism (I coined the term 'information exchange' – *Informations**wechsel*** **–** according to the German terms of

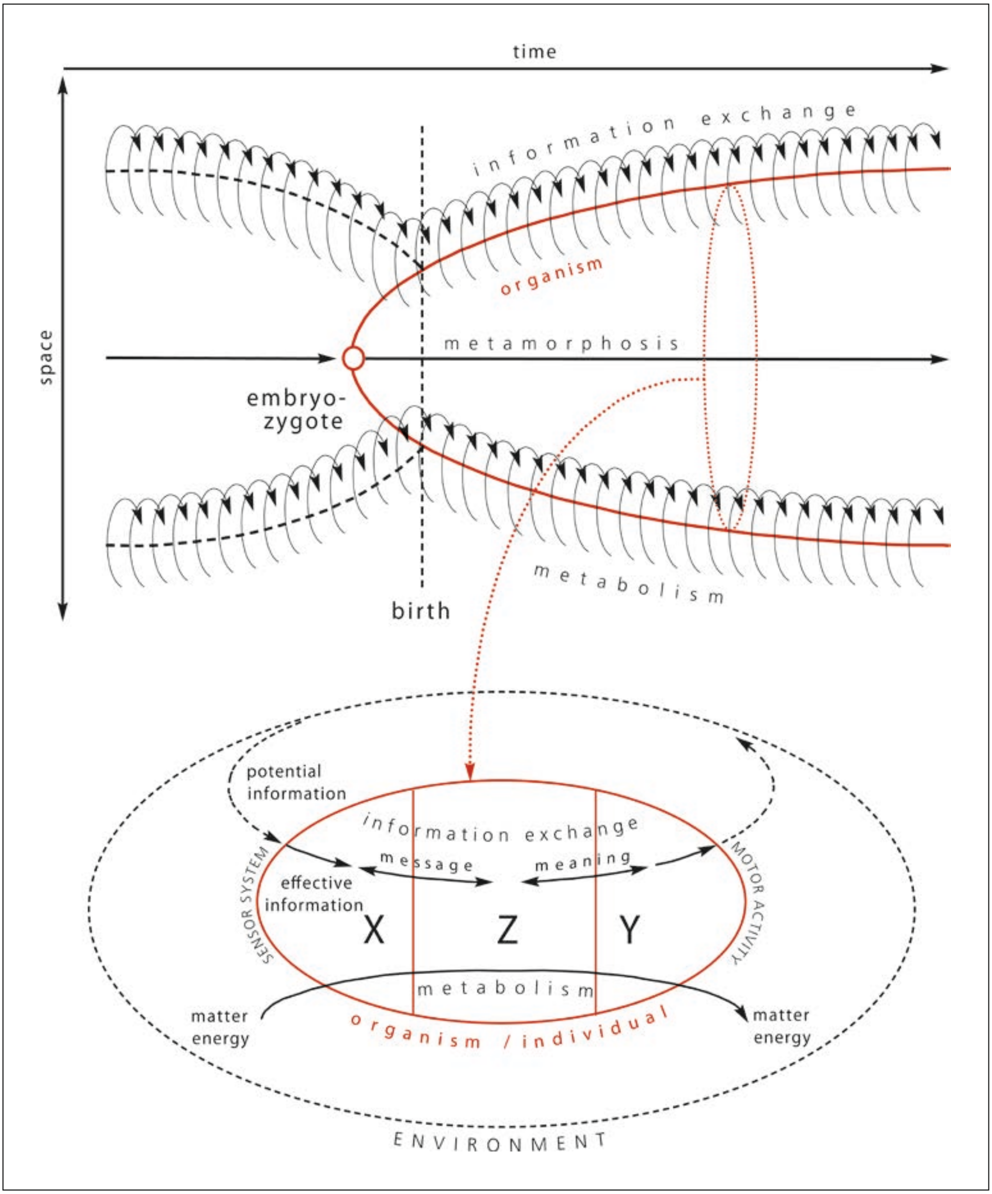


Fig. 7 Organisms become 'subjects' by common effective properties: metamorphosis (physical characteristics), metabolism and information exchange, the last two linking the 'open system' with the environment. Below are the 'three vectors' of the organism depicted which 'organize' its behaviour. (Modified from Tembrock 2003.)

> *Form***wechsel**, metamorphosis, and *Stoff***wechsel**, metabolism) (Fig. 7). These properties coalesce with individuality ('mortality') and reproduction. The information exchange is based on the singular quality of what we call 'life' with the ability to store information (genes, genomes) and the informational relationship between organism and environment (*Umwelt*) (Fig. 8).

The concept assumes a dualistic structure of organisms where the subjective parameter is ascribed to quantum physics (Fig. 9). As a consequence, special representations developed during the application of the 'three-vector-model' (Fig. 10). The input vector (sensorial and material input), the internal state vector (stationary dynamic state) and the output vector (motoric and material output). During the phase after 1963, however, 'classical' methods were addressed such as research with mazes. These investigations were also interpreted physiologically. The approach is virtually a continuation of efforts to conceive 'behaviour' in all its facets.

From the very beginning (1949), the books cited here have been indicative of a comprehensive concept of behaviour – however named – having been in the focus of attention, and as a consequence a corresponding study group had been built. When in further

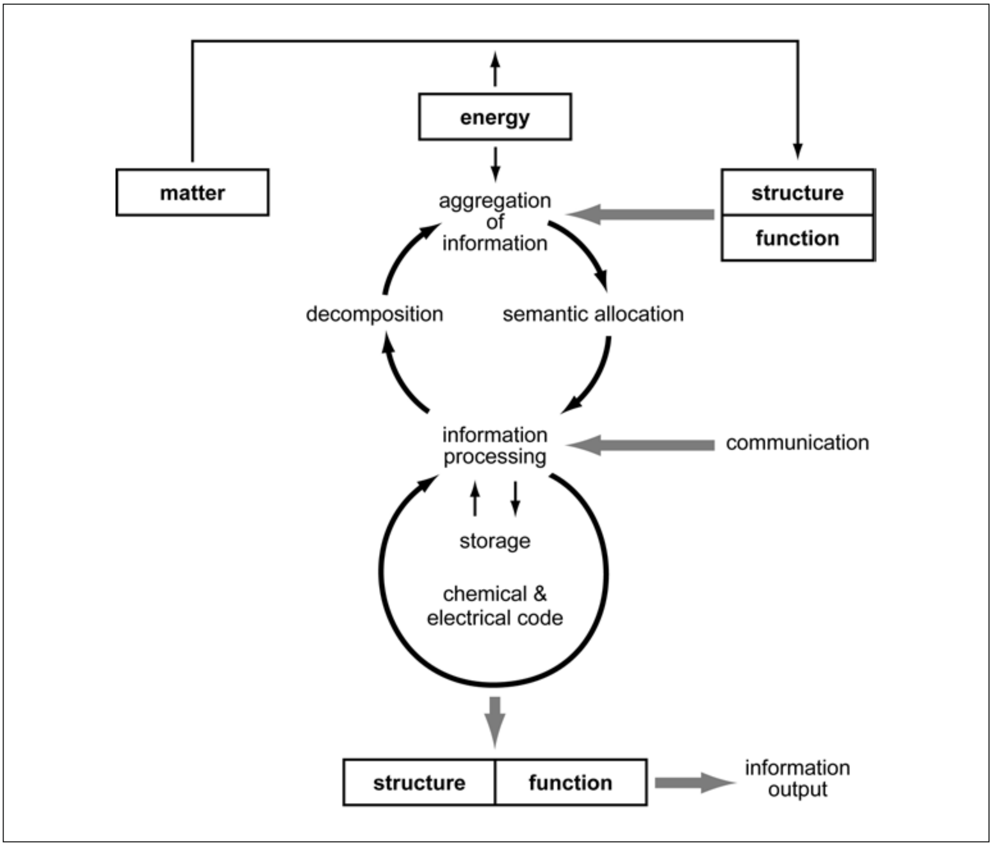


Fig. 8 Scheme of the process of information exchange

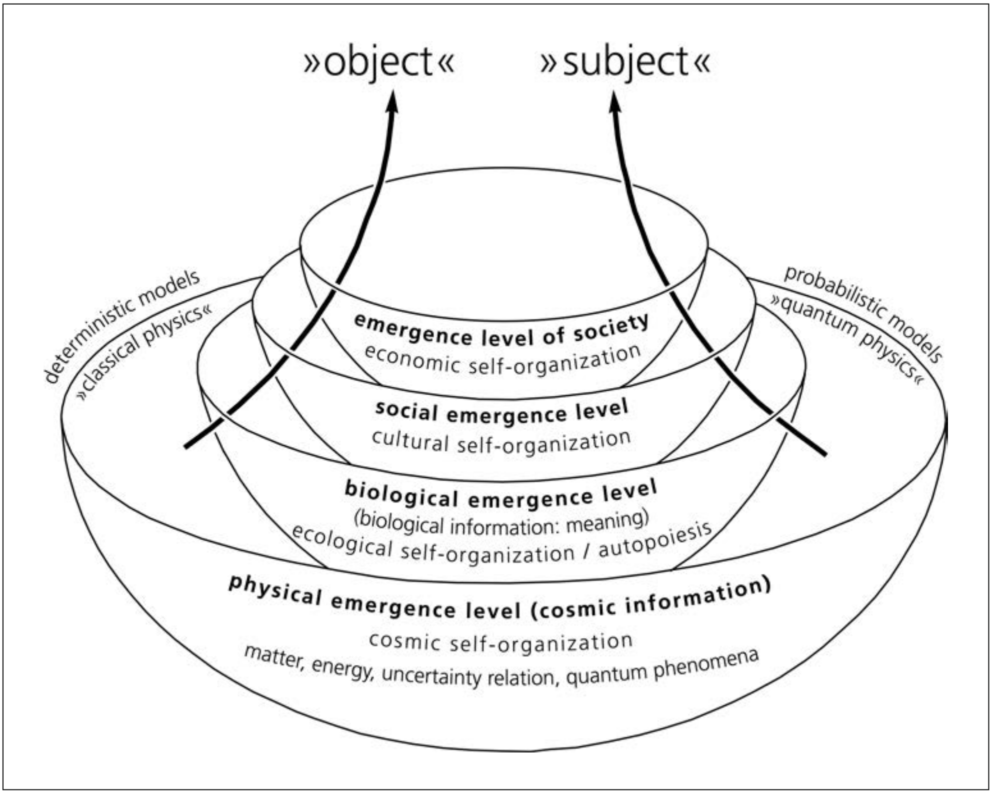


Fig. 9 Illustration of levels of emergence underlying the presentation. 'Emergence' stands for the formation of something new, more precisely the development of a new quality. The levels shown here embrace the following in the sense of an encapsis. 'Object' stands for observed properties, 'subject' for the 'observer' (a living organism). (Inspired by approaches from Görnitz and Görnitz 2002, and discussions thereafter.)

years a discipline was installed at a university then in conjunction with a head of department who would focus on a special topic. The research approach developed here in 1948 ran another path, and the books reflect the conceptional background. Hence, it has become discernible that there have been many obstacles, but the groundwork remained. Within the already mentioned department of behavioural sciences (1971) the structure of research of my chair was such: it consisted of two sections: (A) 'information exchange' und (B) 'system analysis (communication)'. Group (A1) with the emphasis on information transmission, behavioural algorithms, information aggregation, in each case altogether 15 people dealing with special topics mostly doing their theses. In this group I was also actively pursuing research concepts. Group (A2) comprised 5 people having the overall issue: recognition of signs and patterns. The remaining groups belonging to section (B) were divided into three 'sub-groups': fishes, insects, and mammals, where 19 persons participated, three external associated scientists included. These teams originated in 1968/69 within the context of the Third University-Reform resulting in completely different working structures which nevertheless upgraded my position at the same time to such an extent that I had a share in the further implementation of scientific-administrative matters on higher levels, too. Our

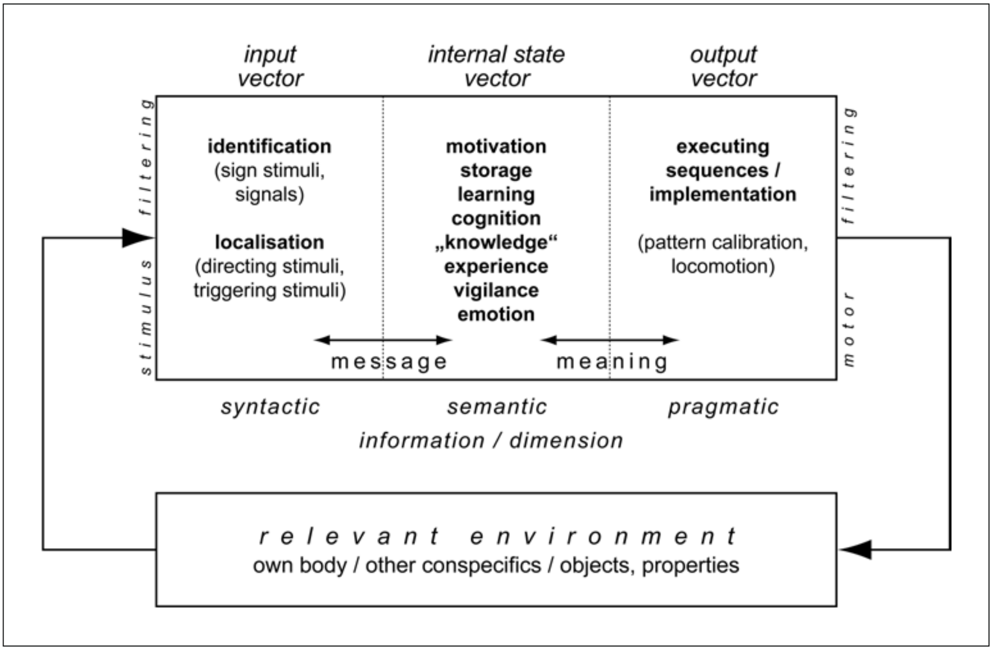
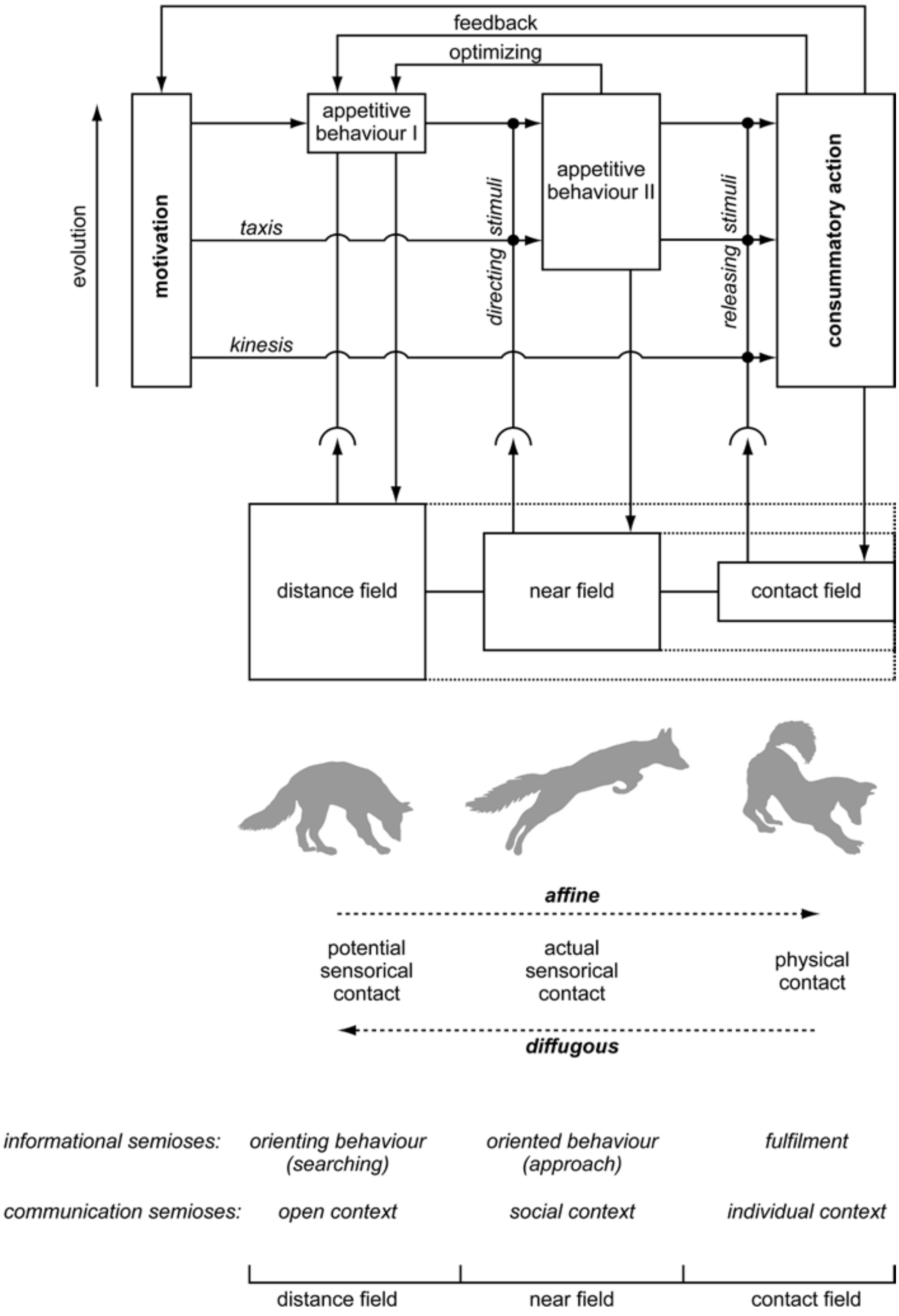


Fig. 10 Three-vector-model. Illustration of the structure of organism-environment-interaction on the basis of motivated behaviour that determines the aims (relevant environment) of the process. Three vectors can be distinguished within the organism: input vector, active information perception; internal state vector, information processing using and expanding contents of storage; output vector, motor activity in a wider sense, including vegetative phenomena.

thoughts repeatedly included synopses referring to major causal relationships last not least to the importance of the noosphere (Fig. 6, see also Fig. 15). The level talked about here and the overriding issues culminated in a singular book: *Biocommunication: Information Transfer in Biology* (Tembrock 1971). This book appeared in 1971 on the basis of information theory which led to my independent definition of an organism having three premises: metabolism, information exchange and metamorphosis as a functional spatial-temporal unit from bacteria to humans (Fig. 7). The information exchange may also mean communication.

Fig. 11 Three-phase model of motivated behaviour. Motivated behaviour aims at ensuring the fulfilment of a specific motivation by implementing adequate consummatory actions following appetitive behaviour. This model permits to distinguish between three ‘fields of events’ of behaviour (*Ereignisfelder des Verhaltens*). The distance field is defined by the condition, that there are no releasing stimuli present which could release the consummatory act (thus, orienting behaviour is activated). Internal factors, e. g. search images, may be guides for implementing the strategy of orienting behaviour. The near field is characterized by directing stimuli meaning that the goal was identified, as well as its position in space (thus, oriented behaviour is possible). Complex strategies have been evolving being enriched in many species by learning. The animal can only seek for those things about which existence it has ‘knowledge’. Intra- and inter-individual variations of motivated behaviour on all levels help to optimize this strategy. The consummatory act, e. g. eating, results in a negative feedback on the initial motivation. We have to assume that these phases of motivated behaviour appeared in evolution in inverse succession, as seen in many cases in the ontogeny of individual behaviour. (Modified after Tembrock 1980, 1982a) ►


feedback
optimizing
evolution
motivation
appetitive behaviour I
appetitive behaviour II
consummatory action
taxis
kinesis
directing stimuli
releasing stimuli
distance field
near field
contact field
affine
potential sensorical contact
actual sensorical contact
physical contact
diffugous
informational semioses:
orienting behaviour (searching)
oriented behaviour (approach)
fulfilment
communication semioses:
open context
social context
individual context
distance field
near field
contact field

A so-called three-phase model of motivated behaviour led to the definition of three ‘fields of events’ of behaviour (*Ereignisfelder des Verhaltens*) (see Fig. 11). Relating to the stimuli with respect to the distance (in space and/or time) the three fields can be termed as distance field (out of direct, immediate, but within possible and known reach), near field (within sight, hearing and/or smelling distance), and contact field (body contact). In the 1950s, I developed a concept dealing with intraspecific distance regulation. Certain behaviour elicits distance reduction which I named ‘affine’. Distance increase I called ‘diffugous’ and its maintenance within a certain distance ‘intermediary’. These fields and their

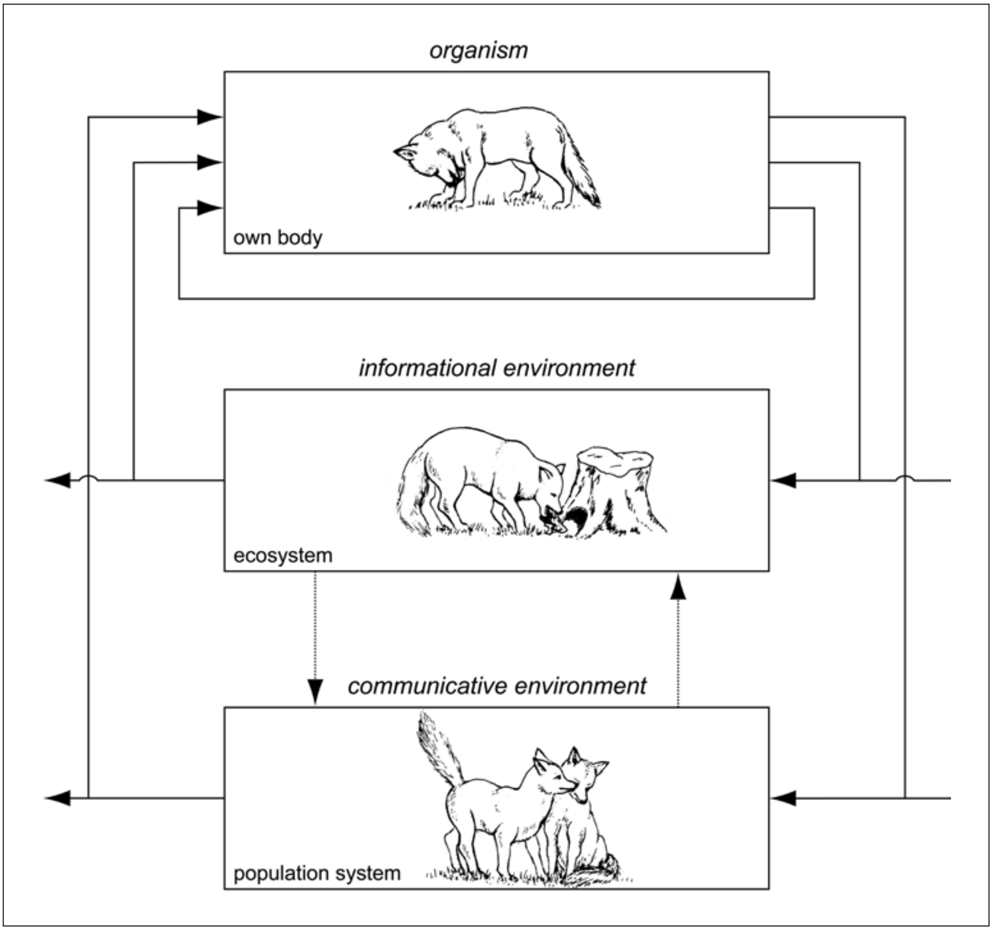


Fig. 12 Schematic illustration of the ‘three environments’ of the organism. The informational environment is a precondition for information exchange and the structure of organism-environment-interaction built on it. The ‘Eigenumwelt’ is defined by the own body’s constitutional properties, these may be sources of information as well as targets of output behaviour, e. g. when grooming. Sources of information as well as targets of output behaviour lying outside the own body constitute the informational environment (‘Fremdumwelt’, ecosystem). All information is structure-bound the meaning only being assigned by the receiver. For the communicative environment (population) all information is bound to communicative signals, the meaning already assigned by the sender and therefore ‘understood’ by the ‘addressee’. Some of these signals may be constitutional properties of the sender, others – which are commonly available in greater diversity – operate on the efferent level.

characteristics also define conditions of communicative behaviour. The environment relevant to the organism can be divided into three categories as shown in Figure 12.

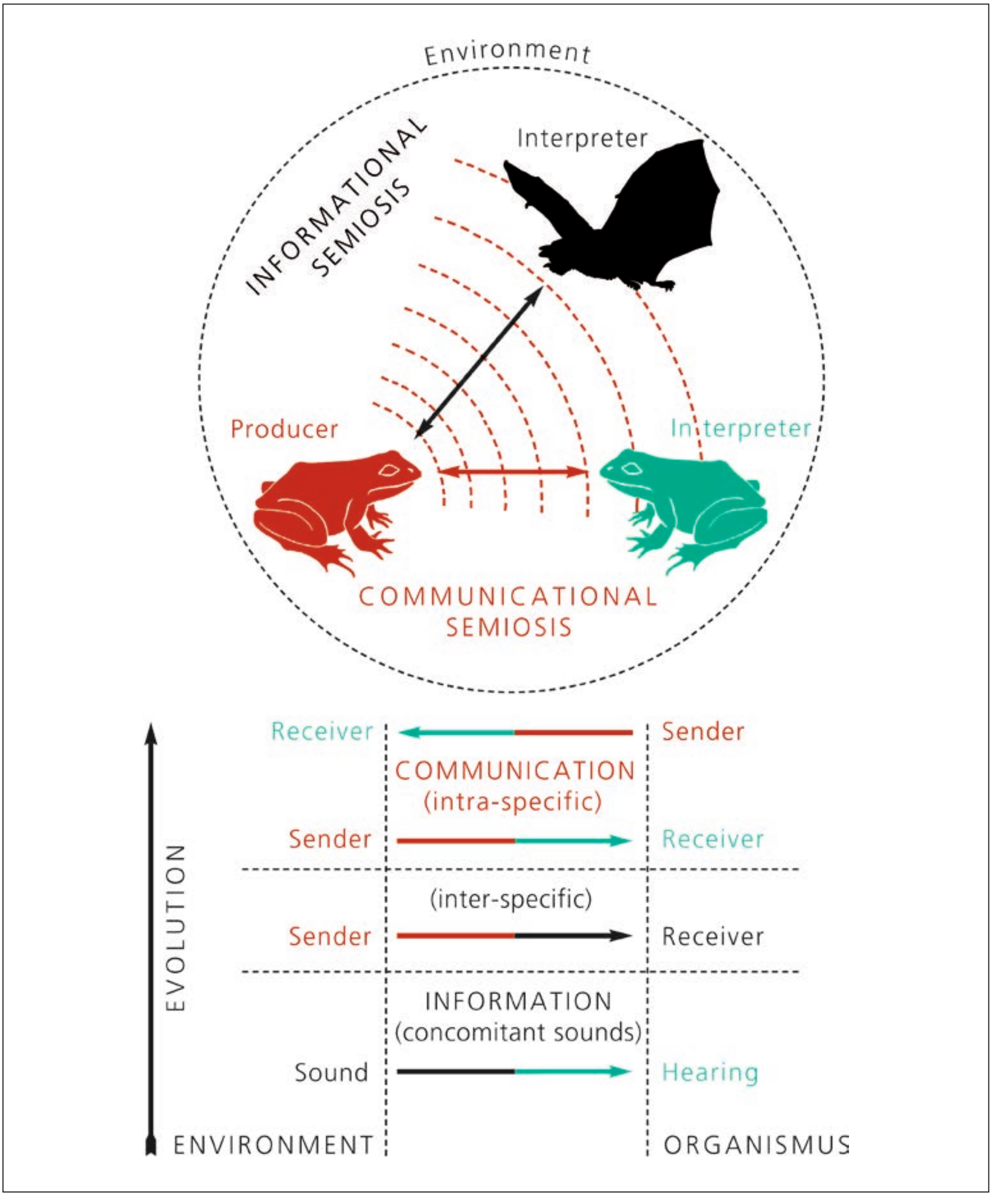


Fig. 13 Semiosis stands for information transferred by signs. The producer is the source of signals, the interpreter the receiver. Within a communication semiosis the male Tungara frog sends acoustic signals to the females (and possibly to competitors). Communication is given when there is a sender and a receiver both assigning the same meaning to the signal/sign (i. e. ‘understanding’ each other). The fringe-lipped bat here uses the calls as signal for identifying potential prey, i. e. not as ‘subject’ but as ‘object’ with certain properties. Thus, an information semiosis came about. The same applies to humans watching without understanding the subjective process between the frogs.

These approaches led to the following concept in ‘biocommunication’: fundamental issues of communication, physiological issues, genetic issues, phylogenetic issues, chemical, thermal, electric, mechanical, visual information transfer, complex systems of communication, general considerations and models. An impressive example is the frog sending communication signals to conspecifics and whose calls are used by a bat species for prey catching (Fig. 13). When applying the ‘three-vector-model’ within this context, one may deduce phylogeny and ontogeny to basic steps (Fig. 14). Against this background semiotics became an essential part within the context of information, which later on I integrated as a contribution about ecology to an encyclopaedia (Tembrock 1997).

Nevertheless, at that time already 30 years of many-layered developments had passed so that an institutional state within the framework of behavioural sciences had stabilized. In 1968, the elementary sentence can be found: “Ethology is the science of natural behaviour. [. . .] The natural behaviour of animals is the result of phylogeny.“[2] At that time I developed the ‘three-vector-model’ for the behaviour of the individual which – refined – is still valid today (see Fig. 10) (Tembrock 1974). About ten years later I took on Friedrich August von Hayek’s (1899–1992) concept (see von Hayek 1979) and extended it substantially whereas his three potentials relating to humans were differentiated as layers: biogenetic, tradigenetic and ratiogenetic potential. I added the evolutionary potential (Fig. 15). As an example this model can be applied explaining the acquisition of language (Fig. 16).

In this phase of development our work in progress focussed on overriding principles whereby having been accepted as a member of the Academy of Sciences Berlin (1975) was helpful. Among the first topics presented at the academy was: The ‘optimizing strategy of behaviour’ (Tembrock 1976). Organisms were regarded as multi-stable open systems with the following premises: homeostasis and behaviour, locomotion and orientation, metabolism and protection, adaptation on the basis of individual experience. Within this context ‘fundamental issues of behaviour regulation’ (Tembrock 1977) were covered in the acad-

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[2] Tembrock 1968, p. 11.

Fig. 14 Three steps of the evolution of biocommunication. The microgenesis of a motivated stimulus-released behaviour is illustrated: A passerine bird perceives a raptorial bird in the air. This means for him ‘aerial enemy’. After this process of identification and designation as a function of the input vector ($\underline{X}$), the internal state of ‘fear’ ($\underline{Z}$), will be established in consequence, that means the bird is ready to perform a specific behaviour pattern. This leads in the output vector ($\underline{Y}$) to a flight behaviour typical for this species. If we accept these general phases of the behavioural interaction with the environment, we can derive three steps of the evolution of biocommunicative behavioural processes: (*1.*) Transmission of the behavioural processes of the output vector (functional transmission), i. e., the output (vector) of the sender determines all three vectors of the receiver. The receiver executes the same behaviour as the sender, that may be an allelomimetic phenomenon, but it does not include a specific internal state. (*2.*) Transmission of the internal state by signals of the sender; in our example the readiness for flight behaviour. The signals designate the state of ‘fear’, or what we understand by this. The receiver is now in the same (internal) state as the sender (but without information about the cause of this state); he may show flight behaviour. (*3.*) Transmission of information about the sender’s perceptions; in our example the ‘aerial enemy’, in some bird species indicated by specific acoustic signals. Here, the receiver is able to react as if the perception was performed by himself. This level of biocommunication builds up two principal degrees of freedom in the receiver: the choice of the internal state and the choice of the external (output) behaviour patterns. The upward-pointing arrows in the right column indicate each the possible (and adequate) subsequent behaviour. (Combined and modified from Tembrock 1980, 1985.)

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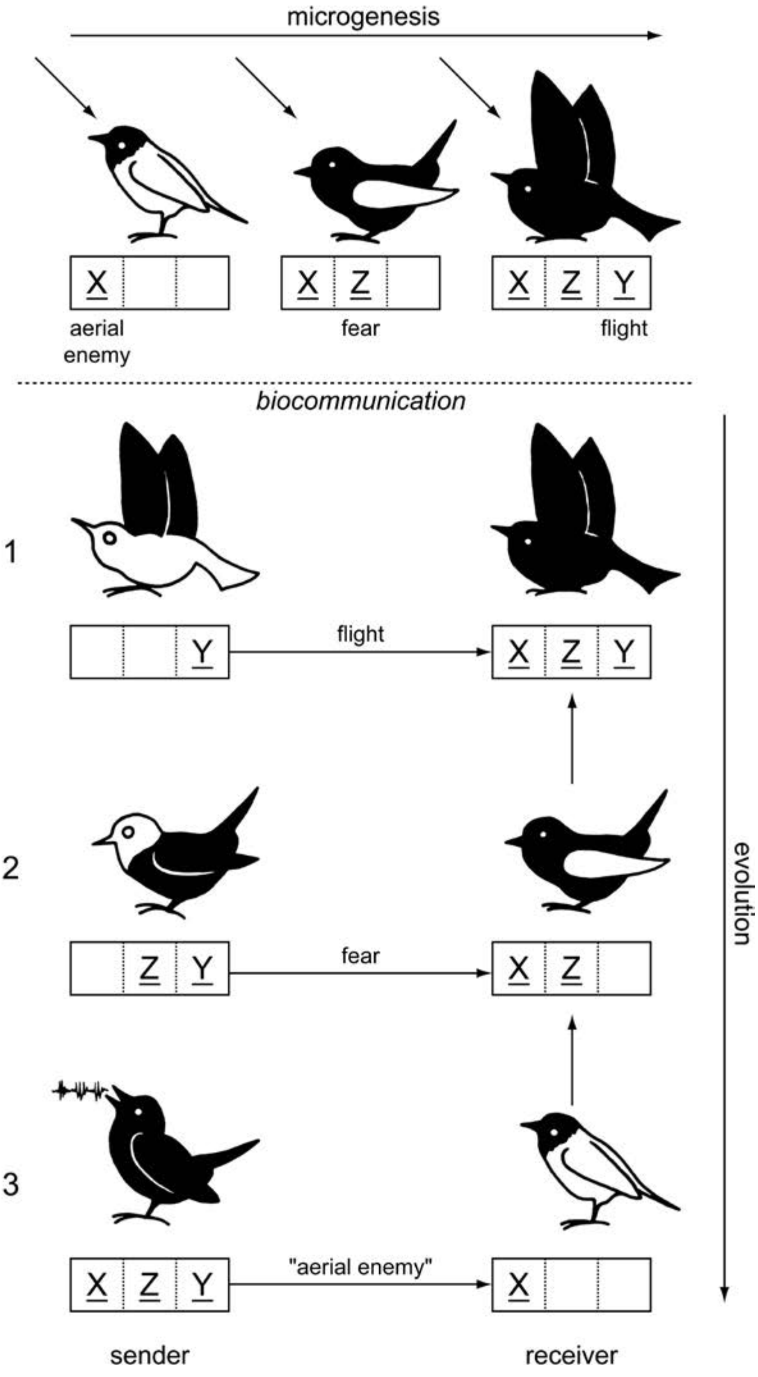
microgenesis
X
X Z
X Z Y
aerial enemy
fear
flight
biocommunication
1
Y
flight
X Z Y
2
Z Y
fear
X Z
3
X Z Y
"aerial enemy"
X
sender
receiver
evolution

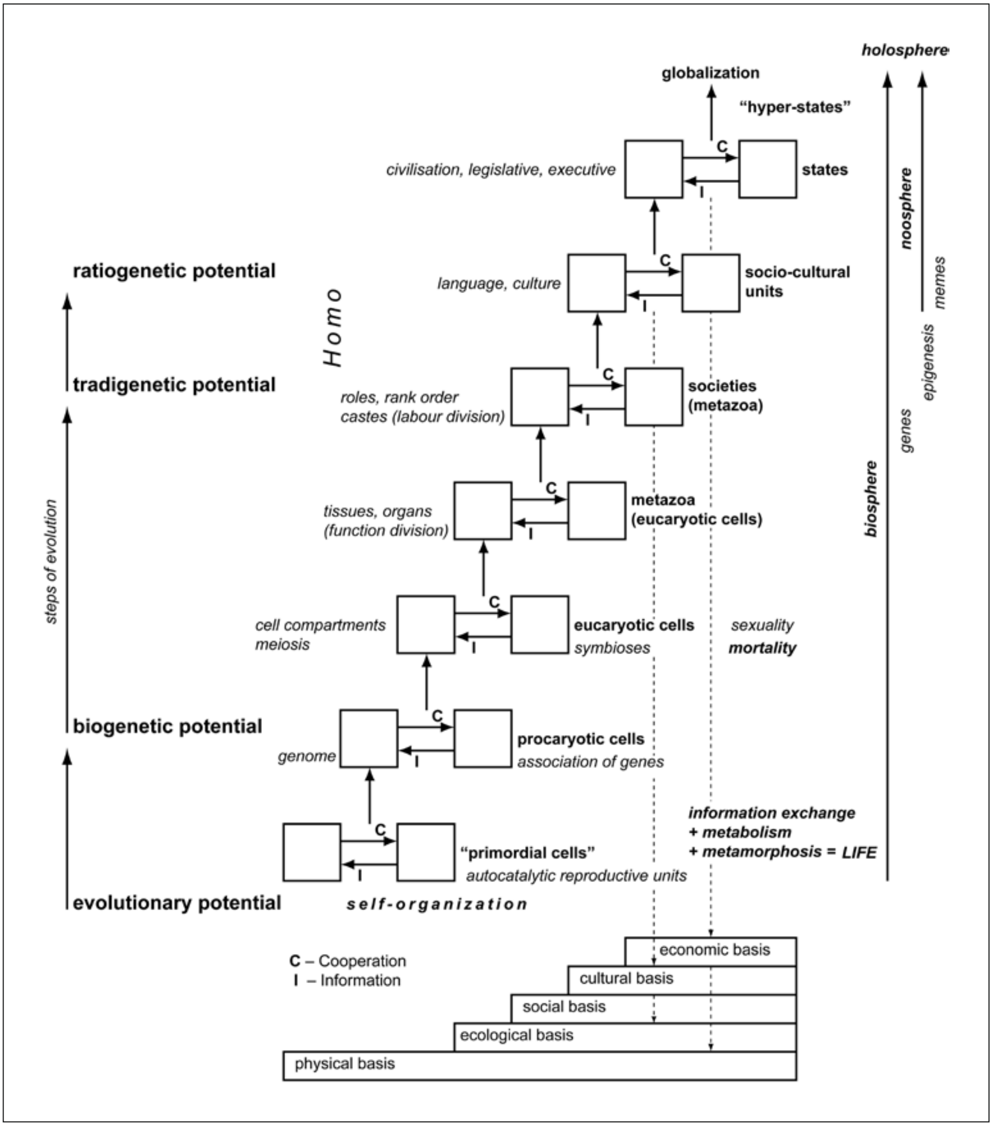

Fig. 15 Steps of evolution. Levels of hierarchies of elementary system parameters with regard to adequate environmental conditions determining interactions, self-organization and adaptation in the course of evolution (inspired by approaches from Müller 1987 and Oeser 1988). The two human specific levels are characterized by an own quality of consciousness, verbal communication and an autonomously emerging change of the 'basis'.

emy. It included a fundamental scheme of information exchange developed at that time as well (Fig. 8). The lectures at the academy of sciences are especially orientated towards perspectives. This also applied in 1977 to the topic of *Bioacoustics, Music and Language* (Tembrock 1978). The developing bioacoustical investigations led, apart from 'collecting' recordings of animal sounds, to comparative studies as parameters for assessing kin-

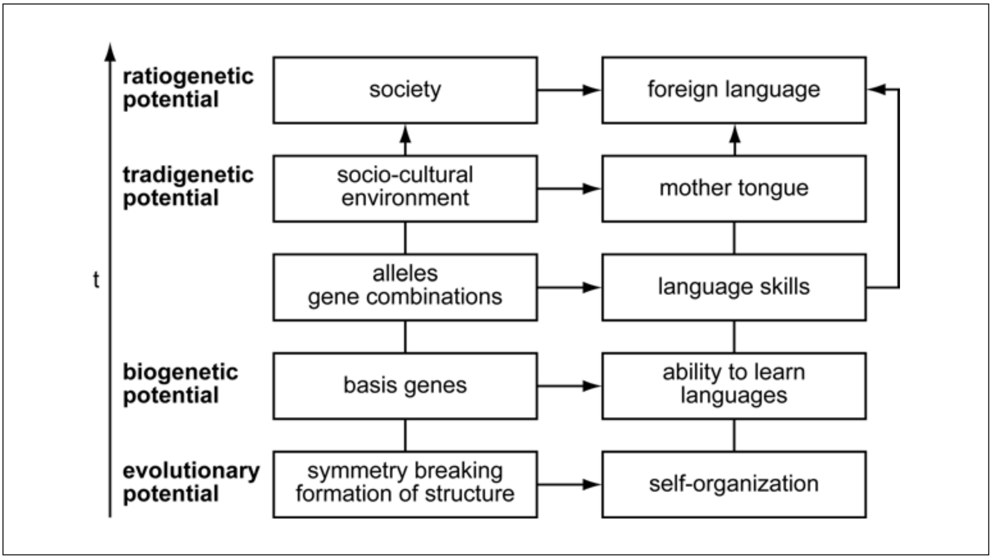

Fig. 16 Illustration of hypothetical levels of potentials which during the cosmogeny of our planet were superimposed on top of each other; the biogenetic potential coalesces with organismic evolution. An example on the right: the evolution of language.

ship, but included other topics such as comparative studies on humans and primates in relationship to the 'mechanisms' of phonation, too. In this context the following findings are shown: 'Bioacoustics as Science' investigates sound events under the following aspects:

(*1.*) Structure and function of sound production;
(*2.*) structure and function of sound perception;
(*3.*) biological sound as information (signalparameters: phonetics, metrics, sigmatics, syntax, semantics, pragmatics);
(*4.*) changes in time (individual, supra-individual, developmental aspect).

Our scientific way of dealing with animal sounds and communication was determined by some key aspects: in 1956, the 'International Committee on Biological Acoustics' was implemented at the University of Pennsylvania followed in 1959 at our institute by 'bioacoustics' which special structure was accounted for as a scientific concept labelled as 'sender and receiver'. I accentuated that when designing the cover of this book (see Fig. 5). In 1968, Felix von Trojan (1895–1968) employed after a longer contact with me the term 'Biophonetics' (Trojan 1968), discussions about the relationship of the animal and the human voice on a semantic level are reflected in my contribution to a later edition of the book (Tembrock 1975, see also Tembrock 1998b). There was another exchange of experiences with Klaus R. Scherer leading to his book about vocal communication including my contribution (Tembrock 1982b). Likewise, there were contacts with Nils L. Wallin (1924–2002) who denotes his basic approach with the term 'biomusicology' addressing a comprehensive concept: 'Neurophysiological, Neuropsychological and Evolutionary Perspectives on the Origins and Purposes of Music' (1991). Then, there was a longer relationship rich in substance with Georg Knepler (1906–2003) leading to his *History as a Means of Understanding Music* (1977).

As a member of Leopoldina (since 1965) I participated in a symposium under an overriding concept concerning language: ‘scientific linguistics’ led by Joachim-Hermann Scharf and Wilhelm Kämmerer (1905–1994) in 1976, organised by nine representatives of the field: Bernhard Hassenstein, Gerhard Joppich (1903–1992), W. Kämmerer, Friedhart Klix (1927–2004), K. Lorenz, Detlev Ploog (1920–2005), J.-H. Scharf, G. Tembrock und Konrad Zuse (1910–1995). Seven topics were treated by competent representatives of different academic disciplines. Still nowadays, the volume comprehending 865 pages is a ‘treasure trove’ (Scharf and Kämmerer 1981). Topic III (Martin Lindauer [1918–2008] and G. Tembrock) dealt with ‘non-verbal communication of organisms’. My contribution was named: ‘signal systems of primates’ (Tembrock 1981). Within this context own investigations on mimics of chimpanzees are illustrated. Special conditions have been postulated for primates leading to a complex communication as it is generally combined with social behaviour. The information may be transmitted *via* mechanical, optical and acoustic signals. The paper in question (1981) applied new representations: the subtleties of muscular movements of chimpanzees (mimics) becoming operant in expressional movements. These investigations were followed later on by another study on combinations of those optical with acoustic signals. One should consider that almost all species concerned here are active during daylight. Incidentally, I also included the human voice in this study and looked at an issue not yet examined till then: the age-related changes of the singer’s voice particularly concerning the frequency of the vibrato which reduces ‘at an older age’ (around 60) from 6 Hz to 5 Hz, related to 1 second as long as the voice is still preserved as such. Formants remain constant, the upper harmonics change. The same phenomenon applies to the hand vibrato.

The continuous expansion of the collection of animal sounds increasingly led to working on special issues determined by behavioural biological concepts. Thus, my next book was titled *Behavioural Biology* (Tembrock 1987). An insightful result of these monographies of an author and his ‘60 years of behavioural history’ which at that time emanated from a concept evolved during the then 39 years of applied scientific debate with our discipline at the Humboldt University. Thus, in 1987, behaviour was defined as such: “Behaviour is organismic interaction with the environment on the basis of an information exchange ensuring individual, ecological and inclusive fitness.”[3] Three examples are: handling of objects, dealing with organisms and dealing with conspecifics. Another aspect denotes environmental behaviour. The behavioural physiological aspect is differentiated as follows: (*1.*) neuroethology and (*2.*) behavioural endocrinology. Ethology now exceeds far beyond the formal description, the comprehensive term is henceforth ‘biology of behaviour’. In the book mentioned here concrete concepts for capturing parameters are deduced from parameters of behaviour. Thus, from those concepts dealt with here special questions emanated such as assessing the behavioural state from the heart frequency of a fish. What distinguishes this book from its predecessors is its introduction of tangible tools for research. Along with it, new questions arise for gaining insight into ecological, geographical, physiological, morphological, and ethological isolation mechanisms as well as gametic and post-zygotic ones. Of course, this also addresses evolution. As an impor-

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[3] Tembrock 1987, p. 15.

tant factor of evolution 'improvement of locomotion' is turned to as well as to the shifting from an axis to extremities, the evolution of the exoskeleton (arthropods) and the skeleton (vertebrates). Furthermore, it is referred to the evolution of birds from reptiles, a particularly impressive example for the ecologically orientated evolution of behaviour as concerns thermoregulation.

Thus, behavioural biology proves itself to be a behavioural science. Into this concept 'adaptation' is integrated. Terms like 'fixed action patterns' and 'ritualization' have their own significance: 'behaviour adapted for other purposes' ritualizes to 'signalling behaviour'. For the deduction of 'signalling movements' twenty different forms are defined. Thus, behavioural observations can be looked at under various aspects: observations, functional explanations. Consequentially, points of application may be deduced for selection, differentiated into group selection, individual selection and kin selection.

Another chapter deals with the physiological bases of behaviour. It is revealing to compare these developments with those already sketched in my book *Animal Psychology* from 1956. For the physiological illustrations the ground-breaking research of the developmental endocrinologist Günter Dörner (Charité Berlin) with whom I have been cooperating for a very long period has been incorporated.

Yet another chapter (1987) attends to 'motivated behaviour' including results of our research groups. A separate chapter was dedicated to the 'genetic presuppositions'. Another chapter addressed ontogeny. It is ethologically relevant to differentiate into 'nidicolous nestlings' 'altricial young' and 'nidifugous nestlings'. Humans are always included into these considerations. Generally, transformational phases, sensitive phases and imprinting are discussed. This illustrates the attempt to interpret behaviour in terms of behavioural science which covers all organisms.

Thus, 'phylogeny' follows in the next chapter as a result of natural selection. This also applies to general concepts of the evolution of behaviour. Here the notes of Charles Darwin from 1835 should be recalled: "When I see these Islands in sight of each other, & possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. […] If there is the slightest foundation for these remarks the zoology of Archipelagoes will be well worth examining; for such facts would undermine the stability of Species."[4] Species are not unmodifiable, against this background the book mentioned here provided in 1987 the following concept under the notion of 'variability levels': (*1.*) Individual variability, (*2.*) Inter-individual variability, (*3.*) Regional variability (geographical), (*4.*) Species-specific behavioural variability, and (*5.*) Characteristics of different kinship. Within this context, learning processes and their relationships are addressed which I have already been differentiating into obligatory and facultative learning for a long time. The obligatory ones have the character of 'imprinting' and are bound to certain areas of the brain which does not apply to facultative learning. Imprinting processes are distinguished into three forms of imprinting: the *sensory imprinting* bound to the input vector, the *readiness for imprinting* operating on the internal state vector, and the *sensomotoric imprinting* which finds its species- and individual-specific implementation in the output vector (see Fig. 10).

Within this context one should also remind of the habituation usually termed 'adjustment' in colloquial language. The development of behavioural science is connected with a

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[4] See Barlow 1963, p. 262.

deepening and broadening of insights into the causal structure of observed processes which reveal even deeper insights *via* appropriate experimental set ups. In this regard we also conducted a range of investigations and experiments concerned with the three vectors ('input, internal state, output'). Again, these questions associate with a fundamental issue: the environmental requirements determining behaviour. They characterize the nature of 'life' as 'elementary requirements'. Thus, 'environmental requirements' and 'individual environmental requirements' and 'traditional (handed down) environmental requirements' concatenate. Individuals need to meet demands of space and time. They require contact space and locomotion space as long as they are not sessile. Swallows perching on wires keep a minimal distance from each other which allows them to fly off unimpeded.

The description addressed here shows that it was a long way till then to comprehend 'behaviour' in its inner causality. Against this background numerous special topics were investigated such as the swarming behaviour of fish whereby the issue of 'temporal demands' led to special studies, within the particular context of the 24-hour-rhythm as well as the annual rhythm. From very early on, chronobiology engaged me in taking my first recordings of toads and ground beetles from 1943 onwards.

In the book of 1987, the notion of 'functional cycles' having already been developed before that period is used, functional cycles are defined ethologically, they ask for cause and effect. In that book functional cycles are classified according to the behaviour: orientational behaviour, metabolic behaviour, protective behaviour, burrowing behaviour, intraspecific competitive behaviour, migratory behaviour, reproductive behaviour, biosocial behaviour and play behaviour. This concept also underlies the book comprising over 1000 pages, and 5160 references, which I prepared with regard to the evolutionary aspect under the title *Systematic Behavioural Biology of Animals* (Tembrock 1983) and which 'illustrates' behavioural biology with 553 figures. It was a long way leading from *Animal Psychology* in 1956 to this *Systematic Behavioural Biology* in 1983. This book was supplemented in 1984 by the title *Behaviour in Animals* equipped with 110 figures, complemented on the background of our numerous study groups and again presenting 'up-to-date science' (Tembrock 1984). A completely new chapter was named: "Animals and Humans". Also, the attempt is taken to process the array of aspects regarding their relationships. Hence, complex questions arose leading to special investigations. In those general representations of 'Behaviour in Animals' a range of studies from co-workers is included such as research on grooming. Special questions on the 'mimic' expression of mammals were examined. Relationships between 'human – animal' were classified in (1984) as follows:

(*1.*) Meaning of humans to animals: 'enemy', 'prey' (rare), 'hosts' (ecto- and endo-parasites), 'environment' for certain species, 'biosocialpartners'.
(*2.*) Meaning of animals to humans: 'enemy', 'prey', 'parasite', 'carriers of diseases', 'commensals', 'beneficiaries', 'nutrients', 'symbionts' (mutual beneficiaries – bee, dog, cat), 'partners' (working animals), and yet an extensive topical range: 'animals as objects of satisfaction of special needs'.

Within this context another concept was developed leading to new study groups: 'behaviour as bioindicator' (1989, see Tembrock 1990). An issue of that time was 'stress reactions' with the following emphases:

(*1.*) Modification of spatial and/or temporal relationships with regard to the source of stress;
(*2.*) application of constitutional properties of the body in connection with motoric patterns;
(*3.*) alteration of attributes of the environment.

Within this range processual spheres of action can be distinguished:

(*1.*) Effects on the body and its constitutional properties: (*a*) species-specific, (*b*) gender-specific und (*c*) individual-specific;
(*2.*) effects of behaviour within the framework of interactions with the ecological niche in the context of using resources;
(*3.*) effects on behaviour within the framework of interactions with the conspecific population in the context of signalling behaviour and biosocial functions.

Single individuals are subject to varying stressors on the processual sphere of effects: the processor intervenes directly in the course of behaviour; the stressor intervenes in the physiological causal mechanisms which makes the actual course of events possible.

'Ethostressors' and 'sociostressors' were used for data assessment, e. g., by exploring indicative valences of 'decisions deviating from the rule'. Within this context our working groups arose being stimulated by my concepts. First investigations on humans regarding this topic were done by Michael T. McGuire. From our own research an array of possibilities of bioindications was deduced.

The chapter headings of the second edition of *Behavioural Biology* (1992) had moved on to the following topics: (*1.*) The science of behaviour, (*2.*) Methods of behavioural biology, (*3.*) General characteristics of behaviour, (*4.*) Physiological principles of behaviour, (*5.*) Motivated behaviour, (*6.*) Behaviour and adaptation, (*7.*) The environmental requirements determining behaviour, (*8.*) Functional circles of behaviour, (*9.*) The environment and the array of effects, (*10.*) Functions of behaviour, (*11.*) Applied behavioural science, (*12.*) Behavioural biology and human sciences. This includes 65 'sub-chapters' showing how the 386 pages are structured.

Generally, the data collection during all those years was done under the following premises:

(*1.*) wild animals in their natural habitat;
(*2.*) wild animals in an anthropogenously 'influenced' habitat (e. g. most forests in industrialized countries);
(*3.*) wild animals in an anthropogenic habitat ('synanthropic species') (e. g. influenced by agriculture);
(*4.*) wild animals kept by humans (e. g. zoos),
(*5.*) wild animals bred by humans (e. g. zoos),
(*6.*) domesticated animals kept and bred by humans (e. g. husbandry).

A special topic, zoo-biology has been termed an 'integrative science' with the components: 'arts (ideographic science)' and 'science (nomothetic science)'. This results in three dimensions of competence:

(*1.*) cognitive (rational) competence,
(*2.*) aesthetic competence,
(*3.*) ethical competence.

These are the conditions for an 'integrative educational mandate'. Zoos are public establishments, thus, humans belong to them in two completely different functions:

(*1.*) caretakers, researchers of the zoo animals;
(*2.*) visitors of zoological parks.

Within this context the 'working group zoo-biology' developed in 1993/94 the following concept of 'animal-appropriate and species-appropriate requirements' on keeping conditions in zoos:

(*1.*) 'Species-appropriate' emanates from the biological species in the sense of Ernst Mayr (1904–2005). Members of a species form a reproductive community. Individuals of a species recognise each other as potential partners. The species is a genetic unity coming from a large gene pool with mutual relationships. Consequences for behavioural biology ensue.
(*2.*) 'Animal-appropriate' ensures individual fitness within the context of species-appropriate premises whereby parameters of individuality, of keeping conditions may lead to ethological modifications.
(*3.*) Tasks of species conservation require both levels.
(*4.*) A fundamental significance is assigned to ontogeny within the sense mentioned here (ontogenetic parameters).

A basic contribution dealt with the issue of zoos of today and tomorrow (Tembrock 1994).

Another point that should be referred to addresses the model of dualistic evolutionary strategies I developed in the mid-nineties inspired by the ideas of Gerd Binnig (1992, see Fig. 17) thereby hoping to stimulate thinking along the following lines. Strategies of replication (= strategies of performance) run in cycles, strategies of storage change internal states and internal selection processes, too. Each cycle of reorganization reinforces asymmetry with the increase of the complexity of internal storage patterns. Asymmetry creates a 'past', changes the cycles of the replication strategy into spirals and thus constitutes a 'quantization of time' intrinsic to the system which is experienced as 'subjective time' by humans with a consciousness capable of reflection.

For the development of the "60 years" it is characteristic that not only the collection of animal sounds has been constantly expanded and developed and that it is still active (Frommolt 1996, 2008, see internet: www. tierstimmenarchiv.de), but that academic work could develop further due to the expansion of technical possibilities. Furthermore, other disciplines took notice of us so that I was invited to give talks at the 'Stuttgart Voice Conferences' ('Stuttgarter Stimmtage') from 1998 onwards on topics such as 'Parameters of the Voice within the Social Context – a Comparative Consideration' (Tembrock 2000b). For the evolution of acoustic communication which includes humans, three functional fields can be distinguished: the contact field, the near field and the distance field as related to the voice (see Fig. 11). In the paper concerned (Tembrock 2000b) the following statements were made:

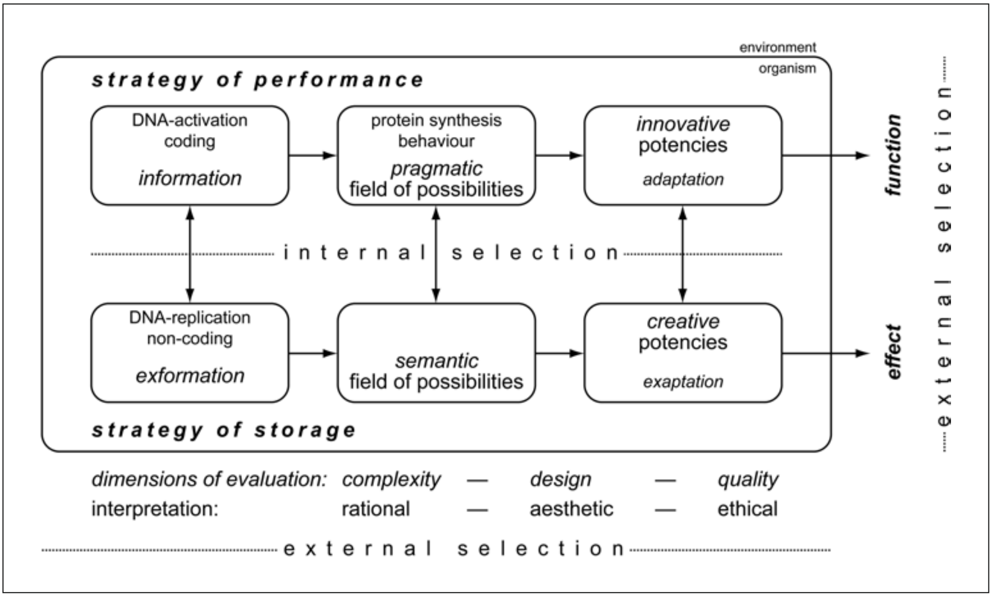

Fig. 17 Dualistic model of evolutionary strategies inspired by a hypothesis of Gerd Binnig 1992

(*1.*) The ‘communication dyad’ (within the contact field): sender–addressee/–receiver (all known to each other, the addressee being meant, but another receiver possibly also getting the message) is often linked with substance transfer (mother’s milk, food, sperm cells) or with other behaviour in body contact.
(*2.*) The intra-social communication (acoustic, visual, olfactory) within a social group (all known to each other), i.e., the near field ensures the perception of other individuals.
(*3.*) The distance field is given when there is no actual contact between social partners, but communication could be established.

Baboons have ‘hominoid’ sounds reminding of humans and also denoted as ‘primeval sounds’. In this context one can mention the human non-verbal ‘filling sound’ (*uh*) while talking. Of particular interest is the fact that in mammals neonates utter similar sounds. My book on the acoustic communication of mammals (Tembrock 1996) joins widely varied investigations on acoustics (among them the ‘Stuttgart Voice Conferences’ till 2004, see Tembrock 1998b, 2000b, 2002, 2004, 2006a) which comprehend a broad research array of the voice, supported by studies on animal sounds.

In 2000, I wrote a book covering the issue of *Angst: Natural History of A Psychobiological Phenomenon* (2000a). The concept is orientated towards the following questions: neurobiological view, behavioural view, individual state, social phenomena, ecological context, dimensions of “angst”, developmental aspects and the way to human beings. About 40 years earlier (1961), I put emphasis on clearly separating “angst” and “fear”: abridged, “angst” means a behaviour that cannot implement species-specific behaviour when in danger, whereas for “fear” species-specific behaviour is available.

We are approaching the "keynote", the "60 years" which were reached in 2008. Here it becomes obvious that this era was determined by comprehensive issues keeping science and arts within their view, and with it the noosphere and a global view. For that matter the *Journal of Human Ontogenetics*[5] has been created, its introduction by the editors-in-chief was formulated thus: "The central idea for human ontogenetics is the methodological concept of the unity of complexity and time (in the sense of PRIGOGINE), which demands considering the complexity within the light of the *'eigentime'* (*Eigenzeit*) of the 'system human being'."[6] The first contribution begins with this formulation: "The concept of the science about humans presented here abolishes the traditional gap between science and humanities. The foundation is a universal concept of development that assumes an evolutionary potential of self-organization as a precondition for the biological potential on our planet to which the biosphere owes its existence."[7] About 5–6 million years ago profound changes of the human brain provoked the establishment of a new dimension of 'life': the noosphere shaped dynamically by humans combined with a vast increase of populations. Self-organization associates with a triadic concept:

(*1.*) the eïstheton as the perceptible dimension,
(*2.*) the noëton as the comprehensible dimension,
(*3.*) the ethiton as the affecting dimension.

These are presuppositions which lead to evolution and with the human evolution to culture which has organismic roots (TEMBROCK 2006b). The roots of culture we owe to the primates.

Quo vadis, Homo?

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[5] *Zeitschrift für Humanontogenetik* (1998–2006, Berlin: Logos, Bielefeld: Kleine); *human_ontogenetics. An International Journal of Interdisciplinary Developmental Research* (since 2007, Weinheim: Wiley-Blackwell).

[6] TEMBROCK and WESSEL 1998, p. 3.

[7] TEMBROCK 1998a, p. 5.

Supplementary Figure Added by the Editors

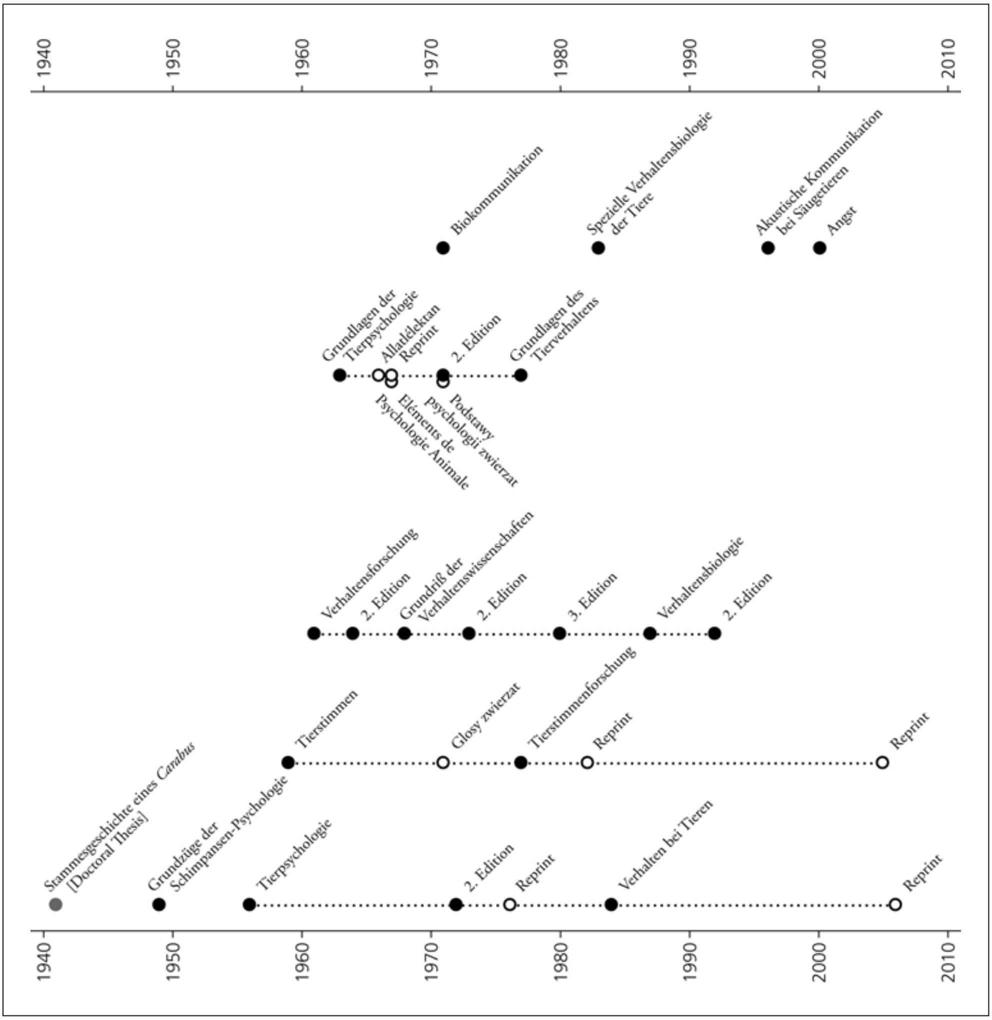

Fig. S1 Overview and ‘evolution’ of the books of Günter TEMBROCK

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Internetresources

Tierstimmenarchiv (*Animal Sound Archive*), Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Research at the Humboldt University Berlin: www.tierstimmenarchiv.de

Note

The lecture manuscript was edited by the author, and translated by Sylvia WENDLAND-TEMBROCK.

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Was ist Leben?

Vorträge anlässlich der Jahresversammlung
vom 23. bis 25. September 2011 zu Halle (Saale)

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Herausgegeben von Jörg Hacker (Halle/Saale, Berlin) und Michael Hecker (Greifswald)
(2012, 284 Seiten, 115 Abbildungen, 3 Tabellen, 29,95 Euro,
ISBN: 978-3-8047-3060-1)

Es gibt nur wenige Fragen, welche die Menschheit seit Beginn ihrer geistigen Auseinandersetzung mit sich selbst und der sie umgebenden Welt unaufhörlich begleitet haben. „Was ist Leben?“ zählt zu diesen Grundfragen des menschlichen Daseins. Angesichts der beeindruckenden Erfolge der empirischen Forschung an Lebewesen wird die Schwierigkeit immer offenkundiger, eine allgemein überzeugende Antwort auf die Frage nach den grundlegenden Eigenschaften derjenigen Systeme zu geben, die wir „lebendig“ nennen. Diese Rätselhaftigkeit fasziniert Natur-, Geistes- und Kulturwissenschaftler und bringt sie dazu, gemeinsam das Wesen des Lebens zu erkunden. In dem Band behandeln hervorragende Vertreter der unterschiedlichsten Wissenschaftsdisziplinen den noch nicht zufriedenstellend geklärten Ursprung des Lebens. Sie untersuchen das neue, umfassende Verständnis der molekularen Grundlagen von Lebensprozessen aus der Sicht der Genomforschung und beschreiben die Möglichkeiten, Leben in Analogie zu Maschinen zu modellieren. Sie behandeln die ungeheure Vielfalt des Lebens, die Beeinflussbarkeit des Lebens durch menschliche Eingriffe und die Grenzen des Lebens aus biologischer, psychologischer und philosophischer Sicht. Dabei wird deutlich, wie hartnäckig sich die Frage nach dem Leben durch die Wissenschaftsgeschichte, ja durch die ganze Geistesgeschichte zieht und welche Brisanz sie angesichts aktueller Forschungsergebnisse erhalten hat.

Wissenschaftliche Verlagsgesellschaft Stuttgart

Nova Acta Leopoldina NF *111*, Nr. 380, 61–75 (2013)

Communication: The Quest for Understanding Behavioural Complexity[1]

Wolfgang M. SCHLEIDT (Wien and Moosbrunn)

With 8 Figures

Abstract

To understand behavioural complexity – how behaviour is composed of its basic elements – we must first define the scenario within which behaviour occurs: the environment in space and time, the actors (individual organisms), and the props (particular things in the environment). *Behaviour, most generally, is any change of an organism,* and *communication can be shown to occur when one organism's behaviour changes the behaviour of another.* There are at least two distinct types of communication: *Phasic Communication* (PC), where a single signal from a transmitting communicant can cause a permanent change in a receiving communicant, and *Tonic Communication* (TC), where a stream of signals from a transmitting communicant can modulate the behavioural state of the receiving communicant and thus create a union between communicants.

Zusammenfassung

Um die Komplexität des Verhaltens zu verstehen – die Art und Weise, wie Verhalten aus relativ einfachen Elementen aufgebaut ist –, müssen wir zunächst die allgemeinen Gegebenheiten kennen, in deren Rahmen Verhalten stattfindet: Die Umwelt, in Raum und Zeit, die „Akteure“ (einzelne Organismen) und die Versatzstücke auf der Bühne des Lebens (die einzelnen Gegenstände, mit denen die Umwelt möbliert ist). *Verhalten ist, auf den Punkt gebracht, jegliche Veränderung eines Organismus*, und *Kommunikation findet statt, wenn gezeigt werden kann, dass das Verhalten eines Organismus das Verhalten der anderen beeinflusst*. Wir können mindestens zwei Arten von Kommunikation unterscheiden: *Phasische Kommunikation* (PC), bei der ein einzelnes Signal des Senders eine dauerhafte Veränderung des Empfängerverhaltens bewirkt, und *Tonische Kommunikation* (TC), bei der ein Strom von Signalen des Senders zu einer Modulation des Empfängerverhaltens führt und damit eine *Union* (Kommunion) der Kommunikanten schafft.

1. Introduction

This is a very brief review of what I have written about behaviour patterns and communication over the last 60 years in several hundred pages. I built on the foundations laid by Jakob VON UEXKÜLL, Oskar HEINROTH, Konrad LORENZ and Niko TINBERGEN, with the help

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[1] Dedicated to the memory of my teachers, especially Konrad LORENZ, Hans BORNSCHEIN, Hansjochem AUTRUM, Jakob VON UEXKÜLL and Oskar HEINROTH.

of new tools and concepts of contemporary physiology and communication engineering. Growing up with household pets and farm animals I was fascinated by the behaviour of animals early on, and soon became aware of the similarities to the behaviour of humans, and especially to the behaviour of human babies.

One of my first papers was about the behaviour of newborn babies of a variety of mammals (Prechtl and Schleidt 1950), and throughout my scientific career I preferred to investigate the behaviour of the vertebrates within easy reach: mice, cats, dogs, chickens, turkeys (e.g. Schleidt 1948, 1961, 1998), as well as humans (Schleidt 1992, Schleidt and Shalter 2003). My first discoveries centred on high-pitched vocalizations in voles and mice that forced me to design and build my own amplifiers, microphones, and loudspeakers (Schleidt 1948, 1950, Zippelius and Schleidt 1956). Thus, my approach to animal communication was always compatible with the concepts of acoustics and communication engineering, and greatly encouraged by Hansjochem Autrum (1942, 1948). "Shannon and Weaver – The mathematical theory of communication (1949)" became my ultimate source of enlightenment.

My early discoveries in animal communication and my skills as jack of all trades were noted by Konrad Lorenz, and, in 1951, I became his first assistant at his research station in Buldern (Westphalia, Germany). As the first scientific task, Lorenz encouraged me to look into unfinished business of 1937, when he and Niko Tinbergen had investigated the responses of various young birds to cardboard dummies of raptors and other flying birds. The intent of these experiments was to test the limits of innate knowledge. The spectacular result was that a particular silhouette (Fig. 1) elicited alarm calls and escape behaviour, when moved in one direction (flown to the right as "hawk", carrying the sign-stimulus 'short neck').

No escape behaviour was released, however, when the model was flown in the opposite direction (to the left as "goose", carrying the sign-stimulus 'long neck'). The original protocols of these experiments had been lost during World War II, and the recollections of Lorenz and Tinbergen differed in several details: whereas Lorenz remembered that the relative speed of the model was the most significant feature, and the hawk/goose effect was

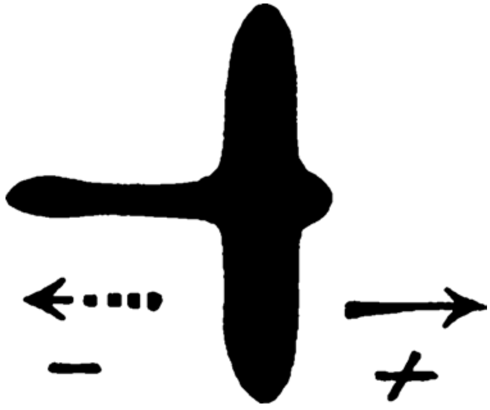

Fig. 1 Tinbergen's famous 1951 rendering of the "hawk/goose dummy" supposedly used by Lorenz and Tinbergen in their 1937 experiments. Image from Tinbergen 1951.

striking only in turkeys, Tinbergen featured the "short neck hypothesis". He claimed that "The reactions of young gallinaceous birds, ducks, and geese to a flying bird of prey are released by the sign-stimulus 'short neck' amongst others" (Tinbergen 1951, p. 77).

Our early experiments in the 1950s with various young gallinaceous birds, ducks, and geese at hand failed to support the short neck hypothesis. In a second phase of our investigation, we concentrated our efforts on establishing a flock of turkeys – the only species in Lorenz's recollection to respond to "short neck dummies", with a sufficient number of turkeys for a detailed experimental study. However, due to problems with an infectious fatal disease (histomoniasis), the decisive experimentation with flying predators was delayed until spring of 1961. Our replication and extension of the 1937 experiments showed, in essence, that the stronger response to the short neck of a moving dummy depended on an earlier experience of the subject. It was not due to an innate *sign-stimulus* 'short neck' but to previous exposures to flying objects and *selective habituation* to common shapes (Schleidt 1961, Schleidt et al. 2011).

The long waiting time between 1951 and 1961 was not wasted, because we always had a few healthy turkey toms around, and their gobbling and strutting became the subject of several investigations (e.g. M. Schleidt 1954, Schleidt and Schleidt 1958, Schleidt 1964, 1974). Since turkeys are highly social and have a rich repertoire of vocalizations, serving social communication and group cohesion, I gained considerable experience with their behaviour. My insight into their communication system became a standard for comparison with communication in other birds, and communication in general.

Finally, I must mention that my original discovery of ultrasound communication in mice, and the subsequent need to gain a minimal level of competence in acoustical and communication engineering laid the foundations for my quantitative approach to animal communication (Schleidt 1973). And, in passing, I note that my discoveries of the ability of various rodents to hear ultrasound and use it in their communication has become a centre of crystallization for research on laboratory mice and rats for neurobiology, psychopharmacology, and psychiatry (with several thousand publications, e.g. Crawley 2007, Wöhr and Schwarting 2007). In addition, my curiosity about the mind of dogs and wolves, at first mainly as predators of rodents, led to novel ideas about co-evolution between humans and wolves (Schleidt and Shalter 2003).

2. Understanding Behavioural Complexity

What do I mean by "behavioural complexity"? That is, the temporal and spatial relation between elementary behaviour patterns we can discern when observing one or more animals. Let me give a brief historical perspective on the discovery of elementary behaviour patterns as constituents of complex behaviour, especially as communication signals.

One of the earliest discussions of *behavioural complexity and communication* can be found in Charles Darwin's 1872 *The Expression of Emotions in Man and Animals*. These issues lay dormant, however, until the discoveries of Heinroth (1911) and Whitman (1919), and then the breakthrough in 1936, 73 years ago, here in Berlin, at the *Harnack-Haus*, when Konrad Lorenz presented a lecture entitled "The concept of instinct then and now". This was an update of an earlier paper on "arteigene Triebhandlungen" (species-specific drive actions; Lorenz 1932), published in its expanded updated form as Lorenz 1937.

Lorenz proposed *Instinktbewegungen* as the central units of observation – translated into English as *Fixed Action Patterns* (*FAPs*; Thorpe 1951). The role of FAPs as communication signals was somewhat simplified within the conceptual framework of *Auslöser* (*Social Releasers*) and *angeborene Schemata* (*Innate Releasing Mechanisms; IRMs*; for a discussion of the concepts of FAP and IRM see Schleidt 1962, 1964, 1974, 1982).

A severe shortcoming of behavioural research *at that time* was the difficulty in *documenting and analyzing the observations.* At best, the most salient observations or results were scribbled in a notebook. In fact, one of the most degrading arguments against Lorenz' research was that he had only *anecdotal evidence* and *was just a story teller.* And, in the scientific literature, quite often the only cited references to Lorenz are his popular books *King Solomon's Ring* and *Man Meets Dog*, even though many of his scientific papers had been translated into English. Konrad Lorenz' role as pioneer of *scientific cinematography* has rarely been recognized. He started filming in 1935 and documented the experiments he performed together with Niko Tinbergen in 1937 (ultimately published as "the behaviour of the greylag goose", Lorenz 1950). He also filmed the courtship of many surface feeding ducks in support of his comparative studies (Lorenz 1941, 1952, 1958, Schleidt and Oeser 2011 a, b), and he was one of the founding members of *Encyclopaedia Cinematographica.*

When Lorenz proposed his concept of *Instinktbewegungen,* behavioural theory was still overshadowed by Descartes' assumption that animals are mere machines. After Pavlov's discovery of the conditioned reflex, Watson's *Behaviorism* transformed Descartes' ideas into a rather simplistic framework of Stimulus-Response behaviour. The underlying assumption was that an individual organism starts with very few innate reflexes and acquires, through learning, all the information needed for its survival. Lorenz' claim that *complex sequences of behavioural acts* can be performed without having to be learned led to endless arguments about *what is innate and what is learned,* while the discovery that *complex sequences of behavioural acts are important building blocks of behaviour* was accepted as a matter of fact.

The amazing technological progress in audio and video recording during the second half of the 20th century and the availability of event recorders and computers for data storage eliminated the scribbled field notes and data sheets. Many of the problems confronted by early ethologists were thus resolved, except for one: *data analysis.* Many ethologists have piled their notebooks and tapes on shelves and locked the door forever because they failed to find ways to analyze their data and extract precious information.

In fact, ethology is still confronted by a problem similar to that *faced by physics about 100 years ago, namely, the lack of mathematical tools to deal with the problems at hand.* David Hilbert (1862–1943), the famous mathematician, used to bemoan poor physicists because he thought *physics was much too complicated for them.* Hilbert had mercy with the physicists and developed new methods of mathematics and geometry that greatly enhanced their skills (Hund 1969).

There were breakthroughs that benefited the experimental design and data analysis in the study of behaviour, especially in psychology by non-parametric statistics (e. g. Siegel 1956), or in orientation (e. g. Batschelet 1981). But to this day, ethologists await a mathematician or statistician of Hilpert's skill and devotion *to develop methods to deal with the analysis of behavioural complexity.*

I realized these shortcomings early on, despite (or because of) the fact that my own mathematical skills are extremely limited. But even though I lack a *mathematical brain,* I am quite good at *basic intuitive geometry* and in *hands-on engineering.* This allowed me, with the help of patient mathematicians and statisticians, to search for and find methods and tools, at least to get the work started.

2.1 Discrete Elements of Organismic Behaviour

As an example of a *complex sequence of behavioural acts* I have chosen a brief sequence of 18 s duration from the first scene of our movie documenting sexual behaviour of turkeys (Schleidt and Schleidt 1962), focusing on a single turkey hen ambling along in search of a mate (Fig. 2).

We can discern four behaviour patterns: walking, standing, alert posture, and the contact call “Drr”, and three additional continual variables: orientation of the body (in reference to the standard compass direction), orientation of the head (in reference to the body axis), and height of the head above ground. There are additional variables that may be of interest, but did not change much in our case, e. g. “height of the centre of gravity above ground” and the “Global Positioning System coordinates” (in that instant near: 47°58'24"N 11°14'09"O). Others, like breathing or eye blink, cannot be recovered at the given resolution of the images. It may be of interest that the “Filmbeschreibung” in the “Filmbeiheft” of this movie provides a detailed list of the most striking behavior pattern starting at a specific frame number (Schleidt 1971).

I must point out that, as a matter of convenience, in the scientific literature a particular behaviour pattern is represented by a characteristic “climax position,” a momentary image used as a mere label for a complex three-dimensional process. Such icons are useful for a space-saving summary of a behavioural inventory (e. g. Lorenz 1941, Schleidt et al. 1984), but must not distract from the fact that by behaviour pattern we mean the whole

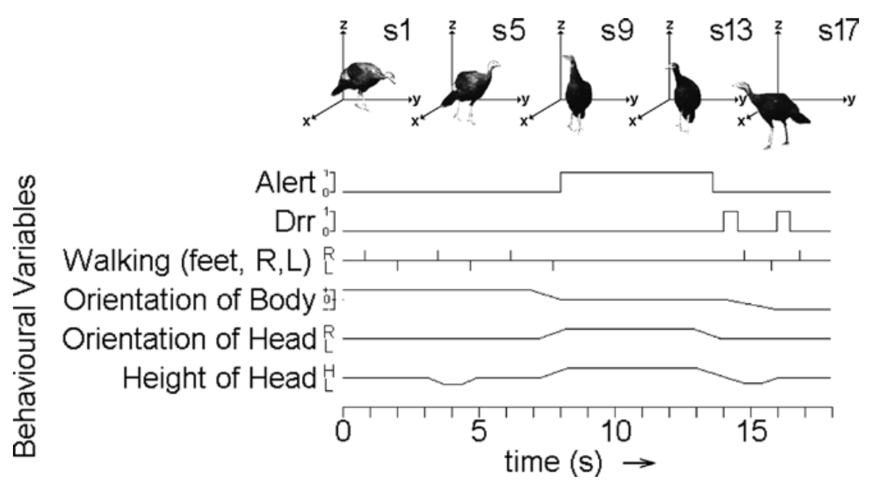

Fig. 2 Example of a 18 s recording of a turkey hen ambling along in search of a mate. Images above depict the stills at the indicated second, and below the schematic depiction of four behaviour patterns and three orientations, readable like a musical score; the two “Drr” start at frame 500 and frame 550 (see Schleidt 1971, p. 13; the drawings are based on scene 1 in Schleidt and Schleidt 1962).

process that is better described by a movie (Lorenz 1950), a sequence of frames (Lorenz 1958), or by an abstract space-time diagram (Finley et al.1983).

2.2 A Basic Geometry for Organismic Behaviour

We generally assume that a duck is a duck is a duck, as a rose is a rose is a rose, and we can assume that a rooster's crowing is a crowing is a crowing. In other words, whenever a thing, an animal, a flower, a behaviour pattern, is easily identified and described, the variability is accepted as a matter of fact. Thus, as a first approximation, we need to define the core features of a thing or a behaviour pattern.

To understand behavioural complexity – how behaviour is composed of its basic elements – we need to define the scenario within which behaviour takes place, the actor(s): individual organism(s) within a specific environment in space and time, and the props (particular things in the environment; Fig. 3).

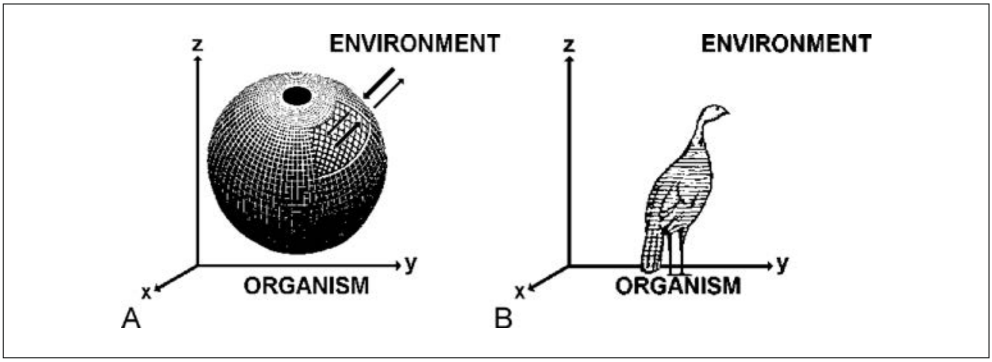

Fig. 3 Organisms within their Euclidian space. (*A*): Most organisms can be approximated by a three-dimensional body, separated from the environment by a semi-permeable membrane, a skin that acts as a two-way filter. (*B*): A turkey hen within her Euclidian space (left drawings based on Schleidt and Crawley 1980).

Behaviour, most generally, is any change of an organism, and can be described in one or several of the following actions: change in location, orientation, surface geometry, surface emission and/or surface absorption of matter, energy and/or information (Fig. 4).

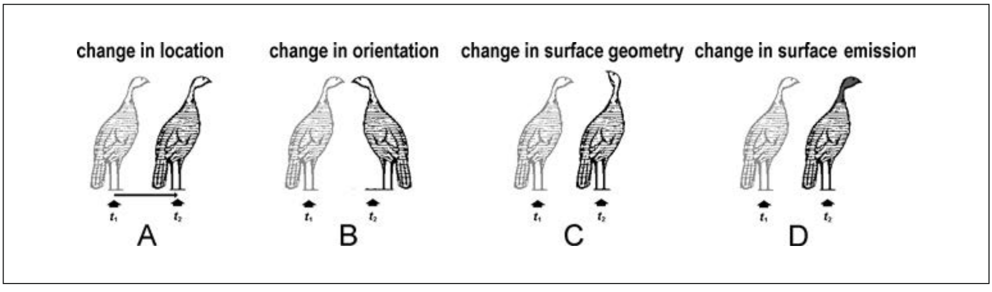

Fig. 4 A turkey hen within her Euclidian space, displaying four basic categories of behaviour as a change between two moments: t_1 and t_2: change in location (*A*), orientation (*B*), surface geometry (*C*), and surface emission and/or absorption (*D*).

Returning to my previous statement, we need to define the scenario within which behaviour takes place, the actor(s): individual organism(s) within a specific environment in space and time, and the props, I can illustrate the props on the stage of real life: particular things in a turkey hen's environment (Fig. 5).

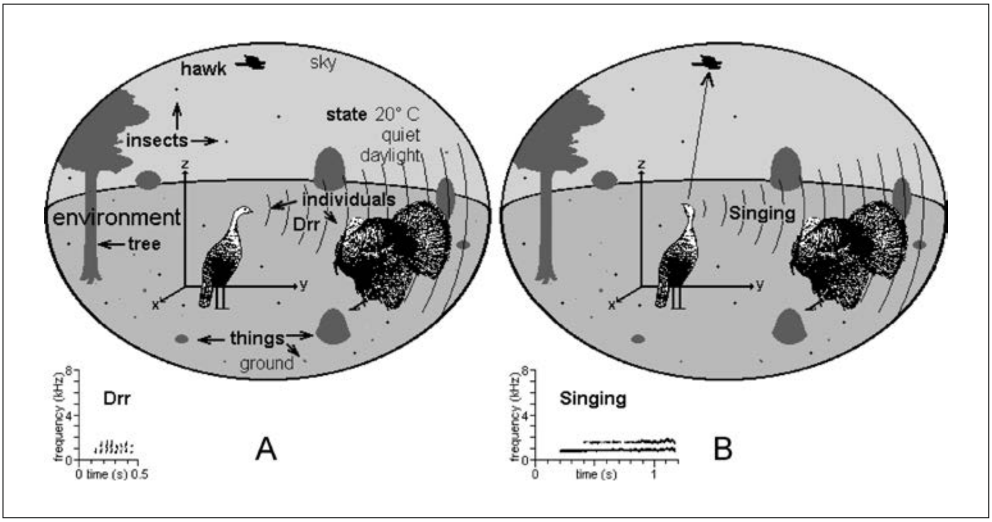

Fig. 5 A turkey hen within her environment, including a potential mate, a hawk (as a potential predator), insects (as potential food) and the props on the stage of real life, things on the ground, trees (to roost at night). There are additional variables, e. g. temperature, ambient noise level, daylight, etc. that are likely to influence the hen's behaviour such as her companions, etc. In the left scene (*A*) the hen is about to let the turkey tom approach her and emits a contact call "Drr". In the right scene (*B*) the hen has noticed the hawk flying overhead and emits an alarm call "Singing". The acoustical signals spread in all directions, but in the figures, they are shown to be addressed to the conspecific, so as not to clutter the drawings with too many lines.

This form of giving due consideration to the environment was pioneered by Jakob von Uexküll (1909) and illustrated unforgettably in his *Stroll through the Worlds of Animals and Men. A Picture Book of Invisible Worlds* (von Uexküll and Kriszat 1934, von Uexküll 1957). With the preceding considerations in mind, we have a conceptual framework available for the quantitative analysis of behaviour patterns that has been freed from the fruitless argument as to whether a particular behaviour pattern is innate or learned, without precluding a future analysis of the genetics and learning processes which have shaped it. Furthermore, we must be aware of human observer bias that has led us to a high preference for observation, recording, and analysis of behaviour within the domains of sight and hearing, at the expense of other sensory modalities such as smell, taste, touch. Many mammals are born with eyes and ears sealed and rely on smell and tactile information to find their mother's nipples, long before they see the light of day (Fig. 6).

Through careful recording of behavioural sequences that allows transformation into numerical data, conventional algorithms of pattern detection, classification, and recognition become useful tools for dealing with the complexity of both behaviour and the environment (Schleidt 1985).

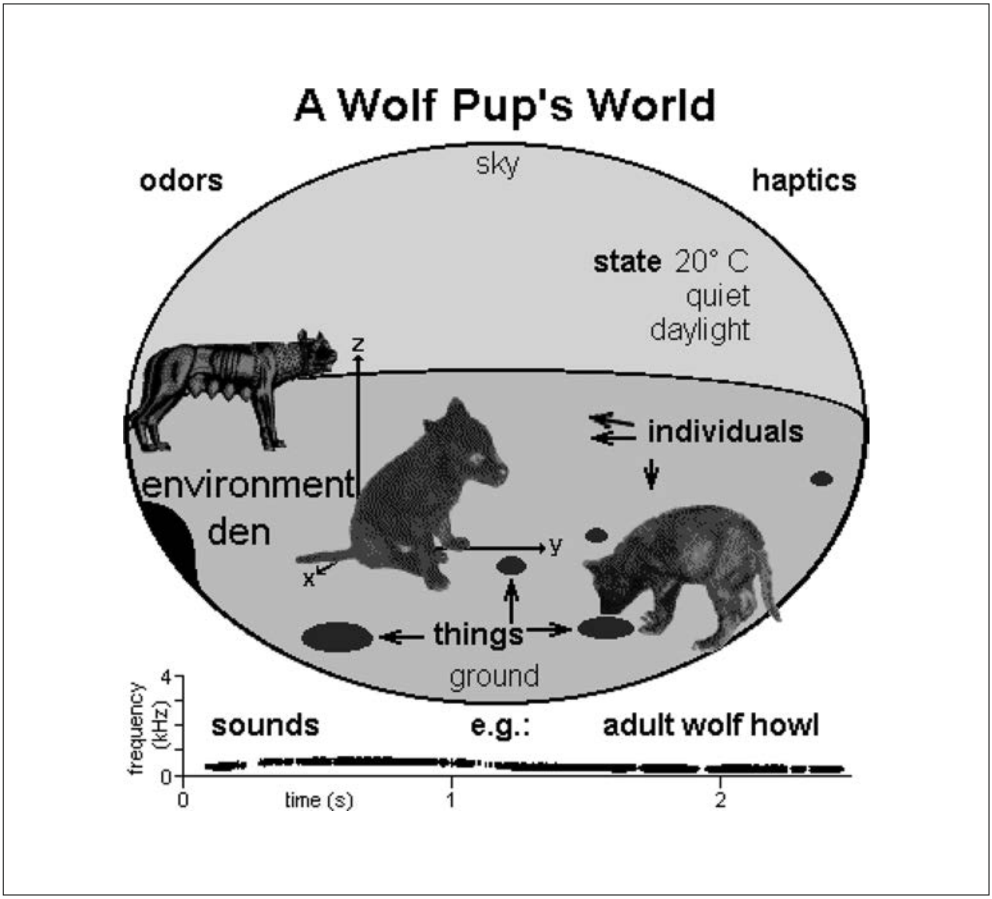

Fig. 6 Wolf pups, emerging from the den, experience for the first time a world in light, adding visual features to their world of touch, smell, sound and taste.

3. Communication among Animals

Before I discuss the role of discrete elements of behaviour as communication signals, we must clarify not only what we mean by communication within the general framework of organismic behaviour, but also give special attention to the cluster of concepts: *signals*, *messages*, and *information*. These concepts are sometimes used interchangeably and lead to considerable confusion: Given that the sensory system of an observed species is similar to that of the observer, familiarity with the species-specific behaviour patterns is sufficient for detecting the most salient signals. The *content of the specific message* encoded in the signal, however, remains cryptic in many cases, and *the specific information* which is being conveyed as well.

This situation is comparable to tracking the path of a registered letter: from the post office at which it has been deposited to the hand of the receiver, attesting with a personal signature its safe delivery. We know that communication has taken place, but have no hint about the message or information transferred.

With these considerations in mind, we can diagnose an ongoing process of communication, the transfer of information between two organisms, without having to know the specifics of a particular message or information. In fact, communication and information transfer can be diagnosed by a relatively simple statistical paradigm: “Communication between two animals occurs whenever the probability of a particular behavior of the receiving communicant is, with positive lag, associated over time with the signal output of the transmitting communicant.”[2]

3.1 The Statistical Analysis of Communication Signals

The “songs” of birds, but also of insects and frogs, because of their beauty at first, but also due to their species-specific nature, have been subject to speculations as to their function since antiquity. With the availability of sound recording equipment, especially sensitive microphones, tape recorders, and loudspeakers since the second half of the 20th century, the analysis of animal sounds was greatly advanced, and has reached a high level of sophistication in documentation, statistical analysis, and experimentation. Because of the available methods in bioacoustics, sound signals have become the preferred subject of studies in animal communication.

Of all the variables for consideration in any statistical analysis, *the frequency of occurrence of a signal* is the most important. For example, a contact call, like the “Drr” of a turkey hen (Fig. 7), emitted in some situations every few seconds, in an ongoing dialog among the members of a flock, can result in hundreds of events in a single day and provide plenty of data.

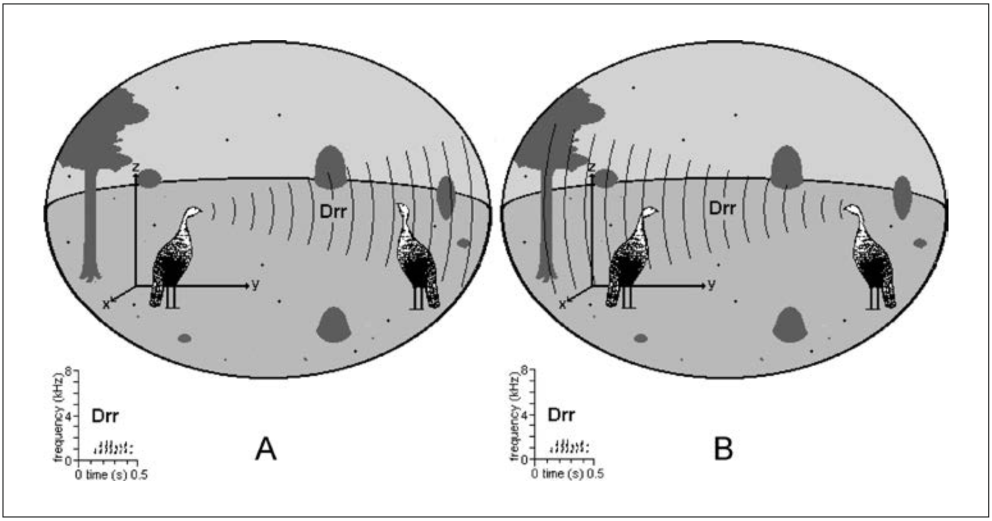

Fig. 7 A turkey hen within her environment, including another hen of her flock. In the left scene (*A*) the hen ambling along emits a contact call “Drr”, in the right scene (*B*) the other hen replies “Drr”. As noted in the caption of Fig. 5 the acoustical signals spread in all directions, but in the figures, they are shown to be addressed to the conspecific, so as not to clutter the drawings with too many lines.

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[2] Schleidt 1973, p. 384.

Other communication signals, like a series of the aerial alarm call "Singing" (Fig. 5*B*), can be elicited by a high-flying raptor only once every few days, even weeks. Thus, frequently occurring signals will be highly preferred over the rare ones. This bias in search of signals suitable for quantitative studies is not only a matter of convenience: reducing time for data acquisition. A short sampling time span is necessary to satisfy a basic requirement of statistical sampling, *homogeneity of the sample*. To insure homogeneity, the system from which the data are obtained must be in a "steady state", steady relative to the signal under investigation.

An aspect of the proposed algorithm for the detection of communication between two potential communicants, spelled out above, is the term "positive lag". *Positive lag* means that the behavioural change of the receiving communicant must start *some time after* the signal was emitted by the transmitting communicant – whereby the time delay is the sum of *travelling time* of the signal (critical in the case of sound), and the *response time* of the receiving communicant.

That this is not trivial can be shown in the case of turkey toms, communicating by their gobbling calls between two nighttime roosts, 2 km apart, early at dawn. A gobbling signal emitted at "roost one" travels at a speed of about 343 m/s, resulting in a delay of about 6 s in its arrival at "roost two". The standard response of a turkey tom's *hearing a gobbling call* is to *answer with a gobbling call.* The response time to elicit gobbling call depends on the loudness, and ranges – from highest to barely perceptible – between 200 ms to more than 1 s. From a distance of 2 km, the loudness of gobbling calls from "roost one" will be only a few dB above ambient noise at "roost two" and this adds another second of response time to the 6 s travelling time. So the total *positive lag must be at least seven seconds.* If the turkeys on "roost two" emit gobbling with a positive lag of about 7 to 9 s since it was emitted at "roost one", we can assume that gobbling on "roost two" *had been elicited by the gobbling call(s) from "roost one"*. Thus, communication had taken place.

Since one roost tree is usually shared by several turkeys, hens and toms, and the response time for gobbling eliciting gobbling within the roost is only a fraction of a second, one tom's gobble elicits a real explosion of gobbling from many or all toms sitting in this tree. Such a collective "monster gobble" is followed by a refractory period of intense listening for a response, lasting a few seconds. In this way, gobbling bouts between neighbouring roosts result in a true dialogue between the two turkey flocks, with a time interval of about 15 s between two gobbling bouts.

The primary function of this early morning gobbling activity is, like most bird songs, to provide other conspecifics with information about the presence and location of their neighbours. Such functional aspects will be discussed in the next chapter.

Another important aspect of communication is that "no reaction" can also be an answer, an indication that communication has taken place, provided we have a data sample of sufficient magnitude to look at the time course of the transitional probability of the response. For example, a turkey tom, isolated acoustically in a sound-attenuated, anechoic chamber will emit gobbling calls spontaneously at a certain rate. Once a gobbling call is played back, it immediately elicits a gobbling call, followed by a long phase of silence, much longer than the time interval between the spontaneous gobbling activity, only a minute ago. Thus, for a turkey tom hearing the gobbling of another there is an *excitatory effect at first*, eliciting one gobbling call, but then *a longer lasting inhibitory effect*: suppressing spontaneous calling and switching to a "listening mode".

A similar principle works in the case of crowing of roosters, where hearing another rooster's crowing inhibits its own crowing momentarily, but after a few seconds increases the probability of crowing. The statistical aspects of sampling and analysis of signals in this and other cases were discussed in some detail by Schleidt (1973).

3.2 Two Types of Communication: Phasic and Tonic Communication

In reviewing a wide variety of cases in which it can be shown that communication is taking place, we encounter a striking difference between signals that occur relatively seldom and those that are emitted frequently. Examples of the first type of communication include alarm calls that are elicited only by specific types of predators and which under natural conditions have a striking effect on the receiving communicants: overt expressions of panic that do not require sampling a large number of responses to prove that communication has occurred; e. g. the case of "Singing" sketched in Figure 5*B* in response to a high-flying raptor. I proposed calling this type of communication *Phasic Communication* because it puts the receiving communicant into a different *phase, mode, mood, or behavioural state*, lasting for a while (for several minutes, hours, for the rest of the day, or even for a lifetime).

Examples of the second type of communication, *Tonic Communication*, include the contact calls of social animals, conveying the message "Here Am I – Where Are You?" (as used by Konrad Lorenz as title for his *Ethologie der Graugans*; Lorenz 1988, 1991). That contact calls are emitted very frequently make it easy to record a large data set to study the changes in probability as an indicator of communication taking place, e. g. the case of the contact call "Drr" in Figure 5*A*, 7. I proposed calling this type of communication *Tonic Communication* because it acts like the stream of nerve impulses that maintain the tonus of a muscle: a stream of repeated signals maintains the contact between emitting and receiving communicants and can modulate each other's behaviour.

3.2.1 Phasic Communication

One of the most spectacular cases of phasic communication is the switch of a broody turkey hen from incubating her eggs to leading her poults through hearing repetitive contact calls emitted by the young, at first while still within the egg shell and later on during hatching and the first excursions from underneath the hen. If the hen cannot hear the contact call, visual cues of the emerging poults (their fur-like downs) elicit in the hen a deadly attack – she mistakes the fluffy balls for predators and kills each with a forceful peck between the eyes (Schleidt et al. 1960). This strange case was discovered by coincidence when a deaf turkey hen had killed all her poults immediately after hatching. In subsequent experiments in which an incubating turkey hen with normal hearing was tested with a fluffy dummy poult with a loudspeaker inside, from which baby turkey contact calls could be played back. When the dummy was brought within reach of the incubating hen, she responded with all signs of nest defence, ruffling her feathers, hissing, and pecking at the dummy. The moment the tape recorder was switched on and the dummy began to emit contact calls, the aggressive behaviour stopped: the hen started clucking and looked underneath herself as if she knew that the peeping must come from her eggs (even though her eggs were also "dummies" made of plaster). Observations of incubating turkey hens while young were hatching showed that when the first dry and fluffy poult appeared from underneath, the hen became highly agitated, even pecking at the poult when it was silent. However, as soon as the poult emitted contact calls or even a pain cry, the hen started clucking and calmed down. Within an hour, all signs of hostility toward the poults had ended and the switch from incubation behaviour to that of a leading hen had been completed.

A similar relatively brief communication process occurs during "*imprinting*" of the young of nidifugous birds (those that leave the nest shortly after hatching) to their parent (Lorenz 1935, Hess 1973). Contrary to popular belief, imprinting is neither an instantaneous process nor inevitably permanent and immutable in all cases. Central to its occurrence, however, is a relatively brief exchange of signals that have a long lasting, phasic effect.

3.2.2 Tonic Communication

As already mentioned, examples for the second type of communication are the contact calls of social animals, conveying the message: "Here Am I – Where Are You?" Contact calls provide information on identity and current location (the social "existence") of the transmitting communicant, and, since they are emitted very frequently, these signals maintain a bond between the communicants, allow them to proceed in a coordinated way, create a union, and transform the communication individuals into a social unit – a family, flock, etc. Their frequent repetition makes it easy to record a large data set for statistical investigations, e. g. the changes in probability as an indicator of communication taking place.

Many bird songs serve also as contact calls and belong in this category, as do the song-like vocalizations of male gallinaceous birds (e. g., the crowing of a rooster, the gobbling call of a turkey tom, or the wet-my-lip call of a male European quail).

A special feature of tonic communication is that the stream of signals can code the magnitude of information transfer independent of distance between the communicants, resulting in a form of coding that in communication engineering is called *pulse code modulation*.

There are at least two distinct types of communication: Phasic Communication (PC), where a single signal from a transmitting communicant can cause a permanent change in a receiving communicant, and Tonic Communication (TC), where a stream of signals from a transmitting communicant can modulate the behavioural state of the receiving communicant and create a union between communicants.

Tonic communication has been found in many different species: whenever a communication signal occurs at a high repletion rate, a tonic function is very likely.

That the songs of male birds function to attract potential mates and repel other males has been recognized for some time, but the complexity of the system has long been underestimated in being interpreted as a kind of unconditioned reflex that lets females approach singing males and keeps neighbours spaced by an equilibrium of attraction and repulsion. I think the first case that indicated the complexity of the problem appeared with the availability of high quality play-back from tape-recorded bird songs. It turned out that, e. g. in ovenbirds, each resident male recognizes his neighbours by their songs, and between his own singing bouts, listens (like the turkey toms and roosters mentioned above) to songs of his neighbours. If the song of a neighbour is played back from a different direction, it is interpreted as an intruder into the "status quo" and is investigated immediately (Weeden and Falls 1959, Falls 1982, 1992).

4. Concluding Remarks

In my introduction, I pointed to *the importance of new tools and concepts* of contemporary physiology and communication engineering for our quest to expand our understanding of behavioural complexity in communication processes. Biology is no longer an isolated discipline but rather has become an integral part of natural sciences.

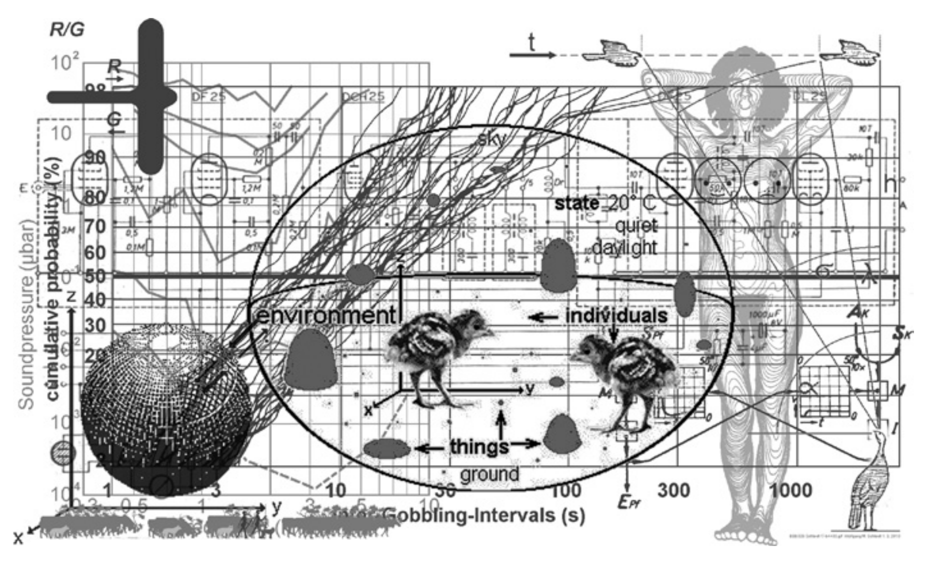

Fig. 8 A glimpse into W. M. Schleidt's analytical toolbox.

When dealing with overt behaviour, a solid base in physics is of utmost importance, as are chemistry and physiology when considering the internal mechanisms, e. g., motivation. A few specific algorithms for investigating behaviour and communication – instructions for using and honing the tools I found most helpful – are listed in the references. In Figure 8 I offer a glimpse into my analytical toolbox.

Acknowledgements

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Nachhaltigkeit in der Wissenschaft

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Im Mittelpunkt der weltweiten Überlegungen zur Bewältigung zentraler Herausforderungen des 21. Jahrhunderts steht das Konzept der Nachhaltigkeit. Damit dieses Prinzip sich in konkreten Handlungsvorschlägen widerspiegeln kann, bedarf es der Präzisierung. Der Band untersucht daher die Nachhaltigkeit in der Wissenschaft, der wichtigsten Informationsquelle der Gesellschaft. Dabei wird Nachhaltigkeit sowohl der Strukturen als auch der Aktivitäten in Forschung und Lehre betrachtet. Behandelt werden die „Erforschung von Nachhaltigkeit“, die Strategien zum besseren Verständnis liefern soll, der Komplex „nachhaltig forschen“, der Voraussetzungen, Verläufe und Folgen von Forschung gemäß den Kriterien der Nachhaltigkeit analysiert, und die „Nachhaltigkeit von Forschung“, die Wesensprinzipien der Wissenschaft – etwa die Falsifizierbarkeit ihrer Resultate – im Lichte der Idee der Nachhaltigkeit untersucht. Schwerpunkte der Analyse bilden in allen Bereichen einerseits das Spannungsverhältnis zwischen Freiheit und Nachhaltigkeit der Wissenschaft sowie andererseits die Auswirkungen der Debatte auf die Strukturen des Wissenschaftssystems.

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The Quest for Understanding Social Complexity

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Abstract

Complex social systems are loosely characterized by individualized long-term dyadic relationships embedded in interactive groups. Individual behaviour in such systems is contingent on what the others do and is based on species-specific behaviours as well as physiological mechanisms. Hence, social complexity, i. e. individual variation of performance in social webs can only be understood *via* the contingencies and interactions between proximate mechanisms and ultimate functions. Amazingly parallel patterns of social organization are even found between distantly related vertebrates, such as mammals and birds. Understanding the reasons for these parallels also contributes to explain social complexity in general. In the present contribution I discuss major elements of the mechanistic base of these parallels, including conservative social brain networks, bonding and emotional systems, as well as the brain and physiological systems for coping with stress and modern brain areas developed in parallel in mammals and birds which allow proper control of social behaviour. The setpoints and functions of these mechanisms may be dramatically affected by social ontogeny, allowing to adapt offspring behaviour to prospective environments and generating some continuity in social styles between generations.

Zusammenfassung

Individuen in komplexen sozialen Systemen unterhalten besondere langzeitliche Beziehungen innerhalb von interaktiven Gruppen. Individuelles Verhalten in solch komplexen sozialen Netzen hängt natürlich von den anderen Mitgliedern des sozialen Netzes ab. Individuelle Komponenten sind artspezifische Verhaltensweisen und zugrundeliegende Mechanismen. Um individuelles Verhalten in komplexen sozialen Netzen zu erklären, ist ein Verständnis der vielfältigen Kontingenzen zwischen proximaten Mechanismen und evolutionären Funktionen nötig. Generell zeigen sich erstaunliche Parallelen in den sozialen Organisationsmustern von Wirbeltieren, sogar zwischen stammesgeschichtlich entfernten Taxa, wie etwa Säugetieren und Vögeln. Diese Parallelen zu erklären, liefert auch einen Beitrag zum Verständnis sozialer Komplexität. Im vorliegenden Beitrag werden die wichtigsten Elemente der mechanistischen Basis des Sozialverhaltens der Wirbeltiere diskutiert. Dazu zählen konservativ über die Stammesgeschichte erhaltene Hirngebiete für sozio-sexuelles Verhalten, Bindung und Emotionen sowie die Systeme zur Stressbewältigung. Zur Impulskontrolle und zum Treffen von Entscheidungen wurden bei den Säugetieren und Vögeln analoge Vorderhirngebiete entwickelt. Über frühe soziale Interaktionen werden die grundlegenden Einstellungen der basalen Systeme und die zugehörigen kognitiven Repräsentationen individuell geprägt, wodurch Nachkommen auf die zu erwartenden Umwelt- und Sozialbedingungen eingestellt werden und eine Tradition sozialer Stile entstehen kann.

1. Introduction

Social behaviour means relating to others. Nothing seems to fascinate most humans more than their own relationships to others and learning about the relationships between others. Still, towards the midst of last century, the prime interest of ethologists was to explain individual behaviour (see contribution by W. Schleidt in this volume, Lorenz 1978) *via* focussing on instincts mainly. This was understandable, because the tenet of ethology was that behavioural elements, dispositions, even in the context of learning are strongly genetically heritable (Tinbergen 1951), which is the reason why there is not only species-specificity in anatomy and physiology, but also in behaviour. Hence, the focus of early ethology was at the species-specific inventory of behaviour and on a general explanation how individuals manage to use the proper behaviours in certain contexts. Individual variation was long considered as a nuisance rather than a clue hinting at the mechanisms of individual ontogenetic development.

But one of the characteristics of social interactions is that even genetically similar individuals differ in their phenotype, including behavioural (Sih et al. 2004). Hence, social interactions are not merely stimulus-response based exchanges between standardised models performing at a species-specific mean, but are shaped by interaction styles, depending on individual features components. Individual experience, setpoints of the relevant physiological systems, dyadic relationships, but also conditionality of social performance due to individual standing in the social network are non-independent elements of social individuality (Kotrschal et al. 2010). Among the relevant factors for social behaviour at the interface between physiology and ultimate functions are emotions, bonding/attachment, social support, coping styles, social cognition, eavesdropping/bystanding, etc. (Kotrschal et al. 2010). Explaining (complex) social interactions and individual roles in social webs needs an understanding how these mechanisms interact, how they develop together in ontogeny, how they affect behaviour and how they are themselves affected by feedback from behaviour/social context.

In fact, similar (‘convergent’) patterns and elements of social complexity can be found in mammals and birds (Bugnyar and Heinrich 2006, Byrne and Whiten 1988, Emery and Clayton 2004, Kotrschal et al. 2007, 2010). These include long-term dyadic partnerships, certain patterns of conflict resolution and an often impressive knowledge of third party relationships, even in geese (Aureli and de Waal 2000, de Waal 2000, Kotrschal et al. 2006, 2010, Weiss et al. 2008, Weiss and Kotrschal 2004, Scheiber et al. 2005, Wascher et al. 2008). Such convergence may not only be the result of common selection pressures shaping social systems (Trivers 1985) and systemic ‘self-organization’ (Hemelrijk 1997), but is probably also based at a toolbox (below) of common physiological, ontogenetic and cognitive mechanisms, constraining other solutions and permitting the development of impressive in detail parallels even between mammals and birds, which evolved independently for at least 230 million years.

In the following, I will focus on the mechanistic components of sociality and its modulation in ontogeny. The most important elements of this vertebrate social toolbox include exceedingly conservative elements of the brain, such as the ‘social brain network’ (Goodson 2005), including a bonding mechanism (Curley and Keverne 2005), which is the base for the attachment and caring systems in mammals and in many birds, and including highly preserved brain emotional systems (Panksepp1998). But there is also rapid convergence in the most modern parts of the brain, if needed in a social context, a good example being the parallel evolution of brain control centres (i. e. mammalian prefrontal cortex and bird Nidopallium caudolaterale; Güntürkün 2005). Based on these parallels in the brains, considerable parallels in cognitive mechanisms are found between mammals and birds (Byrne and Whiten 1988, Emery and Clayton 2004, Kotrschal et al. 2007). Other elements of the social toolbox, tightly linked to the brain are the means for (social) stress management, essentially the two stress axes. Based on stress modulation, temperaments ('personalities') seem to vary according to the same principles in the different vertebrate species (below). In the following, some of the mechanistic elements will be discussed which provide the common ground for parallel social structures in the homoeothermic vertebrates.

2. Individual Components of Social Players

2.1 Conservative Vertebrate Brains

The brains of all gnathostome vertebrates show a common 'Bauplan' (Nieuwenhuis et al. 1998). By and large, the brain is relatively conservative with regards to evolutionary change, "it appears that the basic adaptive neural mechanisms had been worked out during early vertebrate evolution" (Welkner 1976). The diencephalic and tegmental brain centres for socio-sexual behaviour govern instinctive socio-sexual behaviour. These areas remained essentially unchanged in structure and function over more than 400 million years of evolution. A diencephalic constituent of this vertebrate brain 'social behaviour network' (Goodson 2005) is the parvocellular preoptic nucleus, which is centrally involved in the development of social bonding between individuals (Curley and Keverne 2005). This nucleus produces two peptides for release in the neurohypophysis: oxytocin (OT) and arginine-vasopressin (AVP); with functionally similar analogues in different vertebrate phyla. Besides their metabolic functions, these hormones and neurotransmitters are centrally involved in the regulation and modulation of sex-specific socio-sexual behaviour, with more oxytocin in the females and more arginine-vasopressin in the males (Goodson 2005). AVP seems specifically involved in courtship in both sexes (Goodson and Bass 2001).

Particularly in mammals, OT and AVP are involved in tuning brains towards bonding with specific individuals, offspring or pair partners. Estrogen and progesterone up-regulate OT receptors in the brain and elsewhere. At birth, OT is released under the influence of cortisol, aiding parturition, milk let-down and facilitating olfactory offspring recognition. Under elevated OT, brain reward systems are activated *via* the appropriate olfactory input, establishing the mother-offspring bond on the side of the mother. In the 'small-brained' mammals (e. g. rodents) this mechanism is primarily used for establishing and maintaining mother-offspring bonding, but also for monogamous pair bond in some species (Carter and Keverne 2002). In the 'large-brained' mammals (e. g. primates) some 'emancipation' from this hormonal mechanism is found (Curley and Keverne 2005), probably because for rearing offspring in a complex social group, such a relatively invariable 'stimulus-response' social coping mechanism may not be fully adequate. Notably, OT is released at female orgasms or at tactile stimulation during allogrooming (de Vries et al. 2003, Uvnäs-Moberg and Francis 2003) and seems one of the major mechanistic underpinnings of 'love' between long-term pair partners (i. e. dyadic attachment: Carter et al. 1995).

Birds show surprising parallels to mammals in their social behaviour (Emery et al. 2007). It is still unknown, however, whether allopreening in altricial birds, in parallel to allogrooming in mammals, also triggers the release of mesotocine (MT), the bird equivalent of OT. Precocial birds, such as greylag geese, do not allopreen at all and still show long-term bonding between parents and offspring, between sisters and between pair partners and other complex social features (Kotrschal et al. 2006, Scheiber et al. 2007, Weiss et al. 2008). This may either mean that the MT-AVP system is not important for social bonding in these birds, or that this system is mainly activated *via* the visual input. Still, particularly altricial birds do allogroom. Particularly many species with long-term pair bond, such as corvids and parrots do. It is quite likely that allogrooming will trigger the MT system in a similar way in these birds as in mammals.

Even within-species, bonding and attachment styles between individuals may vary substantially, depending on species-specific characteristics and early socialization in interaction with basic personality traits (below; Ainsworth 1985, Bowlby 1999, Hinde 1998, Hinde and Stevenson-Hinde 1987). The kind of socialization provides a direct developmental link to attachment style and stress management over generations (Meaney et al. 1991). In fact, *via* social influence on brain development (Mayes 2006), the maternal style may be socially transmitted over generations. Hence, on top of the genetic background, maternal style crucially affects attachment, and therefore, the quality of social bonding individual offspring will be able to engage later in life.

Another functionally important element at least partially associated with the "social behaviour network" of the brain (above; Goodson 2005) are the phylogenetically conservative affective/emotional systems. Social relationships are always and unavoidably affective/emotional relationships. Operationally defined, emotions are conscious qualia, whereas affects remain unconscious. In the following "emotions" is used as the more inclusive term, which however does not imply that all affects are necessarily conscious in humans or non-human animals. Emotions "motivate" social interactions, are affected by social interactions and are directly linked with basic physiology (HPA, SAA) and cognition. Thereby, emotions are directly relevant for the proportion of energy spent in the social domain (e. g. efficiency in the social domain). Such, emotional phenotype ('temperament') will affect social connectedness, 'social efficiency' and finally, fitness in complex social systems. Emotional systems provide the motivational base for 'instinctive' socio-sexual and other basic behavioural systems. But also, depending on their phylogeny and social organization, there will be tight interactions of these systems, with "higher cognition" (Emery and Clayton 2004) and consciousness (Panksepp 2005). For example, Range et al. (2009) showed that dogs are sensitive to unequal treatment (i. e. being not rewarded for giving the paw when the other dog is). The non-rewarded dog in an experimental setting with two dogs not only stops cooperating, but shows signs of stress, frustration and annoyance, for example, may attack the rewarded dog. Hence, the cognitive ability to detect unequal treatment is evidently strongly linked with emotions.

Emotions are involved in every decision the prefrontal cortex prepares for conscious judgement. In turn, all decisions feed back to the emotional systems (Koechlin and Hyafil 2007, Sanfey 2007). These extended and elementary trans-diencephalic, limbic, emotional/affective systems may include 'seeking' (appetitive, interest), 'fear', 'rage' (aggressive), 'lust', 'care', 'panic' and 'play' (Panksepp 1998). *Via* common origin, these basic emotional systems seem to be shared by all mammals and probably, birds (Jarvis et al. 2005). If this phylogenetic distribution is due to common origin, the basic affective systems may root even deeper in phylogeny and may already be present in reptiles and potentially, fish. Because the 'social brain network' (above) contributes to these emotional systems, they may be found, in different shades of differentiation, in all vertebrates (Goodson 2005).

The emotion systems are directly connected with motor systems producing the expressions of emotions (Darwin 1872). Clearly, the behaviour patterns expressing emotions are very different in different species, but there are common principles: As a rule, full individual control over the expressions of emotions is hard to achieve, even in humans. In contrast, adequately socialized individuals are experts in 'emotional ('mind') reading', i. e. in deciphering even the most subtle expression of others' emotions. This seems a core component of empathy and emotional competence in humans (Eibl-Eibesfeldt 2004) and nonhuman animals alike. To maintain group cohesion, such mechanisms are needed to synchronise individual activities, for example to feed where others feed or to depart with the others, etc. This kind of 'social facilitation' may be mediated by 'emotional contagion', based on mirror neuron systems (Rizzolatti and Craighero 2004). Moreover, these brain systems may also be the base for the ability to imitate skilled actions, grasping of the intentions of others, or may even mediate elementary empathy (de Waal 2008, Gallese et al. 2004, Ramachandran 2008). The basic mechanism for empathy, emotional sharing when seeing others suffer, may be involved (Gallese and Goldman 1998, Rizzolati and Sinigalia 2007). At present, mirror neurons serve as a convenient mechanistic explanation of quite some features of behavioural complexity, for example, of social facilitation, social support and even consolation (Aureli and de Waal 2000, de Waal and van Rosemaalen 1979) in mammals and also in birds (Emery et al. 2007, Kotrschal et al. 2007). Such parallels suggest that the common ancestor of birds and mammals, 320 mill. years ago may already have had such a reflexive system.

Selective attention usually focuses offspring towards social role models, such as parents or play mates. Thereby, the linkage between emotions and cognition, which is a crucial element for decision making (Sanfey 2007) seems to be fine-tuned by implicit social learning with regards to deciphering the emotional expressions of others and the social do's and don't's. This seems to be achieved during early sensitive periods of development together with the ontogeny of individual attachment (Ainsworth et al. 1978), in most, if not all social birds and mammals, including humans (Bowlby 1999, Hinde and Stevenson-Hinde 1987, Scott and Fuller 1965).

Reasonably complex social systems do not just rely on these 'old' mechanisms discussed above, but, to the contrary, these old, 'instinctive' mechanisms need to be controlled for contextual adequacy by 'higher' brain centres. Individuals need their instinctive substrate for social behaviour, but they also need to control their instinctive impulses, to respond conditionally to the opponent's/partner's behaviour, to keep track of checks and balances over time (emotionally or cognitively, above), to adjust to categorical (e. g. clan membership) and individual (dyadic) relations with others, to integrate information from different domains into "episodic memory" (Emery and Clayton 2004), or generally, to form relevant concepts about the environment (Koechlin and Hyafil 2007). This is certainly true for many birds and mammals, which often reproduce and raise their offspring in the frame of complex social systems. Hence, even attachment and caregiving need to be adapted to the relevant social context, which may vary widely between individuals necessitating the basic behavioural systems to be open to modulation *via* social cognitive mechanisms.

But 'instinctive' mechanisms do not do the trick when it comes to succeed in complex social systems. This needs brain centres for instinct control. The prefrontal cortex in mammals and the nidopallium caudolaterale in birds were identified as such centres. Complex ecological and social environments (Aureli and de Waal 2000, Weiss et al. 2008) demand appropriate mechanisms of decision-making (Kotrschal et al. 2007, Paulus 2007, Sanfey 2007). The mammalian prefrontal cortex (PC) does exactly that (Damasio 1999, Güntürkün 2005); it is associated with complex learning (Lissek and Güntürkün 2003), economic choice (Kalenscher et al. 2005), context integration (Lissek and Güntürkün 2005), self-control (Kalenscher et al. 2006) and thereby, controls impulsive behaviours, allows social judgement, concept formation and categorization, guides emotion-based decision making and conducts mental and sub-conscious trial-and-error simulations before a final decision is reached (Koechlin and Hyafil 2007).

Structurally, the PC is part of the laminated pallium and hence, is a mammalian privilege (Nieuwenhuys et al. 1998). It is now accepted that the telencephalon in birds and mammals has comparable proportions of pallium (Reiner et al. 2004). Based on connectivity and neurochemistry, the 'nidopallium caudolaterale', a dorso-caudal telencephalic area in birds, was identified as the functional equivalent of the mammalian PC (Divac et al. 1994, Güntürkün 2005) prefrontal cortex. This cognitive 'rehabilitation' of birds (Jarvis et al. 2005, Reiner et al. 2004) reconciles neuroanatomy with evidence that birds frequently innovate (Lefebvre et al. 1997, 2004), show theory of mind-like abilities (Bugnyar and Heinrich 2006, Bugnyar et al. 2007) and may develop social systems of similar complexity as mammals (Kotrschal et al. 2006, 2010, Weiss et al. 2008).

2.2 *Coping with Stress*

Another common principle among homoeothermic vertebrates is that individual variation to the maternal effects (pre-partum) and effects of early parenting/socialization (post-partum) affect stress coping and whether and how social context later in life will affect dealing with stress or itself will represent a stressor. This involves two stress axes which were conservatively maintained over more than 400 mill. years of evolutionary history. These stress axes are usually greatly modulated by social context and *vice versa*, are themselves important modulators of social behaviour. Stress coping is a crucial element of individual social performance (Creel et al. 1996, Creel 2005, de Vries et al. 2003, Mayes 2006, McEwan and Wingfield 2003, Sachser 1998, Sapolsky 1992, von Holst 1998). Therefore, it is not surprising that the 'social brain network' (above) is also involved and that the degree a species tends to be social or territorial, for example, is contingent with these highly conservative (brain) mechanisms of stress coping (Goodson 2005).

There are two vertebrate-general systems for coping with stress, which are strongly linked with the evolutionary conservative brain: the sympathico-adrenergic system (SA), which provides a rapid alarm response (Selye 1951), associated with a quick release of catecholamines from the adrenals triggered by the sympathic nerves, and with rapid changes in heart rate and blood pressure. In contrast, the hypothalamo-pituitary-adrenal system (HPA) produces a slower, but longer-lasting response (Sapolsky 1992, Sapolsky et al. 2000, von Holst 1998). In the latter, a hypothalamic releasing factor (CRF) enters the anterior pituitary *via* the portal vessels and triggers the release of adrenocorticotrophic hormone (ACTH), which initiates the synthesis of glucocorticoids (cortisol in most mammals, corticosterone in birds) in the adrenals. These major metabolic hormones also mediate individual decisions whether to allocate energy to growth, behaviour, storage or reproduction (McEwen and Wingfield 2003, Sapolsky 1992, von Holst 1998).

The two stress systems may provide a direct link between social context, such as bonding, attachment and social support and stress hormone-mediated investments into the social domain (Kotrschal 2005). Glucocorticoids increase blood glucose and stimulate food uptake. Their frequent, short-term activation is part of coping with any challenge, positive or negative and even, part of the appetitive interest and of the neurotrophic support of learning (Sapolsky et al. 2000). Chronic elevation of glucocorticoids is pathogenic, for example mediating type II-diabetes (Vanltallie 2002). Whether or not stressful conditions are pathogenic depends on individual behavioural phenotype, the degree of predictability and the level of individual control (Sapolsky 1992, von Holst 1998). Depending on the nature of social interactions, their stimulatory effects on the two stress axes may vary (Kvetnansky et al. 1995). While many social stimuli effectively activate the SA and HPA axes (von Holst 1998, Wascher et al. 2008), passive social support (closeness, or socio-positive interactions with a social partner) dampens stress responses *via* activating the brain OT system. Thereby, three crucial steps of the HPA cascade are inhibited, CRF, ACTH and glucocorticoid synthesis (de Vries et al. 2003; see also the oxytocin chapter). Thus, social support dampens anxiety and aggressiveness, enhances socio-positive interactions, positively re-enforces social bonds and decreases the physiological and energetic costs of social life. These physiological, psychological and behavioural effects of social support are found in a similar way, in mammals and social birds (Emery et al. 2007, Scheiber et al. 2005, Weiss et al. 2008). In fact, the mechanisms of bonding and social support seem to be part of the basic vertebrate “social behaviour network” in the brain (Goodson 2005).

2.3 *Individuality, Temperament, Personality*

The two stress axes do not only vary between individuals, as related to early social history, but are also main basic factors in the differentiation of individual temperament and personalities (i. e. relatively stable dispositions to respond to the challenges of life in a particular way). This may also be a main reason why humans and non-human animals seem to be differentiated in their personality characteristics along similar axes.

Individual behavioural phenotypes (in the following called ‘personality’) seem to vary along similar axes in a number of vertebrate species and even, in some invertebrates (Sih et al. 2004). The main axis found in most species is essentially ‘reactive-proactive’ (Koolhaas et al. 1999; ‘proactive’ corresponding with ‘aggressive or assortative’, Huntingford 1976, ‘shy-bold’: Wilson 1998, Wilson et al. 1994, ‘slow-fast’: Drent and Marchetti 1999). Proactive individuals in comparison with reactives tend to approach the challenges of life more actively, they tend to become dominant, are quick, but superficial to explore, are prone to form routines, but are reluctant to change them again and they usually do not excel at solving difficult tasks themselves, but profit from the actions of others by copying or scrounging (Giraldeau and Caraco 2000). These behavioural differences are contingent with differently set physiological systems for coping with stress: When challenged, proactives usually show a strong sympathico-adrenergic response, but only a quickly passing glucocorticoid peak and *vice versa* in the reactives (Koolhaas et al. 1999).

Personality features are genetically heritable, may be greatly modulated by 'maternal effects' (i. e. *via* the direct hormonal interaction of mothers with their developing offspring; Groothuis and Carere 2004) and will also be affected by post-natal parenting and early socialization (Mayes 2006), particularly in species with long-dependent offspring. Early exposure of bird embryos to androgens, for example, generally shifts individuals towards a more 'proactive' behaviour style (Daisley et al. 2005, Groothuis et al. 2005).

Per definition, personality attributes are usually consistent over situations and time and also predispose individuals to assume certain social roles (Dingemanse and de Goede 2004, Pfeffer et al. 2002, Sih et al. 2004). In a way, a non-random variation of individual behavioural phenotypes in virtually any group of vertebrates is one of the preconditions for the development of social complexity. If all individuals had the same fission-fusion organization, for example (discussed as one of the driving forces of complex cognition; Dunbar 2007, Marino 2002) it would make no functional sense, because sub-groups may primarily form according to competence/personality features. Also, mate choice, particularly in the case of long-term pair bond, should not only be based on straight indicators of genetic quality of the partner, but also on operational partner compatibility (Dingemanse et al. 2004), including how successful partners will act together and will provide active and passive social support for each other (Scheiber et al. 2005). In general, a predictable and accountable variation of behavioural phenotypes creates a choice of potential partners and allies for different tasks, makes individuals dependable, and dyadic combinations functional.

3. Concluding Remarks

Social complexity, i. e. the ability to engage in long-term and differentiated dyadic relationships, to form social traditions on the level of the individual, dyad or group, to engage in fission-fusion group organization, etc. comes in convergent patterns even in evolutionary distant groups, such as mammals and birds. As discussed, a major reason for this may be the common underlying mechanisms and principles which are shared, to differing degrees, by most vertebrates. Bonding may be regarded as the core biopsychological mechanism underling complex social organization, explaining how individuals manage to stay together to raise offspring or just to engage in mutual support of various kinds over time. The ability of individuals to bond or attach to others is mainly shaped before birth, by maternal effects, but even more importantly, by early parenting/caring styles. This affects the setpoint of the stress axes and of other physiological systems relevant in the social context, personalities and the way how individuals approach and relate to others later in life. Hence, we start to understand the contingencies between parental and offspring social styles, but much remains to be investigated. Attachment (*sensu* Ainsworth 1985) in humans, for example, may serve as a working model to approach the physiology and the representations linked with bonding as related to individual performance also in other highly social nonhuman animals.

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Developmental Approaches to Behavioural Biology

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With 7 Figures and 1 Table

Abstract

The views about instinct of the classical ethologists were based on many compelling observations of animals' behaviour. Some adaptive behaviour patterns are highly stereotyped in their form, and stable across a wide range of environmental conditions. However, the role of experience varies considerably from one type of behaviour to another. When the requirements are complex, a combination of different developmental processes are required in order to generate the highly tuned skills seen in the adult. Many behaviour patterns have some, but not all, of the defining characteristics of instinct, and the unitary concept starts to break down under closer scrutiny. The various theoretical connotations of instinct – namely that it is unlearned, caused by a genetic difference, adapted over the course of evolution, unchanged throughout the life-span, shared by all members of the species, and so on – are not merely different ways of describing the same thing. The modern study of epigenetics has provided tools for understanding the interplay between the developing organism and its environment. The silencing and activation of genes are of central importance in understanding why individuals differ from each other.

Zusammenfassung

Die Sicht der klassischen Ethologen auf den Instinkt beruhte auf zahlreichen zwingenden Beobachtungen tierischen Verhaltens. Einige adaptive Verhaltensmuster sind im höchsten Maße stereotyp und bleiben auch unter verschiedensten Umweltbedingungen stabil. Es gibt jedoch bei den verschiedenen Verhaltensformen erhebliche Unterschiede, welche Rolle die Erfahrung spielt. Bei komplexen Anforderungen ist oft eine Kombination von verschiedenen Entwicklungsprozessen nötig, um die hochgradig abgestimmten Fähigkeiten der Adulti hervorzubringen. Viele Verhaltensmuster haben zwar etliche, aber nicht alle, der bestimmenden Merkmale von Instinkten, und das einheitliche Konzept beginnt, sich bei näherer Untersuchung aufzulösen. Die zahlreichen theoretischen Konnotationen des Instinktes – z. B. dass es nicht erlernt ist, durch genetische Unterschiede bedingt wird, im Laufe der Evolution angepasst ist, sich im Laufe des Lebens nicht verändert, von allen Artgenossen geteilt wird usw. – beschreiben nur auf unterschiedliche Weise ein und dasselbe. Die moderne Epigenetik bietet Ansätze, das Zusammenspiel von Umwelt und sich entwickelnden Organismen zu verstehen. Die Prozesse von Genaktivierung und -stilllegung sind von zentraler Bedeutung zum Verständnis der Entstehung individueller Unterschiede.

1. Introduction

Just over half a century ago, an eminent comparative psychologist, Frank Beach, wrote an article with the title "The descent of instinct" (Beach 1955). He was concerned by the way most psychologists who used the term “instinct” had never worked professionally on the phenomena to which they wished to apply the term. Beach had a great sense of fun and loved puns. Privately he noted that descent could be written as “de-scent” and that his article could have been given the title “Taking the stink out of instinct”. This was too good a joke not to plagiarise (e.g. Bateson 2000). As Beach was writing, the work of the European ethologists was becoming well known. When they talked about instinct, they certainly had worked on the behaviour patterns to which they applied the term. Beach got to know about their research and was a great admirer of Konrad Lorenz, Niko Tinbergen and their students. Nevertheless, many semantic and conceptual problems remained and these have not diminished over the years. The excellent examples that had been described raised a series of independent problems and attracted a number of different meanings. So “instinct” or the nearly equivalent term “innateness” was used to refer to a wide variety of phenomena (see Tab. 1). Difficulties arise when evidence for instinct defined in one of these ways is taken as evidence for instinct defined in another way.

Tab. 1 Different meanings of the term “instinct”

- Present at birth or particular stage of development
- Not learned
- Genetic – highly heritable
- Adapted during evolution
- Develops before function is established
- Shared by all members of species/sex/age group
- A functional behavioural system
- Controlled by a specialised neural module
- Developmentally robust – well canalized

In this article we shall describe how thinking about behavioural development has changed over the years. The static view that divided behaviour into the innate and the acquired has been replaced by a much more dynamic view of the underlying processes. At the same time the massive growth of molecular biology has provided understanding of how the mechanisms of development work. In the final part of the article we enter into some of these technicalities because they are fundamental to the future progress of the subject.

2. The Ethologist’s Approach to Instinct

With the rise of ethology in Western Europe during the middle part of the 20th century, the notion of instinct, which previously had been largely discredited, once again became a focus of intense interest among biologists who were studying the behaviour of animals, particularly Konrad Lorenz and Niko Tinbergen who became known as the founders of ethology – the biological study of behaviour. Lorenz had been struck by how behaviour patterns that had looked so appropriate in the natural worlds to which the animals had been adapted looked so odd when seen out of their normal context. A few days after hatching a hand-reared duckling touches with its bill a pimple above its tail and then wipes its bill over its down. Yet this pimple, which becomes an oil-producing gland in the adult, is not yet functional and the duckling would normally be oiled by the feathers of its brooding mother.

Observations such as this led LORENZ to conclude that behaviour patterns which were well adapted by evolution to the biological needs of the animal are qualitatively distinct from behaviour acquired through learning.

The ethologists emphasized how complex and coordinated behaviour patterns develop without practice. Birds, for example, can usually fly without prior experience of flying. In one classic experiment, young pigeons were reared in narrow boxes that physically prevented them from moving their wings after hatching. They were then released at the age at which pigeons normally start to fly. Despite having had no prior opportunities to move their wings, the pigeons were immediately able to fly when released, doing so almost as well as the pigeons which had not been constrained (GROHMANN 1939). In a similar way, European garden warblers that have been hand-reared in cages nevertheless become restless and attempt to fly south in the autumn – the time when they would normally migrate southwards. The warblers continue to be restless in their cages for about a couple of months, the time taken to fly from Europe to their wintering grounds in Africa. The following spring, they attempt to fly north again. This migratory response occurs despite the fact that the birds have been reared in social isolation, with no opportunities to learn when to fly, where to fly or for how long (GWINNER 1996).

LORENZ, with his academic training in comparative anatomy, believed that behavioural activities could be regarded like any physical structure or organ of the body. They had a regularity and consistency that related to the biological needs of the animal, and they differed markedly from one species to the next. The developmental progression from a single cell to an integrated body of billions of cells, combining to produce coherent behaviour, is astonishingly orderly. Just as animals grow kidneys with a specialised biological function, adapted to the conditions in which they live, so they perform elaborate and adaptive behaviour patterns without any previous opportunities for learning or practice. Particular behaviour patterns are, LORENZ argued, like body organs in serving particular biological functions; their structure was likely to have been adapted to its present use by Darwinian evolution and depends on the ecology of the animal; and they develop in a highly coordinated and systematic way.

Furthermore, certain aspects of human behavioural development recur in everybody's life despite the shifting sands of cultural change and the unique contingencies of any one person's life. Despite the host of genetic and environmental influences that contribute to behavioural differences between individuals, all members of the same species are remarkably similar to each other in many aspects of their behaviour – at least, when compared with members of other species. With few exceptions, humans pass the same developmental milestones as they grow up. Most children have started to walk by about 18 months after birth, have started to talk by around two years and go on to reach sexual maturity before their late teens. Individual differences among humans seem small when any human is compared with any chimpanzee.

Human facial expressions have characteristics that are widely distributed in people of many different cultures. The emotions of disgust, fear, anger and pleasure are read off the face with ease in any part of the world. Towards the end of his life Charles DARWIN (1872) wrote a book that provided the stimulus for observational studies of animal and human behaviour which have continued into modern times (EKMAN 2009, SAUTER et al. 2010). DARWIN concluded: "That the chief expressive actions, exhibited by man and by the lower animals, are now innate or inherited, – that is, have not been learnt by the individual, – is admitted by every one." DARWIN's descriptions of suffering, anxiety, grief, joy, love, sulkiness, anger, disgust, surprise, fear and much else are models of acute observation. He would show to friends and colleagues pictures of people seemingly expressing various emotions and ask them, without further prompting, to describe the emotions. In one case a picture of an old man with raised eyebrows and open mouth was shown to 24 people without a word of explanation, and only one person did not understand what was intended. In a way that shows both his carefulness and his honesty, DARWIN continued: "A second person answered terror, which is not far wrong; some of the others, however, added to the words surprise or astonishment, the epithets, woful, painful, or disgusted." His extensive correspondence with travellers and missionaries convinced him that humans from all round the globe expressed the same emotion in the same way. Subsequently, an enormous archive of photographic records of human expressions in different cultures at different stages of economic development has been collected. The similarities in, for example, the appearance of the smile or the raised eyebrows are striking (EIBL-EIBESFELDT 1970). The cross-cultural agreement in the interpretation of complex facial expressions is also remarkable. People agree about which emotions are being expressed. They also agree about which emotion is the more intense, such as which of two angry people seems the more angry.

Even though LORENZ was a forceful advocate of the concept of instinct, he certainly did not deny the importance of learning. On the contrary, he gave great prominence to developmental processes by which animals formed their social and sexual preferences. He saw such learning processes as being under the control of what he referred to as the 'innate schoolmarm'. She represented the highly regulated acquisition of information from the environment just when it is most adaptive for the animal to get it. Peter MARLER (2004) has forcibly made this point with respect to song learning in birds. Suppose that in a given species of bird a strong correlation exists between having a certain gene and singing in a particular way and suppose further that the acquisition of the song also requires learning. The development of the song requires (among other things) a sort of learning process that normally happens only in birds possessing the gene. The correlation between the gene and the distinctive song is due to the effects that gene produces on development, including the learning processes required for the development of the song. The gene makes it possible for the bird to acquire its distinctive song.

LORENZ (1965) thought of instincts, whether they organised behaviour directly or were the mechanisms that changed behaviour through learning, as inherited neuronal structures which remained unmodified by the environment during development. Behaviour resulting from learning was seen as being separately organised in the brain from the instinctive elements. At their most complex, then, instincts were thought to provide the basis by which the individual gathers particular types of information from the environment in the course of learning.

The acquisition of language by humans has been thought about in much the same way as LORENZ thought about the innate schoolmarm. It is obvious that the differences in spoken language between a French person and a German are not due to genetic differences. Therefore, apart from the act of speech itself, the proposed universal and instinctive characteristics of all humans are not going to be discovered in the surface organisation of such behaviour. Notably, CHOMSKY (1959, 2000) argued that children acquire words and the local rules of grammar from the adults around them, but the way they do so is, he suggested, shared by all humans.

3. Criticism of the Classical Ethologists' Views of Instinct

Despite all the empirical evidence that some elements of behaviour can develop without opportunities for learning, the ethologists' notion of instinct attracted strong criticism in the 1950s from a group of American comparative psychologists who studied animal behaviour. The critics laid out a quite different agenda for studying behavioural development. A leading protagonist in the debate was Danny Lehrman (1953). His critique of Lorenz's ideas was accepted by Niko Tinbergen, who was by then at Oxford and shaped the subsequent thinking of most English ethologists. In particular it impacted on the developmental work carried out at Cambridge under the direction of Robert Hinde (1970).

Lehrman (1970) noted that as far as individual development is concerned, the problem has to be expressed differently from the ways in which the ethologists had thought about it. He made the point this way: "The problem of development is the problem of the development of new structures and activity patterns from the resolution of the interaction of existing ones, within the organism and its internal environment, and between the organism and its outer environment. At any stage of development, the new features emerge from the interactions within the current stage and between the current stage and the environment. The interaction out of which the organism develops is not one, as is often said, between heredity and environment. It is between organism and environment! And the organism is different at each stage of its development."

Many of the theoretical implications of the generalised concept of instinct are difficult to test in practice. Take the definition of instinctive as behaviour that does not involve learning in its development. To establish experimentally that a particular type of behaviour is not learned requires the complete exclusion of all opportunities for learning. This is harder than it sounds. For a start, it is difficult to draw a clear distinction between experiences that have specific effects on the detailed characteristics of a fully-developed behaviour pattern and environmental influences that have more general effects on the organism, such as nutrition or stress. Experiences vary in the specificity of their effects.

Even if all obvious opportunities for learning a particular behaviour pattern are excluded, a major problem remains. This is because animals, like humans, are good at generalising from one type of experience to another. It is therefore difficult to know whether an individual has transferred the effects of one kind of experience to what superficially looks like a quite different aspect of their behaviour. For example, if somebody draws a letter of the alphabet on your hand while your eyes are shut, you should still be able to visualise the letter, even though you have not seen it. In doing this you will have demonstrated a phenomenon called cross-modal matching. A striking instance of cross-modal matching has been found in rhesus monkeys. Monkeys were trained to distinguish between tasty and noxious biscuits in the dark. The noxious biscuits, which contained sand and bitter-tasting quinine, differed in shape from the tasty biscuits. The monkeys quickly learned to select the right-shaped biscuits. When they were subsequently tested in the light, the monkeys immediately reached for the nice biscuits, even though they had never seen them before. They had transferred the knowledge they had acquired from a purely tactile experience – touching the biscuits in the dark – and used it to make a visual choice (Cowey 1975).

Another pitfall in the quest for instinct is that the developing individual cannot be isolated from itself, and some of its own actions may provide crucial experience that shapes its subsequent behaviour. After they hatch, ducklings exhibit an immediate preference for the maternal calls of their own species. Some elegant experiments by Gilbert Gottlieb showed that the ducklings' preferences are affected by their hearing their own vocalisations in the egg before hatching but after they have penetrated the air space of the egg (see Fig. 1). In other words, their 'instinctive' preference is influenced by the sensory stimulation which they generated themselves. Gottlieb (1971) was able to demonstrate this effect by cutting a window in the egg and operating on the unhatched ducklings, thereby making it impossible for them to produce sounds. These silent birds were less able to distinguish the maternal calls of their own species from those of others. However, if they were played tape-recordings of duckling calls, the preference for their own species' maternal call emerged (Gottlieb 1991).

A formidable obstacle to proving that a behaviour pattern is not learned is the capacity that animals have to acquire the necessary experience in more than one way. When scientists attempt to isolate an animal from one particular form of experience that is thought necessary for development, the behaviour pattern may nonetheless develop by an alternative route. Cats, for example, can acquire and improve their adult predatory skills *via* a number of different developmental routes: by practising catching live prey when young, by playing at catching prey when young, by watching their mother catch live prey, by playing with their siblings, or by practising when adult (Martin and Caro 1985). Hence a kitten deprived of, say, opportunities for play may still develop into a competent adult predator, but by a different developmental route.

The demonstrations of cross-modal matching, the impact of self-stimulation on the young animal and the use of different developmental routes to the same end point all sound notes of warning. It is not as easy as it might seem to demonstrate that a behaviour pattern has not been shaped by some form of experience that has a particular influence on the behaviour.

Nevertheless, the idea that instinct is in some sense 'genetic' was deeply embedded in the ethologists' thinking and survives to this day often in the form that innate behaviour is 'genetically encoded'. The metaphor of coding implies a one-to-one relationship and seems warranted when talking about the way DNA sequences are related to some of their immediate molecular products, such as polypeptide chains. However, the idea that DNA codes for

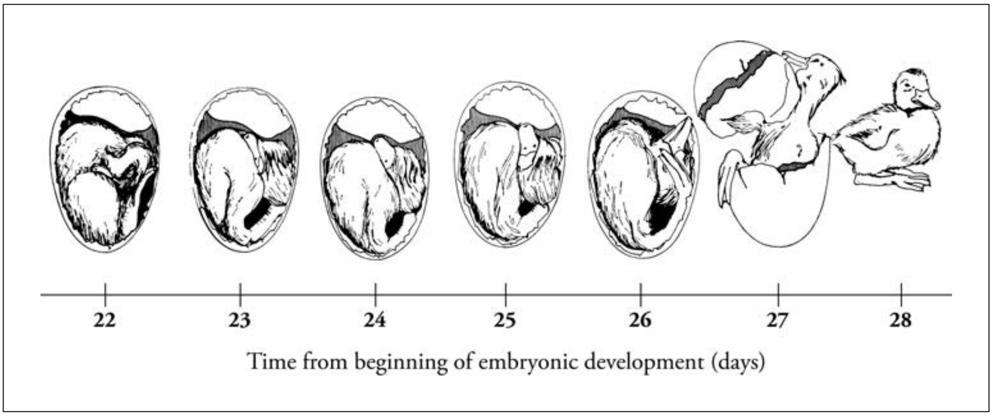

Fig. 1 A duckling shown at different embryonic ages prior to hatching. When the duckling breaks through to the airspace it starts to vocalise which facilitates the development of its preferences for the maternal call of its own species after hatching (modified from Gottlieb 1975).

behaviour is highly implausible given what is known about the dynamics of development. A genetic difference between two individuals may give rise to a behavioural difference, but that does not imply that in either individual a gene codes for that individual's distinctive behaviour (Bateson and Martin 1999). If it is argued that a trait is genetically determined if and only if genes and nothing but genes are involved in its development, the notion of genetic determination relates to no phenotypic trait other than proteins. Moreover, if it is argued that the development of a trait involves gene expression, the notion of genetic involvement applies to virtually all phenotypic traits. Those who concern themselves with developmental processes agree that, except for the immediate molecular products of DNA processing, all phenotypic traits are the result of causal processes that involve both genetic and non-genetic factors. This has been called the *interactionist consensus* (Sterelny and Griffiths 1999).

4. Instinct Dies Hard

Notwithstanding Lehrman's critique and the impact it left on English ethologists, instinct resurfaced strongly in the late twentieth century, in the writings of sociobiologists and evolutionary psychologists. The 1970s style sociobiology 'decoupled' (in E. O. Wilson's phrase) individual development from the project to link evolutionary biology and behavioural biology (Wilson 1976). While few of the 1990s evolutionary psychologists have wished to sink back into a nothing-but genes position, just where they stand on the developmental project outlined by Lehrman is less clear. How can ideas about modular instinctive behaviour patterns being inherited, internally motivated and adaptive be reconciled with the variable and flexible way in which behaviour develops?

The debate has been confused because, as we have already noted, the term 'instinct' means remarkably different things to different people. To some, 'instinct' means a distinctly organized system of behaviour patterns, such as that involved in searching for and consuming food. The different modules of behaviour have been likened by some to the various tools found on a Swiss Army knife. For others, an instinct is simply behaviour that is not learned. As we have already described instinct has also been used as a label for behaviour that is present at birth (the strict meaning of 'innate') or, like sexual behaviour, patterns that develop in full form at a particular stage in the life-cycle. Another connotation of instinct is that once such behaviour has developed, it does not change. Instinct has also been portrayed as behaviour that develops before it serves any biological function, like some aspects of sexual behaviour. Instinct is often seen as the product of Darwinian evolution so that, over many generations, the behaviour was adapted for its present use. Instinctive behaviour is supposedly shared by all members of the species (or at least by members of the same sex and age). Confusingly, it has also been used to refer to a behavioural difference between individuals caused by a genetic difference – so instincts are both universal and part of individual differences. The overall effect of the multiple definitions is, to say the least, muddling (Mameli and Bateson 2006, Bateson and Mameli 2007).

For all that, some examples can be found to which most of the defining characteristics of instinct seem to apply. The ways in which mice, rats and guinea pigs clean their own fur are good examples of behaviour patterns that do have most of the defining characteristics applied to instinct (Berridge 1994). They seem to justify the view that a single coherent and unitary notion of instinct is justified. If one defining characteristic of instinct has been found, then the rest will also be found. The duration of the elliptical stroke with the two forepaws which the rodent uses to clean its face is proportional to the size of the species; the bigger the species the longer the stroking movement takes. This is not simply a matter of physics. The bigger-bodied species are not slower in their grooming movements simply because their limbs are heavier; a baby rat grooms at exactly the same rate as an adult rat even though it is a tenth of the size. Moreover, young rodents perform these grooming movements at an age when their mother normally cleans them and before their behaviour patterns are needed for cleaning their own bodies (see Fig. 2).

Rodent grooming is, in other words, a species-typical, stereotyped system of behaviour that develops before it is of any use to the individual. It has most of the defining characteristics that have variously been attributed to instinct. This case is by no means typical, however, and the various meanings applied to a supposed example of instinct do not always hang together so closely as they do in the example of rodent grooming. A central aspect of LORENZ'S concept of instinct that unravelled on further inspection was the belief that learning does not influence such behaviour patterns once they have developed. Many cases of apparently unlearned behaviour patterns are subsequently modified by learning after they have been used for the first time. A newly-hatched laughing gull chick will immediately peck at its parent's bill to initiate feeding, just as, in the laboratory, it will peck at a model of an adult's bill. At first sight this behaviour pattern seems to be unlearned; the chick has previously been inside the egg and therefore isolated from any relevant experience, so it cannot have learned the pecking response. However, as the chick profits from its experi-

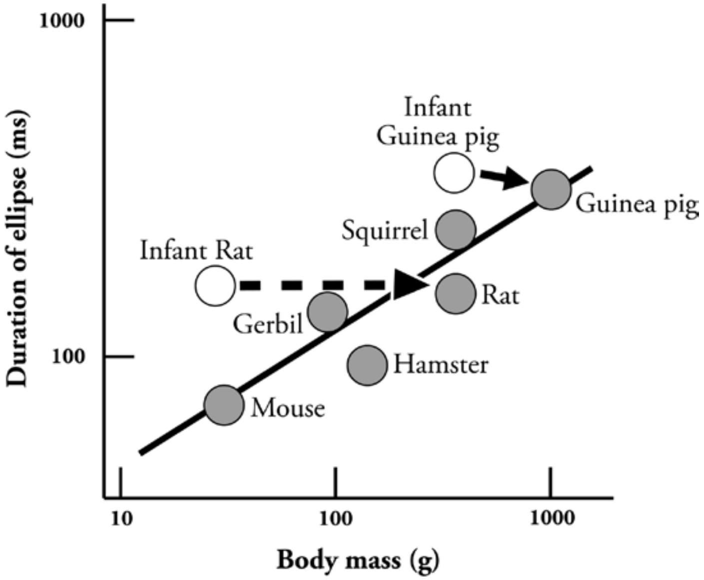

Fig. 2 The time taken for a complete elliptical movement when grooming the face by different species of adult rodents. The time taken is strongly correlated with adult body size. However, in the young rat and guinea pig the time taken is the same as in the adult even though they are much smaller (modified from BERRIDGE 1994).

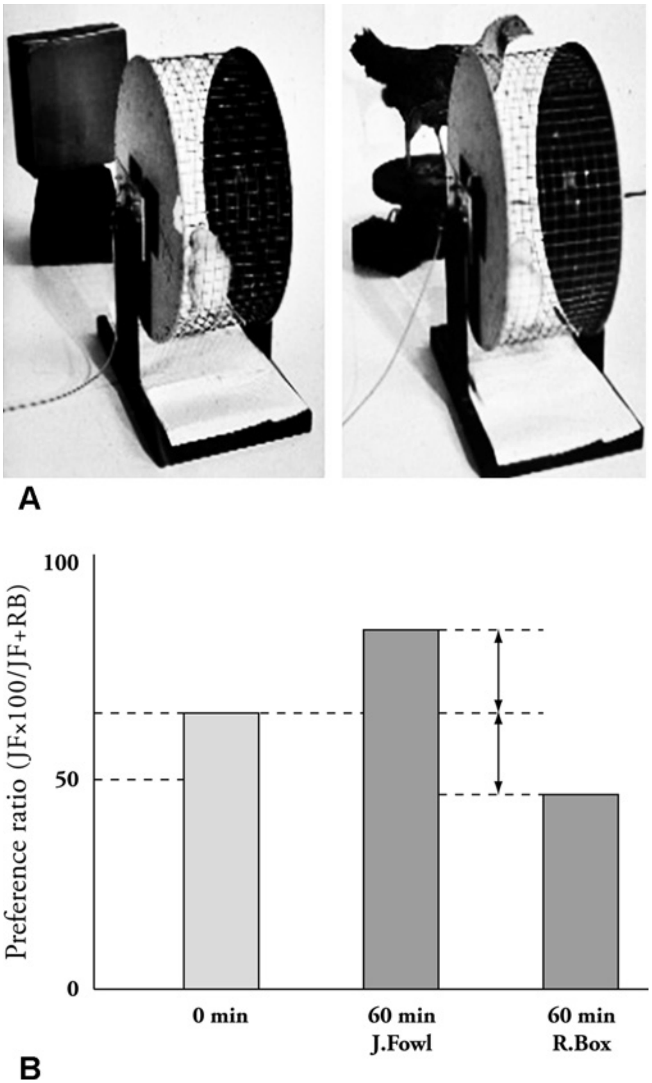

Fig. 3 (*A*) A rotating illuminated red box with two black sides used for imprinting chicks and a stuffed rotating jungle fowl also used for imprinting chicks. The chicks are in wheels in which the rotations are recorded automatically. (*B*) The preferences of dark-reared day-old chicks when exposed sequentially to the red box and the jungle fowl and the preferences of independent groups of chicks imprinted for one hour with either the jungle fowl or the red box. The preferences are expressed as the number of rotations of the wheel when the chick attempts to approach the jungle fowl expressed as a percentage of the same number plus the number of rotations of the wheel when the chick attempts to approach the red box. If the chick has no preference, the ratio is 50 %; if the chick has a strong preference for the jungle fowl the ratio is 100 % and if it has a strong preference for the red box the ratio is 0 %.

ence after hatching, the accuracy of its pecking improves and the kinds of model bill-like objects which elicit the pecking response become increasingly restricted to what the chick has seen (Hailman 1957). Here, then, is a behavioural response that is present at birth, species-typical, adaptive and unlearned, but nonetheless modified by the individual's subsequent experience.

Similarly prior to behavioural imprinting, domestic chicks have strong preferences for certain features such as the head and neck and configurations of patterns of movement (Horn and McCabe 1984, Vallortigara et al. 2005). When chicks' preferences were measured before and after imprinting, the initial predispositions could still be detected after an hour of imprinting (see Fig. 3*a*, *b*) (Johnson et al. 1992).

The idea that one meaning of instinct, 'unlearned', is synonymous with another, namely 'adapted through evolution', also fails to stand up to scrutiny. The development of a behaviour pattern that has been adapted for a particular biological function during the course of the species' evolutionary history may nonetheless involve learning during the individual's lifespan. For example, the strong social attachment that young birds and mammals form to their mothers is clearly adaptive and has presumably evolved by Darwinian evolution. And yet the attachment process requires the young animal to learn the individual distinguishing features of its mother.

Yet another way in which the different elements of instinct fall apart is the role of learning in the inheritance of behaviour across generations. Consider, for example, the ability of birds such as titmice to peck open the foil tops of the milk bottles that used to be delivered each morning to the doors of a great many British homes (Hinde and Fisher 1951). The birds' behaviour is clearly adaptive, in that exploiting a valuable source of fatty food undoubtedly increases the individual bird's chances of surviving the winter and breeding. However, the bottle-opening behaviour pattern is transmitted from one generation to the next by means of social learning. The basic tearing movements used in penetrating the foil bottle-top are also used in normal foraging behaviour and are probably inherited without learning. But the trick of applying these movements to opening milk bottles is acquired by each individual bird through watching other birds do it successfully – that is, by social learning. Many other examples of the acquisition of such 'cultures' in animals have subsequently been discovered (Laland and Galef 2009).

In short, many behaviour patterns have some, but not all, of the defining characteristics of instinct, and the unitary concept starts to break down under closer scrutiny. The various theoretical connotations of instinct – namely that it is unlearned, caused by a genetic difference, adapted over the course of evolution, unchanged throughout the life-span, shared by all members of the species, and so on – are not merely different ways of describing the same thing. Even if a behaviour pattern is found to have one diagnostic feature of instinct, it is certainly not safe to assume that it will have all the other features as well (see Bateson and Gluckman 2011).

5. Heritability

Given that behavioural development depends on both genes and the environment, many have been tempted to partition the influences of the two classes of influence. They ask how much of the variation between individuals in a given characteristic is due to differences in their genes, and how much is due to differences in their environments? Within a single individual this question cannot be answered, but it can be posed for a population of individuals (Bateson and Martin 1999).

The suggested solution was provided by a measure called heritability. The concept of heritability is best illustrated with an uncontroversial characteristic such as human height, which clearly is influenced by both the individual's lineage (genetic influences) and nutrition (environmental influences). The variation between individuals in height that is attributable to variation in their genes may be expressed as a proportion of the total variation within the population sampled (see Fig. 4). This index is known as the heritability ratio. If people differed in height solely because they differed genetically, the heritability of height would be 1.0; if, on the other hand, variation in height arose entirely from individual differences in environmental factors such as nutrition, then the heritability would be 0. Calculating a single number to describe the relative contributions of genes and environment has obvious attractions. Estimates of heritability are of undoubted value to animal breeders, for example. Given a standard set of environmental conditions, the genetic strain to which a pig belongs will predict its adult body size better than other variables such as the number of piglets in a sow's litter. If the animal in question is a cow and the breeder is interested in maximizing its milk yield, then knowing that milk yield is highly heritable in a particular strain of cows under standard rearing conditions is important.

Behind the deceptively plausible ratios lurk some fundamental problems. For a start, the heritability of any given characteristic is not a fixed and absolute quantity – tempted though many scientists have been to believe otherwise. Its value depends on a number of variable factors, such as the particular population of individuals that has been sampled.

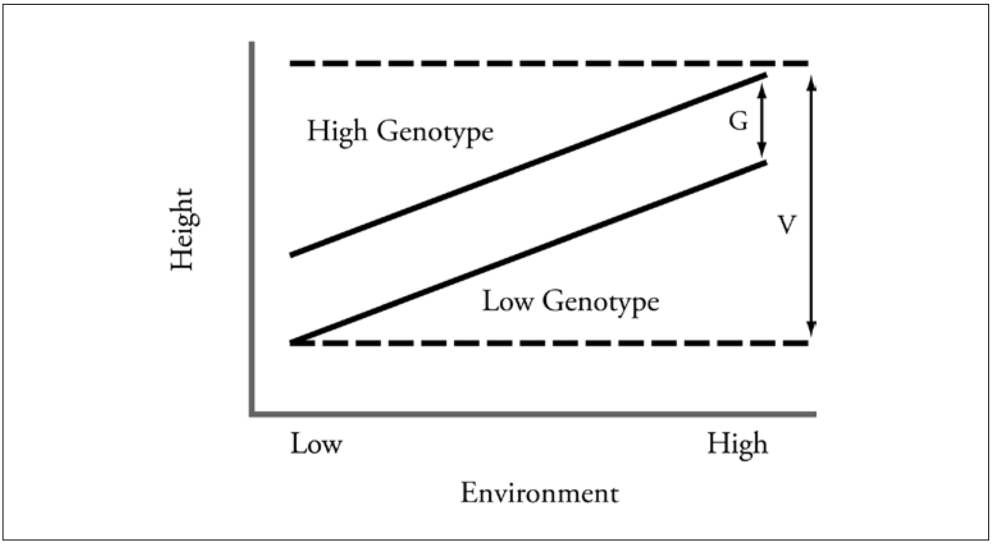

Fig. 4 A hypothetical relationship between the genome of a population and average height of humans growing up in different nutritional conditions. If the nutritional conditions do not interact statistically with the genome, then the variance due to differences in the genome (G) can be expressed as a percentage of the total variance (V) to give an estimate of broad sense heritability. If interaction does occur and the lines are not parallel, then a heritability estimate cannot be obtained.

For instance, if heights are measured only among people from affluent backgrounds, then the total variation in height will be much smaller than if the sample also includes people who are small because they have been under-nourished. The heritability of height will consequently be larger in a population of exclusively well-nourished people than it would be among people drawn from a wider range of environments. Conversely, if the heritability of height is based on a population with relatively similar genes – say, native Icelanders – then the figure will be lower than if the population is genetically more heterogeneous; for example, if it includes both Icelanders and African Pygmies.

Attempts to measure the relative contributions of genes and environment to a particular characteristic are highly dependent on who is measured and under what conditions. Another problem with the heritability ratio is that it says nothing about the ways in which genes and environment contribute to the biological and psychological processes involved in an individual's development. This point becomes obvious when considering the heritability of a characteristic such as 'walking on two legs.' Humans walk on less than two legs only as a result of environmental influences such as war wounds, car accidents, disease, or exposure to teratogenic toxins before birth. In other words, all the variation within the human population results from environmental influences, and consequently the heritability of 'walking on two legs' is zero. And yet walking on two legs is clearly a fundamental property of being human, and is one of the more obvious biological differences between humans and other great apes such as chimpanzees or gorillas. It obviously depends heav-

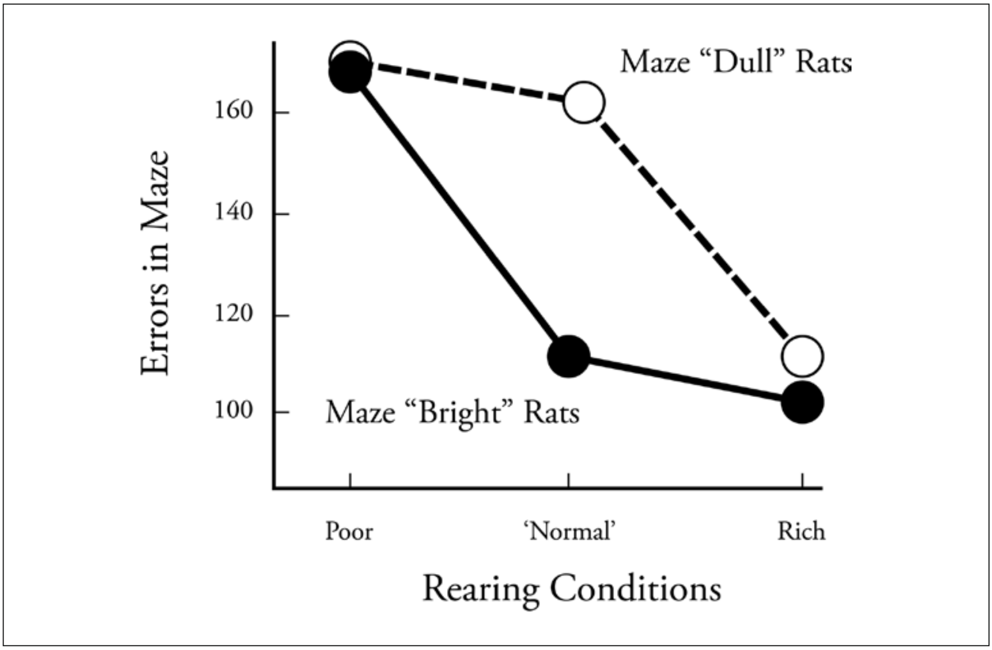

Fig. 5 The number of errors made when travelling through mazes by two strains of rats. The so-called 'Maze Bright' rats did better than the 'Maze Dull' rats when reared in normal cages but the two strains did not differ if they had been reared in impoverished or enriched conditions, demonstrating the statistical interaction between genome and environmental conditions.

ily on genes, despite having a heritability of zero. A low heritability clearly does not mean that development is unaffected by genes. If a population of individuals is sampled and the results show that one behavioural pattern has a higher heritability than another, this merely indicates that the two behavioural patterns have developed in different ways. It does not mean that genes play a more important role in the development of the behavioural pattern with the higher heritability. Important environmental influences might have been relatively constant at the stage in development when the more heritable pattern would have been most strongly affected by experience.

The most serious shortcoming of heritability estimates is that they rest on the implausible assumption that genetic and environmental influences are independent of one another and do not interact. The calculation of heritability assumes that the genetic and environmental contributions can simply be added together to obtain the total variation. In many cases this assumption is clearly wrong. A famous example was provided by Cooper and Zubek (1958). They took two genetic strains of rats and reared them in cages with differing degrees of enrichment. The rats were then tested in their ability to run through a maze. When kept in standard cages with a moderate degree of enrichment the strains differed markedly. However, when reared in impoverished or enriched conditions, no differences were found between the strains (see Fig. 5). This type of interaction between the organism and its environment is fundamental to understanding behavioural development.

6. Alternative Lives

Members of the same species, the same sex, and the same age sometimes differ dramatically from each other. The variation commonly arises because each individual has the capacity to respond in more than one way according to the state of the local environment or its own body. Individuals have many latent capacities that are expressed only under certain conditions. The developmental processes of plasticity that are elicited by those conditions normally provide useful adaptations to the environment. The implication of many of the examples of developmental plasticity is that environmental induction provides a forecast about the conditions of the world that the individual will subsequently inhabit. In mammals the best route for such a forecast may be *via* the mother. Vole pups born in the autumn have much thicker coats than those born in spring; the cue to produce a thicker coat is provided by the mother before birth (Lee and Zucker 1988). The value of preparing in this way for colder weather is obvious. The individual may be likened to a juke box, capable of playing many tunes but, in the course of its life, possibly playing only one of a set. The particular suite of adaptations that is expressed is elicited by the conditions in which it grows up or even by the conditions to which its parents and grandparents were exposed.

Maternal forecasting by induction is now thought to be important in human biology and has implications for adult health when, because of large changes in economic conditions, the maternal forecast is wrong (Bateson et al. 2004, Gluckman and Hanson 2006). The adaptationist argument is that the pregnant woman unwittingly signals to her unborn baby that the environment her child is about enter is likely to be harsh. This weather forecast from the mother's body results in her baby being born with adaptations, such as a small body and a modified metabolism, thereby helping the child to cope with a shortage of food if the forecast is correct. These individuals, having small bodies and specialized metabolisms adapted to cope with meagre diets, run into problems if, instead, they find themselves growing up in an affluent industrialized society to which they are poorly adapted. Among a large group of individuals, who were born at term and breast-fed as babies, those who had the lowest weights at birth had the highest death rate from cardiovascular disease. The argument is that mothers on a low level of nutrition signalled to their unborn child that the environment outside would be harsh. As a result, the babies were born with the suite of adaptations that would have suited them well to diets low in carbohydrates and fat. However, they were poorly adapted to the affluent environment in which they subsequently grew up.

By no means all those working on the developmental origins of health and disease thinks about these effects in terms of the adaptiveness of such plasticity. The extreme alternative view is that every human has a single ideal state on which he or she will converge, given perfect nourishment, stimulation and so forth. Anybody who failed to achieve that state had made the best of a bad job and, at the margins of existence, expressed pathological stunting of body and behaviour.

The opposite side of the adaptationist coin is that people who grow up in good environments may be at greater risk during periods of prolonged famine than those who were born as low-birth-weight babies. Children born to affluent parents are more likely to suffer adverse effects if they are starved in adulthood. In concentration camps and the worst prisoner-of-war camps, anecdotal evidence suggests that the physically large individuals died first while at least some of the small individuals survived. In a famine-exposed Ethiopian population, higher birth weight was associated with a 9-fold higher risk of rickets (Chali et al. 1998). This might have been caused by the children with large bodies having higher needs for calcium and vitamin D than those with smaller bodies, but the point is that these children were at greater risk and had a lower chance of reproducing successfully than the smaller children.

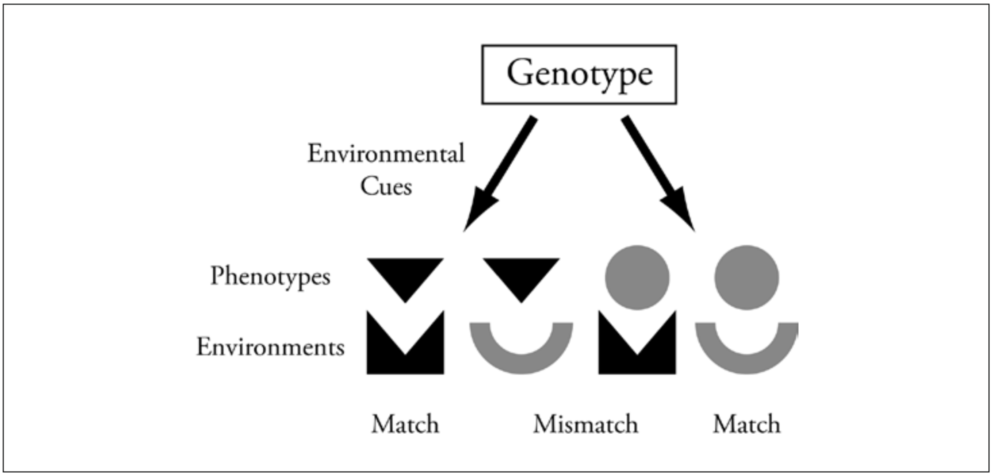

Fig. 6 A given genome can give rise to different phenotypes which generally match adaptively the conditions in which they are expressed, but sometimes a mismatch can occur with the phenotype being poorly adapted to the environment in which it is expressed.

The general point is that such systems of developmental plasticity usually work well, but in a changing environment they generate poorly adapted phenotypes because the environmental forecast proved to be incorrect (see Fig. 6). The triggering of normally appropriate modes of response gives us a fresh way of thinking about individual differences.

7. Dynamics of Development

Modern understanding of behavioural development goes well beyond an acceptance that interaction between the developing organism and its environment is crucial. The interactionist perspective and the conditional character of an individual's development emphasise that we need to understand the processes of development. This is what Conrad Waddington (1957) called the study of epigenetics. He used the term, in the absence of molecular understanding, to describe processes by which the inherited genotype could be influenced during development to produce a range of phenotypes. He distinguished "epigenetics" from the eighteenth century term "epigenesis" which had been used to oppose the notion that all the characteristics of the adult were preformed in the embryo.

More recently epigenetics has become defined as the molecular processes by which traits defined by a given profile of gene expression can persist across mitotic cell division but which do not involve changes in the nucleotide sequence of the genome. The term has come to describe the molecular genetic mechanisms through which both dynamic and stable changes in gene expression are achieved, and ultimately how variations in environmental experiences can modify this regulation of DNA (Jablonka and Lamb 2005; Bateson 2012).

8. The Molecular Basis of Epigenetics

The key concept in the new field of epigenetics is how molecular changes within cells can lead to variation in the expression of genes. These differences, rather than variation in the sequence of genes, are critical in shaping individual differences in phenotype. This is not to say that differences in the sequences of particular genes between individuals do not contribute to phenotypic differences, but rather that even individuals carrying identical genotypes can diverge in phenotype if they experience separate environmental experiences that differentially and permanently alter gene expression. In this section, we shall describe some of the most relevant recent research that demonstrates how these epigenetic changes facilitate plasticity in behavioural development, and provide a molecular mechanism through which environmental experiences and the genome interact.

The level of gene expression that occurs at any particular gene is ultimately determined by the accessibility of the DNA to the RNA polymerase enzyme and other gene-specific transcription factors that regulate transcriptional activity. In turn, the ability of these enzymes and transcriptional modifiers to gain access to the DNA is related to how tightly it is wrapped around its supporting proteins called histones. DNA, histone proteins, as well as these various other modifying proteins and transcription factors make up what is called chromatin, which can essentially exist in two basic states; heterochromatin and euchromatin. Heterochromatin contains DNA that is tightly packed against its histone proteins and the access of RNA polymerase is restricted, and gene transcription is typically repressed. Conversely in euchromatin, DNA is relatively loosely wrapped around histone proteins and thus RNA polymerase and other proteins of the transcriptional machinery are able to access it and increase gene expression (Fig. 7).

The transition between these two states of chromatin is facilitated through epigenetic chemical modifications to both DNA and the histone proteins that cause changes in the respective electrical charges of each leading to them becoming either increasingly attracted or repelled from one another (Keverne and Curley 2008, Kouzarides 2007). Numerous different types of such covalent modification may occur at thousands of possible sites within the DNA or histone proteins, meaning that an almost infinite number of potential combinations of these epigenetic modifications can occur. Determining how each change acting at each site is related to changes in gene transcription is extremely challenging. Nevertheless, several common broad types of alterations can be generally associated with consistent directional changes in gene expression. In particular, histone acetylation (the addition of acetyl groups to histones) is typically associated with elevated transcriptional activity whereas histone deacetylation (the removal of acetyl groups from histones) or methylation (the addition of methyl groups to histones) is typically associated with transcriptional silencing. The acetylation of histones is facilitated by the enzyme histone acetyltransferase whereas histone deacetylase regulates the removal of the acetyl group from the histone tails. The major modification of DNA itself is DNA methylation which involves the con-

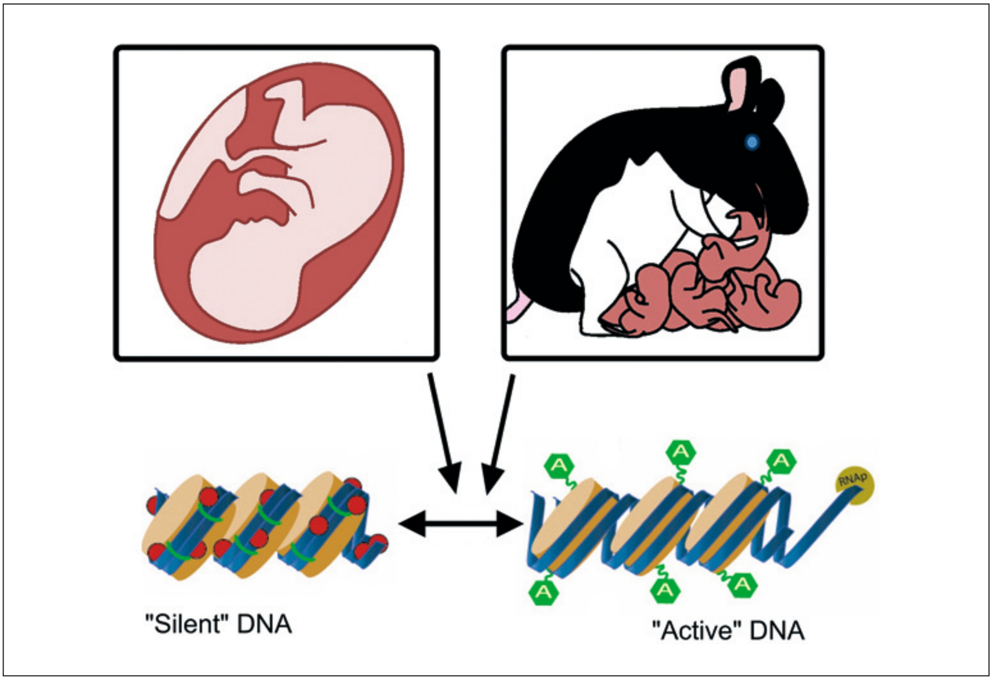

Fig. 7 A stretch of DNA can be subject to molecular change so that its expression is either enabled or prevented. Such changes occur during normal differentiation of cells but they can also be triggered by environmental cues such as the amount of maternal care received from the mother (reproduced with permission of Frances Champagne).

version of cytosines to 5-methylcytosine and is facilitated by methyltransferase enzymes that can promote *de novo* DNA methylation, or the maintenance of already established methyl marks. The transcriptional repression induced by DNA methylation is further sustained through the recruitment to chromatin of other methyl-binding proteins that recruit further co-factors that induce histone methylation and deacetylation. Hence, interactions between DNA and histone modifications can act together to determine gene expression.

The significance of these molecular processes for phenotypic development was first acknowledged with regard to cellular differentiation and proliferation. All cells within the body contain the same genetic sequence information, yet all have undergone specializations to become a skin cell, hair cell, heart cell, etc. and these phenotypic differences are inherited from mother cells to daughter cells. This inheritance of developmental change is achieved *via* the establishment of particular DNA methylation patterns within each cell lineage. These patterns are maintained after cell division and are then passed from parent to daughter cells. Hence, despite containing the same genetic information, the different patterns of epigenetic modifications of the genome that exist within each cell type determine specific levels of gene expression that result in phenotypic variation. In the last decade, it has become increasingly apparent that similar specific patterns of gene expression within individual populations of neural cells can be dynamically and permanently altered through variations in early experiences during development. Much of this work has come from studies in laboratory rodents that have investigated how variations in mother-infant interactions during early life lead to long-term changes in behaviour *via* variations in brain development induced by these epigenetic modifications and their corresponding alteration of neuronal gene expression (Champagne 2010, Champagne and Curley 2009).

We have already touched on the how the human mother's nutritional state affects the phenotypic characteristics of her child. It has recently been shown that individuals whose mothers were exposed to the Dutch famine periconceptually have reduced DNA methylation of the insulin-like growth factor II gene compared to siblings who were not exposed to this undernutrition, which has likely is related to their altered metabolic functioning (Heijmans et al. 2008). Similar effects on offspring development can be found in laboratory studies. Pregnant rat dams placed on low protein diets have offspring with elevated peroxisomal proliferator-activated receptor gene expression in the liver that is associated with decreased DNA methylation of the gene promoter and is partially responsible for the altered metabolic phenotype of these offspring (Lillycrop et al. 2007). The quality of maternal diet can also lead to long-term changes in offspring gene expression. Mice that carry a particular copy of the Agouti gene typically possess a yellow coat colour and obese phenotype. If the mothers of these mice receive dietary supplementation with methyl-donors during pregnancy then the expression of this gene copy becomes epigenetically silenced *via* DNA methylation, and the mice develop a lean phenotype with normal, brown coat colour (Wolff et al. 1998). This environmentally induced phenotype is then transmitted to future generations indicating that such developmental changes can become incorporated into the germline (Jirtle and Skinner 2007).

Other exposures during gestation can lead to developmental disruptions that are the consequence of changes in epigenetic marks. For instance, *in utero* methyl mercury exposure of mice dams leads to their offspring exhibiting increased depressive-like behaviour and reduced brain derived neurotrophic factor expression in the hippocampus associated with increased DNA and histone methylation and reduced histone acetylation of the promoter (Onishchenko et al. 2008). Furthermore, exposure of mouse dams to the endocrine disruptor bisphenol-A, that is commonly found in plastics, leads to large-scale changes in DNA methylation in the fetal mouse brain, including a reduction of DNA methylation at the Agouti gene promoter leading to these mice developing metabolic abnormalities and obesity in adulthood (Dolinoy et al. 2007). Stressing pregnant mouse dams exposes fetal mice to elevated levels of stress hormones such as glucocorticoids and results in these offspring having decreased and increased DNA methylation of the promoters for the corticotrophin-releasing-factor and glucocorticoid receptor (GR) genes respectively in hypothalamic tissue, which is consistent with these mice developing an increased corticosterone response to stress when they are adult (Mueller and Bale 2008). Similar increases in the DNA methylation of the promoter region of the GR gene has been reported in blood cells of infants that were born to depressed mothers during pregnancy (as assessed during the 3rd trimester), with these changes in GR methylation being correlated with cortisol levels between infants (Oberlander et al. 2006). Thus variations in the maternal environment during gestation can have long-term effects on development through alterations in gene expression that are sustained via DNA methylation. Though the focus of most studies so far has been on epigenetic modifications of candidate genes that are known to be involved in the behavioural phenotype under investigation, numerous types of epigenetic changes occur in response to environmental variation leading to a complicated pattern of changes in gene expression and brain development.

Increasing evidence suggests that experiences later in development can also induce long-term changes in phenotype *via* epigenetic modifications, something which was previously thought to be unlikely given the major (and initially conceived to be unique) role of epigenetic changes in regulating embryonic development. For example, rat dams that provide high levels of tactile stimulation to their offspring in the form of maternal licking, have offspring who show as adults a decreased stress-response and increased hippocampal GR expression (which facilitates more efficient negative feedback of the stress response) (Weaver et al. 2004). These differences are not inherited genetically from their mothers. When rat offspring are cross-fostered, it is the maternal behaviour of their foster dam, not their biological dam, that predicts their future phenotype. Significantly, receiving high levels of licking neonatally is associated with reduced levels of DNA methylation of the promoter region of GR gene, which is established by day 6 post-natally and persists throughout adulthood. Moreover, this change in DNA methylation is specific to those GR genes in the hippocampus and not elsewhere in the brain, demonstrating that changes induced by early experience are relatively specific. Mechanistically, it appears that the tactile stimulation that is received early in life stimulates various intra-cellular events in the hippocampus including elevated levels of a particular transcription factor that activates the GR promoter and prevents it from being methylated. Similar mechanisms may occur in human development as it has recently been found from post-mortem tissue of suicide victims that individuals who suffered child abuse early in life have reduced levels of DNA methylation of the GR promoter and reduced GR expression in the hippocampus (McGowan et al. 2009).

Disrupting mother-infant interactions in early life can also lead to long-term behavioural changes that are mediated *via* epigenetic changes. For instance, the daily separation of dams from their offspring for prolonged periods of time results in these individuals exhibiting a much higher stress response as adults, which is partly mediated by high expression of the hormone vasopressin in the paraventricular nucleus of the hypothalamus (Murgatroyd et al. 2009). These neurons, in concert with corticotropin-releasing hormone (CRH) neurons that also reside in the same region of the brain, stimulate the release of adrenocorticotropic hormone (ACTH) from the anterior pituitary which then stimulate the release of corticosterone from the adrenals. In mice, these long lasting increases in vasopressin are due to reduced levels of DNA methylation of the relevant gene specifically in this brain region (Murgatroyd et al. 2009). Conversely, in response to brief daily maternal separations of 15 minutes (handling), offspring develop a reduced stress-response when adults due to these offspring receiving increased tactile stimulation by their mothers when they are returned to them. It has recently been found that these behavioral changes are associated with increased silencing by DNA methlation of the CRH gene (Korosi et al. 2010). The modifications in both of these studies were observed both during the first weeks of life and up to one year later, demonstrating that early social experiences can have immediate yet long-lasting effects on gene expression, brain development and behavioural phenotypes.

These long-term alterations in stress physiology in response to variations in early environments could be considered adaptive developmental shifts if the early maternal environment is a true indicator of the environment that is likely to be encountered by the offspring when adult. Further evidence that epigenetic modifications may underlie such developmental plasticity comes from the development of maternal behaviour in rats that have received high *versus* low levels of licking. Female offspring of high licking dams show low levels of sexual receptivity when adult, though they provide high levels of maternal licking toward their own offspring (Cameron et al. 2008). Female offspring of high licking dams have elevated levels of oxytocin receptors in the brain, as well as increased sensitivity to the up-regulation of these hormone receptors by oestrogen in the hypothalamus (Champagne et al. 2006). This is significant, as following pregnancy and parturition, high levels of circulating oestrogen stimulate the up-regulation of oxytocin receptors in anticipation of the release of oxytocin which initiates maternal care. Congruent with this, offspring of high licking dams have higher numbers of the receptor for oestrogen in the medial preoptic area nucleus of the hypothalamus, which is critical for the exhibition of maternal behaviour. Conversely, in these same females, the number of oestrogen receptors in brain regions that are critical for the regulation of female sexual behaviour are dramatically reduced as a consequence of an increase in DNA methylation of the relevant promoter (Cameron et al. 2008). Critically, cross-fostering studies have shown that all of these changes are related to the quality of the care received postnatally as it is the phenotype of the foster dam and not the biological dam that predicts the reproductive strategy that the offspring undertake (Cameron et al. 2008). In sum, these studies on both stress and reproductive behaviour suggest that variations in early life experiences can induce adapive plasticity in phenotypes through tissue-specific effects on gene expression.

9. Conclusion

For many years the study of development was seen as the Cinderella subject of the four components of ethology identified by Tinbergen (1963). The answer to the question of where an individual's behaviour comes from has not emerged from the conventional opposition between the principal influences on development. Nor has it proved helpful to oppose behaviour patterns that develop robustly in variable environments with those that are highly plastic (Bateson and Gluckman 2011). What is required is understanding of the biological and psychological processes that build a unique adult from a fertilized egg.

As attention is focused on the development of behaviour, more and more is being learned about the underlying processes. Many of the regularities found in development are amenable to analysis. It does not follow that as these regularities are uncovered, behaviour necessarily becomes more predictable. To understand why, consider a rule-governed game like chess. It is impossible to predict the course of a particular chess game from a knowledge of the game's rules. Chess players are constrained by the rules and the positions of the pieces, but they are also instrumental in generating the positions to which they must subsequently respond. The range of possible games is enormous. The rules may be simple but the outcomes can be extremely complex.

Be that as it may, in recent years we have seen how the erstwhile Cinderella subject has become central in the integration of behavioural biology. In this much changed intellectual environment, the time seems right to rebuild an integrated approach to biology. With a whole array of promising new research areas and techniques emerging, integrative biologists have a lot to be excited about. This matters in a highly competitive world in which determined and well-placed people can, in a remarkably short time, change what is and what is not funded, open or close research institutes and radically alter the departmental structure of universities. It is important, therefore, to offer to the new generation of young scientists who are coming into the field a sense of what is becoming once again one of the most exciting areas in biology.

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From Ethology to Biodiversity: Case Studies of Wildlife Conservation

David W. MACDONALD (Oxford, UK)

With 24 Figures

Abstract

Modern biodiversity conservation is multi-disciplinary. Sound biological foundations are combined with insights from wider environmental sciences, and with social sciences, such as economics, development and governance. The boundaries between science, policy and advocacy are increasingly blurred. This essay is based on a lecture delivered in Berlin in May 2009 to celebrate the career of ethologist Günter TEMBROCK, who had offered kindly advice to the author, as a young doctoral student, on red fox behaviour more than thirty five years before. The resulting work on fox behaviour, and its application to rabies control and to other applied problems, was a step towards the creation of the WildCRU – Oxford's Wildlife Conservation Research Unit – and the contents of this essay are drawn from a small sample of that Unit's work to illustrate some issues in modern biodiversity conservation.

Zusammenfassung

Moderne Ansätze zum Schutz der biologischen Vielfalt sind multidisziplinär. Solide biologische Grundlagen werden mit den Erkenntnissen umfassenderer Umweltwissenschaften und den Sozialwissenschaften in den Bereichen von wirtschaftlicher und gesellschaftspolitischer Entwicklung verbunden. Zunehmend verschwimmen die Grenzen zwischen Wissenschaft, Politik und unabhängiger Interessenvertretung. Dieser Essay beruht auf einem Vortrag, der, gehalten im Mai 2009 in Berlin, das Werk des Ethologen Günter TEMBROCK würdigte, welcher dem Autor als jungem Doktoranden vor mehr als 35 Jahren freundlich seinen Rat in Bezug auf das Verhalten des Rotfuchses zukommen ließ. Die daraus entstandene Arbeit über das Fuchsverhalten und ihre Anwendung auf die Tollwutkontrolle und andere angewandte Probleme waren ein Schritt zur Schaffung von WildCRU – der Forschungseinrichtung für Wildschutz der Universität Oxford – und dieses Essay stellt anhand eines kleinen Ausschnittes der Arbeit dieser Einrichtung einige Aspekte modernen Artenschutzes vor.

1. Introduction

When, in 750 AD, Guru RINPOCHE flew into Bhutan to deliver Buddhism, he is said to have done so on the back of a tigress. Later, in 1993, when about 5,000 pastoralists were encircled by the designation of the Jigme Singye Wangchuk National Park, they were therefore warmly disposed towards the tigers (*Panthera tigris*) therein. However, their happiness (Bhutan wisely measures its own success by Gross National Happiness) began to fade when legislation restricted their use of the forest and banned the killing of wildlife (Wang and Macdonald 2006). Using camera traps, we calculated that the park safeguarded 8 tigers (Wang and Macdonald 2009b) (Fig. 1). While many might rejoice at this, some farmers living in the area did not. A fifth of these farmers reported losing stock to tigers and leopards (*Panthera pardus*), costing them on average 84 % of their $250 annual income, and more than half of villagers living in and around the park blamed it for their hardships (Wang and Macdonald 2006). By examining tiger and leopard scats we confirmed that both do eat livestock (Wang and Macdonald 2009a). But farmers could have done more to protect their interests: livestock husbandry was inadequate with about 60 % of farmers failing to construct adequate night-time corrals (Wang and Macdonald 2006).

Fig. 1 Tiger (*Panthera tigris*). (© A. Rouse, with permission)

My point is that where people meet Nature, especially when it's literally red in tooth and claw, and even when the people are culturally well disposed to it, there is often conflict. Whether the issue is parochial – as the fate of the last tadpole shrimps (*Triops cancriformis*) in Scotland, personal – as the fate of our closest cousins, the great apes (*Hominidae*) – or a huge issue of our time, the extinction crisis or climate change – the solution will almost certainly require somebody modifying their behaviour, perhaps even everybody modifying their behaviour (Sachs et al. 2009). That is the theme of this essay which, simply because I know them best, I illustrate with examples of studies by my own team, the Wildlife Conservation Research Unit (WildCRU).

The work reported in this essay began for me at the time of a kindly correspondence with Günter Tembrock, to whom this volume is dedicated. Inspired by the teaching of Niko Tinbergen (1951) and the pioneering field studies of Hans Kruuk (1972), I was accepted as a doctoral student in their group, the Animal Behaviour Research Group in Oxford's Zoology Department. There I determined to study the behaviour of red foxes (*Vulpes vulpes*), both to understand their adaptations to contrasting environments and to apply this knowledge to practical issues such as rabies control (Macdonald 1980, 1987) (Fig. 2).

Fig. 2 David Macdonald with red fox (*Vulpes vulpes*) cubs (© J. M. Macdonald, with permission)

Then, as now, Tembrock's (1957) ethogram of foxes was the most detailed lexicon of vulpine ethology and as a naïve graduate student I wrote seeking his interpretation of some postures and vocalisations with wonderfully onomatopoeic names. I was thrilled to receive his long, kindly and thoughtful responses, and so it is a pleasure to contribute this essay to a celebration of his influence. At the time, attempting to use the academic study of behaviour to solve practical problems in applied science was unusual, and the fox study led to the foundation of the Wildlife Conservation Research Unit (WildCRU) in Oxford's Department of Zoology in 1986 (a history described in Macdonald 2005). Since biodiversity is the engine of all the processes that facilitate the human enterprise, biology will always be essential, although generally not sufficient, for solving environmental problems. The necessary solutions will be dauntingly inter-disciplinary. Hence, many of the topics mentioned in this essay have left these ethological roots far behind. Nonetheless, behavioural ecology remains a foundation of biological conservation, and in this essay I use case studies from WildCRU's work to identify some general principles and, tentatively, a vision of the future. Readers unfamiliar with the topic of conservation should be alerted that the relevant literature is now vast, so the emphasis here on examples from our team provides only a personal and incomplete perspective, but hopefully one that opens the door to the wider field. Many of the wider issues are comprehensively reviewed in two sets of essays in Macdonald and Service 2006 and Macdonald and Willis 2013a.

First, to emphasise the challenge of solving conservation problems, we need to contemplate the enthralling, if sometimes operationally inconvenient, intricacy of animal lives. This intricacy explains why understanding Nature is a prerequisite to managing it, a point well illustrated by the story of the elephant (*Loxodonta africana*), the lion (*Panthera leo*) and the wild dogs (*Lycaon pictus*). These are large mammals, a group whose conservation brings special challenges (Macdonald et al. 2013).

In the 1960 s and 1970 s waterholes were drilled throughout the arid protected areas of Africa to provide wildlife with water. We work in Hwange National Park, Zimbabwe, where there are now about 55 pumped waterholes. Herbivores congregate at waterholes, and more waterholes translate into larger numbers of wildebeest (*Connochaetes taurinus*), zebra (*Equus quagga*), and buffalo (*Syncerus caffer*) (this increased prey-base attracting more lions) and elephants (which are well-known ecosystem engineers). In Hwange, the density of elephants (an impressive 2 per sq km) is determined by the density of waterholes (Chamaillé-Jammes et al. 2008, O'Kane et al. 2011). GPS tracking of lions revealed that water holes act as service stations on their route-maps, and lions loiter close to waterholes, and cruise at twice the speed between them (Valeix et al. 2010) (e.g. Fig. 3). Additionally, lioness home ranges are smaller where there are more waterholes (Loveridge et al. 2009). These effects create contours in a landscape of risk for herbivores (Valeix et al. 2009b), which face greater risks of being killed by lions when close to water holes – where 40 % of kills occurred (Macdonald et al. 2010c, Valeix et al. 2009a). Grazers, such as buffalo, normally visit waterholes in the cool of twilight, but when lions are around they visit at midday, when the cats are too hot to hunt (Valeix et al. 2009b). Some herbivores increase their level of vigilance when lions are in the vicinity of the waterhole (Periquet et al. 2010). At the landscape scale, the risk of encountering a lion influences the distribution of browsers, such as kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), and giraffe (*Giraffa camelopardalis*) (Valeix et al. 2009b); these shifts in herbivore distribution, and hence herbivory pressure may ultimately affect vegetation structure – a ripple effect known as a trophic cascade (Ripple and Beschta 2004).

Into this story lopes the heart-breakingly endangered African wild dog (Fig. 4) – Greg Rasmussen confirmed that their survival hinges, vulnerably, on pack size (Angulo et al. in press, Courchamp and Macdonald 2001, Rasmussen 2009). The number of pups born, per capita productivity, survival of dispersers and pup survival all collapse in smaller packs. Larger packs both grow faster and last longer. So, loss of a pack-member, to lion predation or human persecution, can cast the dogs into a reproductive poverty trap. The common currency in Nature is energy. Substituting into the dogs' daily schedule the costs of running, resting etc., reveals the energetic Achilles heel to their cooperation: not only do dogs with inadequate packing power need to run further to catch their prey but, having caught it, they face the cruel bind that they are unable to squeeze all their gains into their fixed stomach capacity before it is stolen by rivals such as hyaenas (*Crocuta crocuta*) and lions (Rasmussen et al. 2008). So, their maintenance costs soar, leaving them less to invest in reproduction. To add to this misfortune, the dogs meet people. While dogs protected in Hwange hunted at night only when the moon was full, those persecuted on farmland hunted even by the dimmest of waxing and waning moons. This reduced by two thirds their likelihood of encountering people intent on killing them, but increased by an estimated 37 % the risk of an unhappy collision with lions, or by an estimated 70 % the theft of their prey by hyaenas (Rasmussen 2009, Rasmussen and Macdonald 2012, Rasmussen et al. submitted).

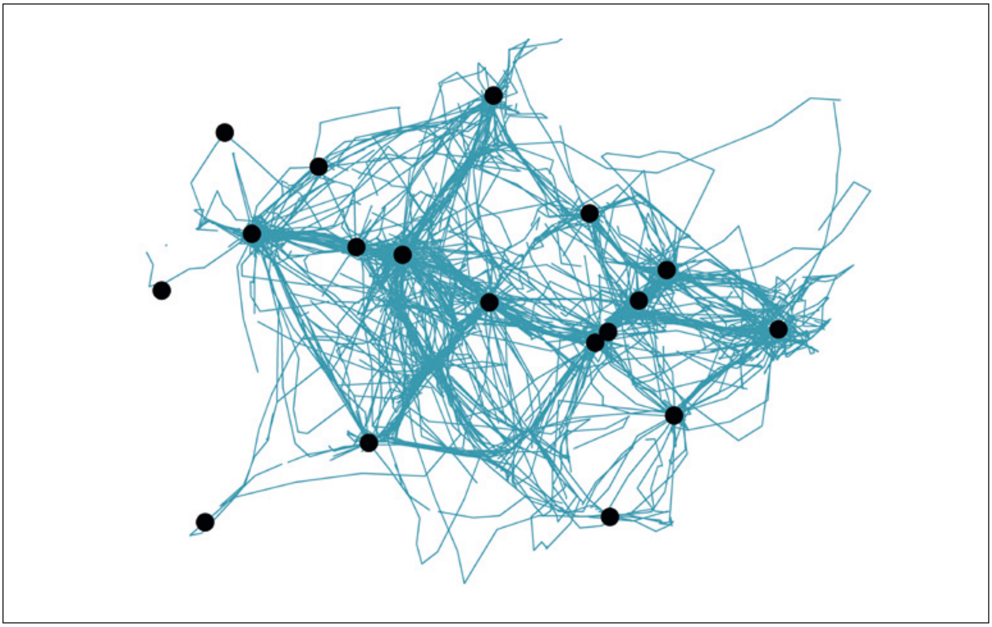

Fig. 3 Map showing trajectories for study lion male 7 in Hwange National Park; black triangles represent main waterholes in the study area (from Valeix et al. 2010, with permission)

Fig. 4 African wild dog (*Lycaon pictus*) (© A. L. Harrington, with permission)

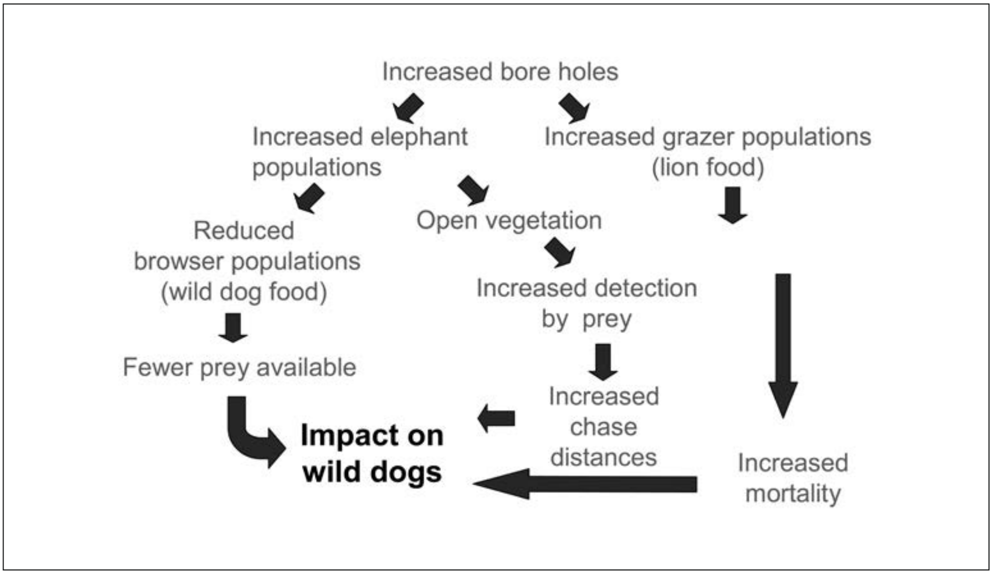

Fig. 5 Waterholes provoke energetic cost cascades among wild dogs (unpublished schematic by G. Rasmussen and D. W. Macdonald).

Cascade effects, and thus the perils of unintended consequences, are rife in conservation. Pumping more waterholes triggers a cascade of consequences (Rasmussen 2009) (Fig. 5). The grazing prey relished by lions increase, fuelling the production of more lions, which increasingly encounter dogs near waterholes, and kill them as an expression of intra-guild hostility (whereby larger carnivores harass smaller ones) (Hersteinsson and Macdonald 1992, Macdonald et al. 2010a). Meanwhile, the waterholes reduce the cost of living for elephants, which proliferate, possibly at the cost of species that are prey for dogs (Valeix et al. 2008) – browsers such as kudu and impala, which congregate where elephants have flattened the vegetation, enabling them to see the dogs coming, and hence prolonging their chases, further draining their energy. The dogs bump painfully down this cascade of consequences, haemorrhaging energy at each step (Rasmussen et al. submitted). The people who put in the waterholes doubtless did not anticipate this, as they did not anticipate similar cascade effects of providing water in other African parks (Mills and Retief 1984).

2. Modifying Human Behaviour

The impacts of human behaviour can be large, widespread, and sometimes unexpected. To make matters worse it can be very difficult to modify human activity, even in the face of overwhelming evidence that such change would be beneficial; take for example resistance towards efforts to address anthropogenic climate warming (*IPCC* 2007, Root et al. 2007, Stott et al. 2010). One cause of behavioural entrenchment has been an unhelpful politicisation of the climate change debate. We might caricature it as a cause taken up as a crusade by the political left, while derided as a fantasy on the right (one influential commentator recently referred to anthropogenic climate change as 'totalitarian gobbledegook' (Phillips 2010)).

The need to modify human behaviour for conservation is set against a man-made extinction crisis of palaeontological proportions (DICKMAN et al. 2007, NEE and MAY 1997). This should concern everybody because 'biodiversity' encompasses the cast of millions that, globally, provide the ecosystem services that support all human enterprise (SACHS et al. 2009).

As I write, the Secretariat of the Convention on Biological Diversity, in their third Global Diversity Outlook (*Secretariat of the Convention on Biological Diversity* 2010), concluded that "the target agreed by the world's Governments in 2002, to achieve by 2010 a significant reduction of the current rate of biodiversity loss at the global, regional and national level as a contribution to poverty alleviation and to the benefit of all life on Earth, has not been met". Moreover, they warn that the principal pressures directly driving biodiversity loss are either constant or increasing in intensity. Amazingly, our aeroplane flies, and amongst the myriad species that slither, slink and scuttle on this planet are the rivets holding it together (EHRLICH and EHRLICH 1981). As a way of categorising the threats posed to biodiversity by human behaviour, and of structuring this essay, I will follow a variant of Jared DIAMOND's Evil Quartet (DIAMOND 1989). I will resist calling them the Four Horseman of the Apocalypse, although Lies, Violence, Famine and Disease all feature in this Revelation. *First*, is transporting species beyond their natural range (invasive species); examples are legion (DAVIS 2009), and they pose a web of biological and ethical dilemmas (MACDONALD *et al.* 2007c). A prime example is the American mink (*Mustela vison*), transported to Britain, where they have driven Kenneth GRAHAME'S Ratty, the water vole (*Arvicola terrestris*), from 90 % of its range (BARRETO et al. 1998a, MACDONALD and HARRINGTON 2003, MACDONALD and STRACHAN 1999). The science of mink control (BONESI et al. 2007) is rife with practical challenges (HARRINGTON et al. 2009a), complex community interactions (BONESI and MACDONALD 2004, CLODE and MACDONALD 1995, HARRINGTON et al. 2009b), all beset with difficult ethical judgments (MACDONALD and BURNHAM 2010). The science of discovering the causes of water vole decline (American mink and agricultural intensification [BARRETO and MACDONALD 2000, BARRETO et al. 1998b, STRACHAN and MOORHOUSE 2006]) underpins the applied science of breeding them in captivity (GELLING et al. 2010, MOORHOUSE et al. 2007) and restoring them and their habitat to the wild (MOORHOUSE et al. 2008, 2009).

Our work in elucidating the best practical mechanisms for water vole reintroductions constituted one of the first attempts globally to conduct a rigorously replicated reintroduction experiment (MOORHOUSE et al. 2009) and demonstrated that, aside from the removal of American mink – a pre-requisite for any reintroduction being the prior removal of inimical factors – the single critical factor governing the population density of the resultant water vole colonies was the width of the margin of riparian vegetation bordering the water course (Fig. 6). The value added to this purely practical outcome was that the same experimental design also permitted us an insight into the basic ecology of water vole populations. On examining the range sizes and growth and maturation rates of our newly established individuals we discovered that the sites with higher population densities supported individuals with smaller range sizes, and a correspondingly smaller quantity of forage available to them. As a result, individuals at higher density sites had smaller growth rates and became sexually mature more slowly; females took 7 days (18 %) longer and males 5 days (13 %) longer to reach breeding condition at the sites with the shortest mean range lengths (MOORHOUSE et al. 2008). This discovery was the first evidence of a feedback mechanism in small mammals by which increased population densities may reduce maturation rates through a reduction in mean range size. Although only one example, this story is typical of the relationship between the science of ecology and its practical application: an understanding of the former both derives from and is essential for the execution of the latter.

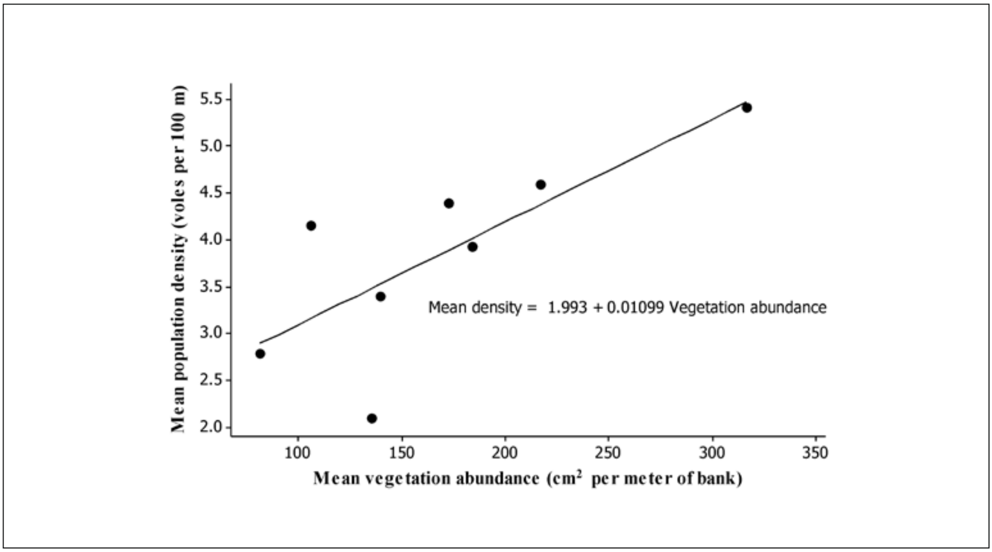

Fig. 6 The relationship between mean population density and mean vegetation abundance at sites where reintroduced water voles established (MOORHOUSE et al. 2009).

Fig. 7 Ethiopian wolf (*Canis simensis*). (© M. HARVEY, with permission)

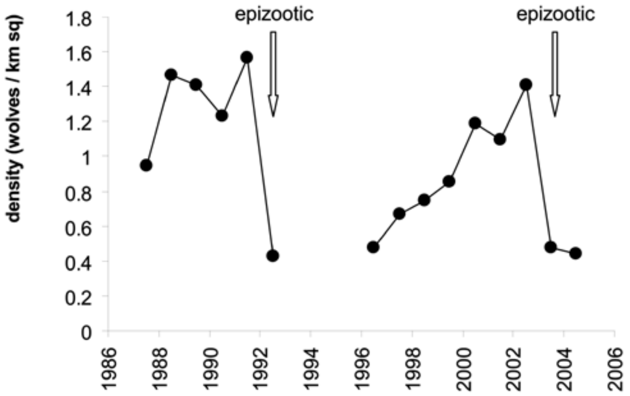

Fig. 8 Ethiopian wolf population densities based on total counts of adults and yearlings in a subset of focal packs in the Web Valley from 1987 to 2004. Rabies outbreaks occurred in 1991–1992 and 2003–2004. Political upheaval in the region interrupted monitoring from 1993 to 1995 (Randall et al. 2006, adapted from Marino et al. 2006).

Then there is disease (Riordan et al. 2006) – not just ‘natural’ disease but diseases exacerbated by human activity – and the risk of transmission from domestic animals to their wild relatives (Macdonald and Laurenson 2006, Woodroffe 2004). A prime example is the precariously rare Ethiopian wolf (*Canis simensis*) (Sillero-Zubiri et al. 2004) (Fig. 7). These most endangered wild canids (Sillero-Zubiri and Macdonald 1997, Sillero-Zubiri and Marino 2004) contract rabies transmitted by dogs (Randall et al. 2006, Sillero-Zubiri et al. 1996) which threatened to drive them extinct (Haydon et al. 2002, Marino 2003) (Fig. 8). Intensive monitoring and the high resolution data obtained by the Ethiopian Wolf Conservation Programme, a WildCRU project led by Claudio Sillero, makes this one of the best studied disease situations among carnivores (Randall et al. 2006). Marino et al. (2006) monitored density dependent processes of populations affected by rabies and discovered that pack extinctions slow the speed of recovery from an outbreak (Marino et al. 2013). Computer models based on these long-term data informed the emergency vaccination intervention that successfully curtailed the spread of rabies among Ethiopian wolves in 2003 (Haydon et al. 2006), as well as underpinning the integrated disease management approach that also serves as a model for disease control strategies in other threatened species (Randall et al. 2006). Tackling this problem requires work with both the wolves and the dogs – the Ethiopian Wolf Conservation Programme has vaccinated 10,000 dogs yearly and levered millions of pounds into community development.

People moving species and diseases beyond their natural ranges are problems now complicated by accelerated anthropogenic climate change (Pounds 2004, Root 2003), an aggravating backdrop to the Evil Quartet (see general review of climate effects in Walther 2002). Indeed, warming creates a risk of pushing these wolves off their mountain tops and into oblivion (just as it has enabled red foxes to thrive further up mountains, and further north, to the detriment of Arctic foxes [*Alopex lagopus*] [Angerbjorn et al. 2004, Gottelli et al. 2004, Hersteinsson and Macdonald 1992]). Other examples include Vargas et alia's discovery that increasingly frequent El Niños already imperil the Galapagos penguin (*Spheniscus mendiculus*) as with the associated weakening of Equatorial current, surface water warms, macronutrients are reduced, primary productivity decreases, and fish numbers diminish. El Niños have thus been found responsible for 65–77 % subsequent crashes in the penguin population (Vargas et al. 2006). Another example is Macdonald et alia's findings, from monitoring now almost 1,350 badger (*Meles meles*) life histories over 24 years (Macdonald et al. 2009), which revealed an initial trebling of the focal study population size (Wytham, UK, see Buesching et al. 2010), due to warmer winters increasing juvenile survival and extending the productive part of the year over which badgers could forage actively (Macdonald and Newman 2002) (Fig. 9).

Fig. 9 European badger (*Meles meles*). (© A. Rouse, with permission)

Poignantly, this trend is now countered by increasing rates of road deaths: as February nights have become warmer, badgers now cross roads when they might otherwise have been expected to be dormant underground (Macdonald et al. 2010d). Incidentally, winter temperatures also affect the sex ratios of cubs born the following spring with milder conditions producing a male bias (Dugdale et al. 2003). Changes in distributions due to climate change are facilitated indirectly by carbon pollution. So, are the resulting newcomers, such as the small red-eyed damsel fly (*Erythromma viridulum*) recently arrived in England (Keat et al. 2005), to be welcomed, or should we regard their assisted passages from the Continent as invasions (even if benign ones)?

Each of these varied phenomena illustrates the complexity of challenges to modern biodiversity conservation, and each touches on huge topics with many ramifications. However, in this essay I will focus instead on the third member of the Quartet: over-use and her twin-sister persecution, which have, to humanity's shame, driven extinct three of the eight sub-species of tiger during our lifetimes, although it emerges now that the Caspian tiger (*Panthera tigris virgata*), disgracefully driven extinct in 1970, still exists in the genes of its Siberian cousin (*Panthera tigris altaica*) and thus could be restored (Driscoll et al. 2009). I will also consider habitat loss: in the last century 93 % of Sumatra's orang-utans (*Pongo abelii*) fell to logging (Singleton et al. 2004), and our team is working on one of their last strongholds, along with gibbons (*Hylobates albibarbis*), in Kalimantan (Cheyne 2010). However, here, I focus later in this essay on restoring habitats, choosing English farmland as an example from our own backyard. Nonetheless, a general point emerges, and we have illustrated it with regard to two charismatic taxa, the Primates and the Carnivores: they often occur in the same places (Burnham et al. 2012), and suffer the same problems, so there is great scope for efficiencies in seeking shared solutions (Macdonald et al. 2012).

3. Overuse and Persecution

3.1 Overuse through Hunting

So, first to hunting, and to the circumstances affecting overuse. Evidence of human excess has long been recorded by artists, for example in Uccello's famous (1468) portrayal, and in comfortingly faded photographs of earlier eras. But the evidence is also vivid and current in numerous case histories, for example the collapse of saiga antelope (*Saiga tatarica*) hunted for horn and meat (Milner-Gulland et al. 2001). Hunters have many motives (Macdonald and Johnson 1996). Consider first sport hunting. This frequently operates within a form of conventional market with price indicating desirability. We looked at the market for African game hunting to investigate how individuals of different species are valued in an attempt to identify what makes a species vulnerable to overuse (Johnson et al. 2010). We know that humans value rarity in commodities as diverse as caviar and postage stamps (Courchamp et al. 2006).

A sinister variant of the phenomenon whereby 24 cent stamps (known as Red Jennies) now sell for more than US$900,000 (http://en.wikipedia.org/wiki/Inverted_Jenny), led to the demise of the prophetically named giant yellow croaker (*Bahaba taipingensis*). This fish, discovered only in 1937, had swim-bladders that were so valued in Traditional Chinese Medicine that soon 50 tonnes were being landed annually. But by 2000, over 100 boats managed to catch just ten specimens (Sadovy and Cheung 2003), a single fish caught early in 2010 fetched $500,000 (www.scientificamerican.com/blog/post.cfm?id=downcast-critically-endangered-baha-2010–02–16). The croaker may have croaked, but the enduring point is that its value was inflated so spectacularly *by* rarity that its exploitation remained economically worthwhile even as it approached extinction (Courchamp et al. 2006). Our exploration of the African game hunting market revealed just such an effect of rarity for bovids (Johnson et al. 2010). The market for this hunting is largely controlled by licensing, but our observations suggest that perceived rarity might affect the demand for species hunted in 'open access' systems. We have recently observed that prices to hunt game species have risen more for those where a change in IUCN status has signalled greater global vulnerability (G. Prescott et al. 2012). Of course, the chain of cause and effect is difficult to establish, but it is possible for conservation action of this kind to have the perverse effect of increasing exploitation in cases where perceived rarity increases demand.

We also quantified a ‘sizeist’ effect, where large species were more expensive to hunt, which was particularly striking for felids. Lions are both large and scarce, inter-related effects combining to affect their vulnerability to exploitation. Hundreds of lions are shot for trophies annually (*WCMC-CITES* 2009), each at many thousands of US dollars, all in economies where both hard currency and lions are scarce (Loveridge et al. 2010a, b). For example, in Botswana, in 2006, tourist hunters paid US$140,000 to hunt a male lion (Fig. 10). This recreation is abhorrent to some, but others argue that it offers hope for the survival of lions in many parts of Africa (arguments explored in Macdonald and Willis 2013b).

Fig. 10 African Lion (*Panthera leo*) (© D. W. Macdonald)

So, returning to Hwange National Park, is the viability of the park’s lion population affected by the quota licensed to the adjoining hunting estates? Since lion society is founded on male coalitions, an obvious starting point is that shooting a male lion might disrupt his coalition, prompting faster turnover, increased infanticide and other multiplier effects cascading from just one death (a perturbation effect, *sensu* Macdonald et al. 2006). We estimated that 22 males roamed the park. Each coalition’s range overlapped 2–6 prides of 2 or 3 lionesses. Some ranges straddled the park boundary, raising the question of whether their use beyond the park was sustainable. In 2000 the quota of trophy lions on land surrounding the park totalled 60 males. Since there were fewer than half that number of adult male lions in those areas, the quota could not be fulfilled; however 72 % of the adult males we tagged in the park were shot outside it. Most lions shot (82 %) were within 1 km of the park and hunting accounted for 44 % of the adult male park population each year. The average trophy was 5 years old, and a third of trophy lions had not reached 4 years. Hwange lions reach full sexual maturity at 8 years old, when their manes achieve full luxuriance, so the average trophy was a relative stripling. The result is two-fold – hunters are embarrassed to have adolescent trophies, and the lion population is deprived of mature males. So, a park of 15,000 km^2 was effectively rendered too small because a vacuum effect at the boundary drew males from the park interior into the firing line outside (Loveridge et al. 2007).

Following the findings of Loveridge et al. (2007), trophy hunting of lions was suspended in 2005. What would happen? Male numbers trebled, and coalitions doubled. Prior to the moratorium, the few surviving males ranged widely; afterwards their ranges halved, most came to encompass only a single female pride. Keynes famously quipped that in the long run we are all dead (Keynes 1923), and this is exactly why, in a climate of political uncertainty, short-termism had caused the off-take of males to double, halving sex ratio (Fig. 11).

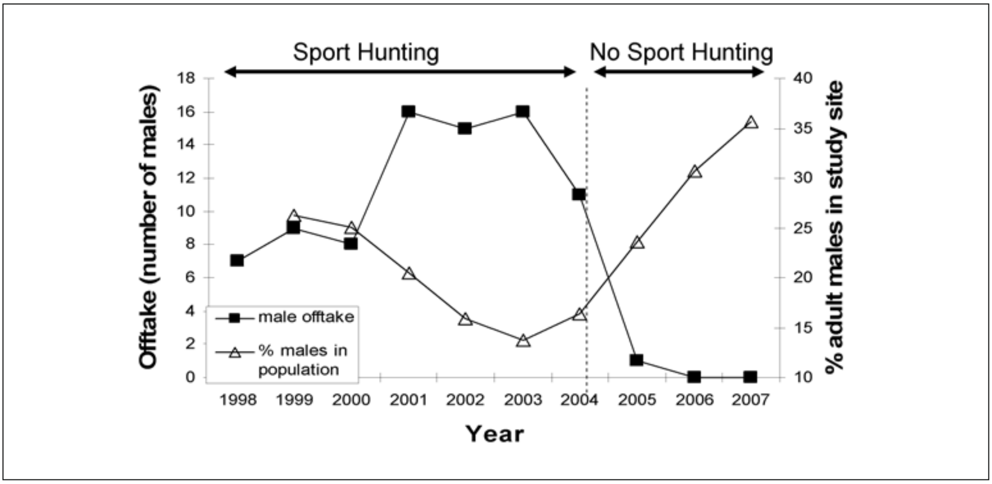

Fig. 11 Percentage of male lions in the Hwange National Park adult population and the number of adult males taken from the hunting concessions directly adjacent to the park between 1998 and 2007 (Loveridge et al. 2010a, modified from Loveridge et al. 2007) (Fig. 11.5 from “Biology and Conservation of Wild Felids” by Macdonald and Loveridge 2010, by permission of Oxford University Press)

Four years of moratorium restored it to 1 male per 2.3 females. As the social perturbation triggered by hunting was quelled, coalition take-overs, and thus infanticide, declined, and cub survival to two years rose from 41 to 64 % (Loveridge et al. 2010a). Hunting resumed in March 2009, but with a quota of only four lions. In summary, the attempt at sustainable use went wrong because the original quotas were set in the absence of adequate data – *firstly*, all the land-owners saw lions, but they all saw the same lions, and so over-estimated their abundance; *secondly*, things got worse because political insecurity in the human population made the future uncertain and sustainability irrelevant; and *thirdly*, they got even worse because of a perturbation effect – in this case prompting territorial strife and infanticide among lions.

Darwin’s contemporary, the philosopher Herbert Spencer, offered a Utopianly egalitarian view which counterpoints the reality of human-wildlife interactions; he opined: “Every man is free to do that which he wills, provided he infringes not the equal freedom of any other man" (Spencer 1982). Well, this is a difficult one, because the same lion is a trophy to one man, photo-opportunity to another and damned nuisance to yet another. Nonetheless, information, education and regulation, within a market context, led here to people modifying their behaviour for the better of biodiversity conservation. Unfortunately, the next case is less encouraging.

3.2 Overuse through Consumption

If hunting for sport has a long history, hunting for the pot is clearly the most ancient human motive for exploitation of animals. For much of human history, and still for much modern exploitation, this is sustainable. But for wildlife consumed in the tropics, now widely referred to as 'bushmeat', there are substantial doubts about sustainability. One of the areas of greatest concern is the Congo Basin in Africa. A recent review of bushmeat exploitation in the region (Fa and Brown 2009) draws attention to the scale of the problem in West Africa.

Increased commercial hunting is one important factor. Hunting for trade has been promoted by an increased penetration of remote forests by logging roads, and by the greater access to modern weapons by hunters. At the same time, low incomes and lack of alternatives push hunters to sell bushmeat directly to other consumers, or to markets *via* middlemen. Most pressing though, is probably the attrition of wildlife inside protected areas as these become a main (or even the last) source of wild meat in many regions. Yearly, bushmeat equivalent to 4 million cattle is harvested in the Congo Basin, while the human population grows by [up to] 2.4 %, and 1 % of the forest is felled (Fa et al. 2006).

We investigated sustainability in 35,000 km^2 of tropical forest between the Cross River in Nigeria and the Sanaga River in Cameroon (Fa et al. 2006). The Sanaga-Cross region is a 'hot spot' of endemism, home to such charismatics as the mandrill (*Mandrillus sphinx*), the Cross River gorillas (*Gorilla gorilla diehli*) and chimpanzees (*Pan troglodytes verus*), Preuss's guenon (*Cercopithecus preussi*), and Preuss's red colobus (*Piliocolobus preussi*). We sampled all known markets in nine areas, totalling 118 villages. Fourteen graduate 'market observers' coordinated weekly reports from 80 'market assistants' and in turn reported to a research assistant in each country. Each Nigerian market traded almost 3,000 carcasses pa, and Cameroonian markets a little more than a thousand. Of the 100,000 bushmeat items we logged, 95 % were mammals. Of the mammals, most were ungulates and rodents, but overall around 16 % were primates.

For species like the putty-nosed monkey (*Ceropithecus nictitans*), these extraction rates are a signpost to extinction, the observed extraction rates are unlikely to be sustainable, given the reproductive capacity of the species and its likely density (Fa and Brown 2009). Furthermore, where prey disappears, predators follow, as Henschel illustrated for leopards in Gabon (Henschel 2008). There is comfort in the fact that this area is well-endowed with protected areas – but remember the lesson of lion hunting edge effects. Endangered Preuss's red colobus, and other species, were traded more, closer to protected areas. Of the 10,000 or so Blue Duiker traded in three months, price rose with distance from protected areas, raising fears of a vacuum effect outside the park, and poaching within it (Macdonald et al. 2011) (Fig. 12).

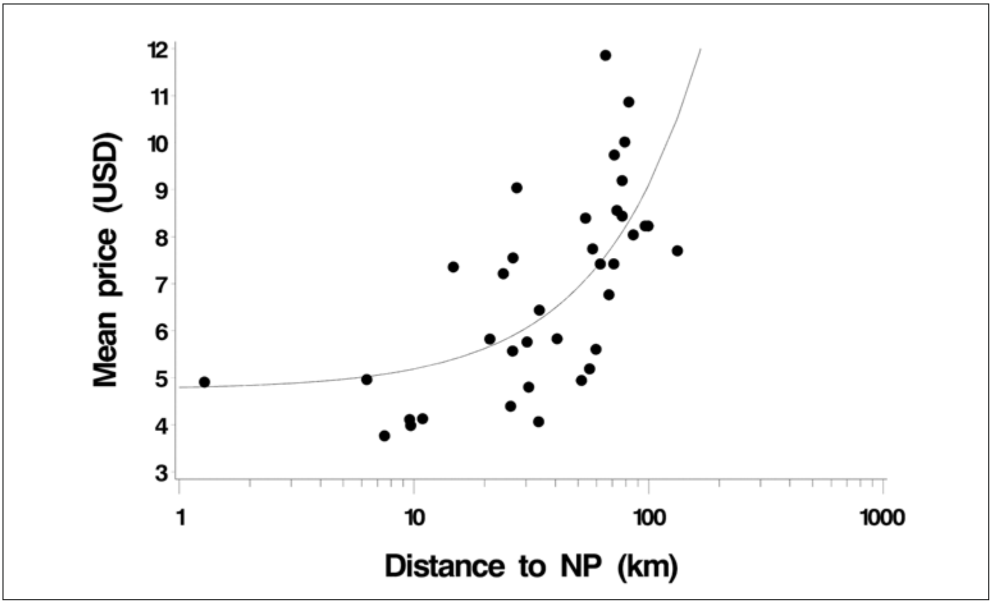

Fig. 12 Price of blue duiker sold as bushmeat against distance from protected areas in Cameroon (Macdonald et al. 2011).

In Equatorial Guinea we recorded the amount and type of bushmeat recorded at one market, in Bioko Island, over almost 3 years. Monkey carcasses got fewer – even the number of rodent carcasses available for sale crashed from 100 to 20 per day – and more expensive, while forests got emptier – so empty, that by the end of 1998 the proportion of carcasses imported to that island market from the mainland had doubled (Albrechtsen et al. 2007).

And remember consequence cascades. In the forest, the loss of primate species due to hunting disproportionately hits big species. Hunting larger, more vulnerable species, such as the Bioko Red Colobus (*Procolobus pennantii pennantii*), probably leads to competitive release of more resilient, often smaller, ones such as the red-eared guenon (*Cercopithecus erythrotis* ssp. *erythrotis* on Bioko). Of course, even if yield of the red-eareds, which increasingly dominate as hunting pressure escalates, can be sustained or increased, that isn't sustainability if it comes at the cost of an impoverished community and reduced biodiversity. This risk highlights the need to be alert to the danger of a shifting baseline in what is regarded as acceptable (Macdonald et al. 2010b).

For conservationists tackling the bushmeat issue, identifying the consumers is important. Is bushmeat a luxury of the wealthy or an essential, but unfavoured source of protein for the poor? In continental Equatorial Guinea, we found that the wealthier were more likely to report eating *domestic* meat in the 24 hours before our survey, though the effect was not marked. In Bata city, where average wealth was 'high' (at about $138 per year), those at the upper end of the wealth spectrum were more likely to report eating bushmeat (Fig. 13) and more likely to record eating both bushmeat and domestic meat (Fa et al. 2009). In rural areas of Equatorial Guinea, the proportion of people who reported eating bushmeat in the day before our study varied substantially between sites (between approximately 2 % and 40 %) and was not related to wealth (which averaged $9 per adult per year) (Fa et al. 2009).

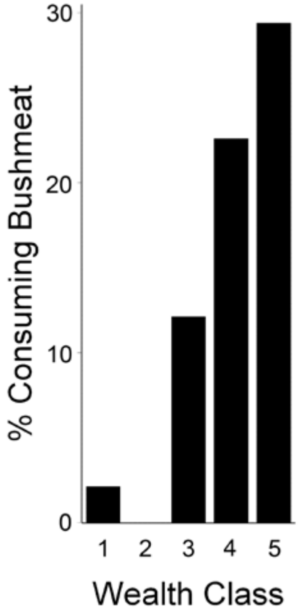

Fig. 13 Effect of wealth on likelihood of recording bushmeat consumption in Bata city. Household wealth is categorized into five quintiles (modified from Fa et al. 2009).

But who drives demand? Although about a third of people lived in towns in our Cross-Sanaga study area of Nigeria and Cameroon, only 5 % of bushmeat traded in markets was sold to them, so for the *average* urbanite this source of bushmeat was nutritionally trivial: about a tenth of a gram per day, set against a daily requirement for about 55 g of animal protein. The vast majority of bushmeat biomass traded (95 %) was dispersed amongst the two thirds of the population supplied by rural markets, providing an average rural consumer with only approximately 0.9 g of animal protein daily in Nigeria and 3.5 g in Cameroon (again a nutritionally trivial amount in comparison to the 40–100 g per day per American Male Equivalent [AME] reported by Fa et al. [2009] for mainland Equatorial Guinea, and which was broadly comparable with other studies in central Africa). The mainland Equatorial Guinea study reported greater average amounts of domestic meat consumed at both rural and urban sites compared with bushmeat, though the median household consumption for both were zero everywhere (most households reported eating no bushmeat or domestic meat in the 24 hours before our survey). In a separate study, we observed that on Bata island, Equatorial Guinea, wealthier consumers were more likely to eat bushmeat, similar to the mainland urban dwellers (Albrechtsen et al. 2005). While we found some evidence for consistent preferences for some taxa across the region, there was little evidence that preference was linked to rarity; price was principally determined by the size of taxa (Macdonald et al. 2011). Policies enforcing restriction of trade in rare taxa may be more likely to succeed than more general attempts to regulate the trade. More intense enforcement near national parks may yield additional protection. In the Sanaga-Cross region, bushmeat is more expensive further away from national parks, suggesting these may be significant sources for the trade.

An overview of these findings, which represent a work still in progress, is that bushmeat in cities may be largely a luxury for the middle class. Set against the extinction risk it exacerbates, any unsustainable elements of this trade merit limited sympathy or tolerance. However, this flow – although it might eventually be staunched by economic development and improvements in education and regulation – is a secondary problem. Most bushmeat is eaten by the rural poor. Tragically, while its average contribution to their nutrition seems trifling, its aggregate drain on some elements of biodiversity is devastating. Considering first the carrot, then the stick, the supply chain might be broken by luring hunters to an alternative livelihood – for example, the Lebialem Beekeepers' initiative (http://www.bee-4bushmeat.org) trains hunters, who take the pledge to refrain from taking bushmeat and instead to produce honey and beeswax for an international 'fair-trade' market. However, as one cohort of hunters is reformed, surely an endless pool of candidates waits to take their places. So to the stick, in October 2007, amidst commendable fanfare, President Obiang of Equatorial Guinea passed legislation prohibiting nationwide the hunting, sale, consumption and possession of primates. The impact was immediate, but sadly not long-lasting. Until now, no hunter or seller has been fined. Much of the bushmeat tragedy is played out in kleptocracies where governance is as threadbare as are larders. The rural poor may currently have no alternative to bushmeat, and providing an agricultural one may lead to forest destruction. This dilemma seems likely to worsen as human populations increase, and insofar as they cannot eat cake, a tragedy of the commons seems set to ensue.

3.3 Persecution

So, what if wildlife is not so much the victim but more the problem? Returning to Zimbabwe's lions, reprisals for their perceived depredations, and an accidental by-catch of poaching, result in a second haemorrhaging at Hwange's boundary – this time of lionesses (Loveridge et al. 2010a). Prides near the core of the park average 3.5 lionesses, almost twice those at the perimeter, where only 42 % of prides survive intact for two years, and only 48 % of their cubs survive to one year. Sixteen of 17 lioness deaths recorded at the park edge were caused by people, whereas all six deaths in the interior were from natural causes (Loveridge et al. 2010a, submitted).

A human community might modify its behaviour towards predators if the losses incurred by some sectors were more than offset by the gains in others. Hemson et al. (2009) explored these optimistic propositions with regard to the 32–41 lions in Botswana's Makgadikgadi Pans National Park, surrounded by a countryside carpeted in cows (Valeix et al. 2012). It appeared that not everyone was delighted to share their home with hungry lions and, in retaliation for an outbreak of stock-raiding in 2000, 8 lions from the park were killed.

However, on the face of it this should not have happened. Botswana is the only member of the Southern African Development Community (SADC) with a state-funded predation compensation system, and it also has a profitable "eco-tourism" industry that might provide people with incentives to value wildlife. There was clearly scope for people to be compensated for their losses and even to profit from the hard currency flowing into their area. Why kill the golden goose? Questioning the inhabitants revealed that many people were hostile towards lions, and people living in cattleposts and sharing their environs with lions had much more negative attitudes towards wildlife, conservation and particularly lions, than those living in nearby villages. Despite the clear risk of lion depredation, husbandry was remarkably lax, 13 % of cattle roamed the park at night and more than three-quarters of herders confessed, unabashed, to not gathering all their stock at night. Perhaps then it was no surprise that reported losses to lions seemed little affected by the size or type of bomas (or corrals), numbers of dogs or herders. That, however, did not make the 59 % of them reporting lion depredation in the previous year any less cross or willing to kill lions if presented with an opportunity (Hemson et al. 2009, Macdonald et al. 2010b)!

Hemson et al. (2009) reported an annual Profit-and-Loss account such that the average cattlepost lost US$284 to lions, totalling a community-wide loss of US$33,643 pa. That compensation, at 80 % of market value, could not be claimed for cattle killed within the park was evidently insufficient incentive for retrieving stock at night. Consequently, only 42 % of stock lost to lions was compensated. On the profit side, tourism (to which lions are crucial) earned $317,200 per year (and for example one tourist operator paid the central government approximately $150,000 in tax per annum, while the Central District Council received $55,000 as a resource rental, so there is no shortage of funds from which offsets might be drawn). Nonetheless, most people disliked living near a national park, mostly because of stock losses to predators, and only 15 % of herdsmen professed any inclination to improve their stockmanship. Almost everybody thought the benefit of lions accrued to somebody else – generally the government – and that it was they who should take responsibility for them. Almost two-thirds of herdsmen (61 %) thought the park should be fenced, and 16 % thought the lions should be killed. The nub of the problem was that the benefits were distributed equally into a community that did not share the burden of living with lions equally. Those that lost the most did not gain enough to offset their losses while those living in large villages far from the national park were much more positive towards lions, wildlife and the tourism industry. Indeed, while scientists like to work with averages, and development planners like to think about communities, no relevant ‘community’ existed at Makgadigadi in this context – only individuals prioritising their own families, and to whom the fact that lions ‘paid for’ a school or hospital 30 km away was of little consequence (Hemson et al. 2009).

A more operational sense of community is illustrated in Maasailand, southern Kenya (Maclennan et al. 2009). Amboseli, the third most visited National Park in Kenya, nestles amidst a constellation of unfenced ranches, across which roam wildlife – including predators which kill livestock daily. Lions are crucial to Amboseli’s US$3.5 million tourist revenue. In 2001–2002, partly in retaliation for livestock losses, the Maasai community owning the Mbirikani ranch (1200 km^2) speared 24 lions. Fearing their local annihilation, in 2003 a local NGO drew on international donors to establish the Mbirikani Predator Compensation Fund. So, wider society – in this case the NGO representing the ideological interests of conservation and the financial interests of ecotourism – wanted lions sufficiently to pay herdsmen not to kill them. This, in contrast to the hitherto more familiar ‘polluter pays’ principle of environmental regulation, is a case of the developing genre of ‘beneficiary pays’ programmes, collectively known as Payments for Ecosystem Services – in this case the continued presence of lions. Maclennan et al. (2009) examined 1,694 stock killings – there were an average of 52 claims per month. Eight monitors were employed to verify claims, and if anybody in the community killed a carnivore, the entire community lost its payments. Predators took 2.3 % of livestock annually. Owners received compensation at full market value, but most were penalised by 50–70 % for avoidably sloppy husbandry, so the US$33,000 per annum paid out in compensation was less than half the value of the predated stock (Fig. 14). Lions accounted for only 7 % of stock-killing, and keeping the average lion alive cost US$6,124 a year in compensation and monitoring costs (MACLENNAN et al. 2009).

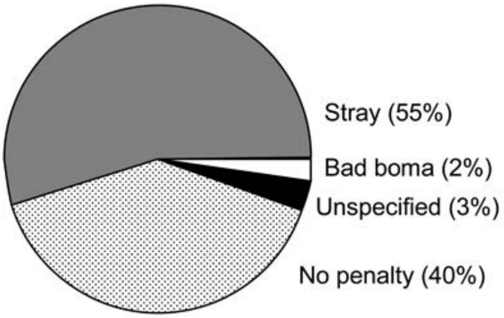

Fig. 14 Penalties assigned to livestock claims made to the Mbirikani Predator Compensation Fund. Cases in which the penalty status was not specified are categorised as ‘unspecified’ (based on MACLENNAN et al. 2009).

Has the investment of $44,000 per annum, in compensation payments and administration costs, over 3.5 years worked? It is too early to say, but in the interim a short-term metric of success might be the number of lions killed on the ranch, and this has surely diminished (although it may simply be that there are few left to kill, and remaining lions are more difficult to hunt as they spend more time in inaccessible lava beds). Lion numbers did not increase, because they were killed on neighbouring properties. A study of the attitudes of people living on Mbirikani Ranch found that more people said they liked living with carnivores (45 %) than those living on a nearby ranch without a compensation scheme (3 % – one person) (GROOM 2008). Without the scheme even fewer lions might have survived, and now the scheme is being extended to the neighbouring properties too.

So, when it’s in your own back yard, it can be seriously difficult living with wildlife – especially the sort that can eat not only your livelihood, but also your family. Incentivising people to do so raises a mix of questions in psychology, sociology and economics – perilous topics for an ethologist (MACDONALD et al. 2007a, 2010b, MACDONALD and SILLERO-ZUBIRI 2004, MACDONALD and WILLIS 2012). A good example is provided by jaguars (*Panthera onca*), which are persecuted by ranchers from Mexico to Argentina (Fig. 15). Indeed, all nine healthy jaguars tracked by Sandra CAVALCANTI ate domestic stock (CAVALCANTI and GESE 2010, CAVALCANTI et al. 2010). However, as Silvio MARCHINI’S (2010) study of ranchers in the Pantanal and Amazonia revealed, peoples’ mind-sets vary from place to place, irrespective of the impact of jaguars on their livelihoods. The attitudes of the Pantaneiros, typically from long-established, land-owning dynasties of cattle ranchers, were different from the Amazonians’ who were mostly immigrants with small properties and scant experience of jaguars or forest. Pantaneiros, especially those with most economic pessimism, regarded jaguars as a menace to their stock, whereas the Amazonians, those with smaller properties and less knowledge about jaguars in particular, were more worried about jaguars attacking them than their cows (MARCHINI and MACDONALD, in prep.), even though jaguar attacks on humans are equally rare in both areas and have happened almost exclusively in hunting situations. The perceived impact of jaguars on livestock and human safety often exceeds the evidence for it, and it is affected mostly by people's perceptions of the economic situation and their knowledge about and attitudes towards jaguars.

Fig. 15 Jaguar (*Panthera onca*). (© A. Rouse, with permission)

Do these mindsets translate into active persecution? Both Pantaneiros and Amazonians expressed a continued willingness to persecute jaguars. However, their motivations to kill jaguars differed strikingly: Pantaneiros were heavily influenced by their perception of what was acceptable to their peers – who tended to view killing jaguars as a legitimate element of their group identity – whereas Amazonians were mostly motivated by the fear of jaguars (Marchini and Macdonald 2012). Amazonians were oblivious to peer endorsement, but believed that jaguar killing was a common and therefore natural practice among their neighbours, and this perception also determined their intentions to kill jaguars. Intention to kill jaguars turned out to be less associated with stock-losses, and more with identity and the social acceptance that killing jaguars was part of the natural order of things. As a result, our project shifted attention from the largely nugatory task of persuading jaguars not to eat cattle (commonly the aim of human-wildlife conflict resolution), to teaching children to value jaguars, and thereby to exert moral pressure on their parents to do the same (see Macdonald et al 2010b).

Tolerance of conflict may also sometimes be determined more by feelings than by economics. The game theorist and economist Thomas Schelling (1960) contends that situations of pure conflict in which two antagonists are completely opposed are rare, and arise only in wars of complete extermination. As a result, 'winning' in conflict does not have a strictly competitive meaning of winning relative to one's adversary, rather it means gaining relative to one's own value system. In areas of small subsistence livestock holdings within the Arucania Lake District of Chile, Murphy and Macdonald (2010) found that beliefs played a greater role in tolerance of puma depredations than did the number of sheep owned by a stakeholder or the total economic value of sheep-holdings as a percentage of total livestock holdings. Moreover, almost 50 % of stakeholders were willing to accept the loss of at least 1 sheep (though always less than 4) to pumas per year without seeking retribution against them. These results may help explain why compensation schemes have been employed by conservationists throughout the world with such mixed success (Nyhus et al. 2005). Whether stakeholders intend to kill felids regardless of losses (as Marchini 2010 observed in the Pantanal) or whether they tolerate some small losses without seeking retribution (Murphy and Macdonald 2010), they are hoping to 'win' relative to their own values, not relative to jaguars or pumas (*Puma concolor*).

Turning from adaptation to mitigation, history provides a wheel ripe for reinvention: mediaeval livestock guarding dogs, as depicted in the 14th Century Psalter commissioned by the Visconti rulers of Milan: the dog guards the sheep (*Domini canis*: dog of the Lord) while one shepherd sleeps and others are distracted by the heavenly host – it was ever thus – and how perfectly the artist portrays the Maremma-type dog that perpetuates this profession (Fig. 16). Anyway, in reality livestock guarding dogs have been genetically selected to think of themselves as sheep, with which they are brought up from puppies, and they develop a strong protectiveness towards their woolly companions! In Slovakia, following protection in 1975, wolf (*Canis lupus*) numbers have recovered to about 300, and although wolf depredation is nationally inconsequential, there are local hotspots of predation to keep the embers of hatred glowing. Rigg et al. (2011) reintroduced Slovensky cuvacs, cutting predation by an average of 69 %, and might have done better but for the inefficiency of the shepherds.

A long way from mediaeval Europe, Namibian ranchlands are home to a third of the world's 9,000 or so cheetah (*Acinonyx jubatus*) (a century ago there were ten times as many) (Marker 1998). There, Marker et al. (2003) have sought to reconcile the conflict that arises when cheetah on these 8,000 ha farms attack calves, and farmers retaliate by killing cheetahs (reviewed in Marker et al. 2010). This conflict has had a huge impact on Namibia's cheetah population – nearly 7,000 were trapped and removed (usually killed) from Namibian farms between 1980–1991 (*CITES* 1992), which is, staggeringly, almost the same number as persist worldwide today. In order better to understand cheetah ecology and conflict, Marker et al. radio-tracked 41 cheetahs, which were found to range across vast areas, each typically crossing 21 farms, making obvious the potential impact of a renegade farmer or a renegade cheetah (Marker et al. 2008). A survey of farmers conducted in the early 1990 s revealed the impact that they were having on cheetah populations – on farms where the owners perceived cheetahs as problematic, they removed an average of 29 cheetahs every year (Marker et al. 2003). The key problem was livestock depredation, with the 241 farmers in the study collectively reporting the loss of 138 sheep and goats annually to cheetah. In an attempt to combat this problem, Marker et al. (2005a, b) imported ten Anatolian sheep dogs to Namibia, from which 143 more were bred and given to farmers (Fig. 17). After having the dog for a year, three-quarters of recipient farmers (73 %) reported a large decline in stock losses (Marker et al. 2005a). Before dogs, almost no farmers believed they were free of losses to cheetah and 71 % reckoned they lost 10 or more head of stock to predators but after receiving a livestock guarding dog, 65 % of farmers recorded no losses to cheetah (Fig. 18). This partly explains why the average number of cheetah removed annually on problem farms declined from 29 to 3.5 per farmer. *Domini Canes* indeed!

Fig. 16 14th century Psalter (ms. Landau Finaly Ms 22, folio 11 recto) held in the Biblioteca Nazionale Centrale di Firenze. (By kind permission of the Ministero per I Beni e le Attività Culturali della Repubblica Italiana / BNCF.)

Fig. 17 An Anatolian sheep dog puppy meets his flock. (© A. L. Harrington, with permission)

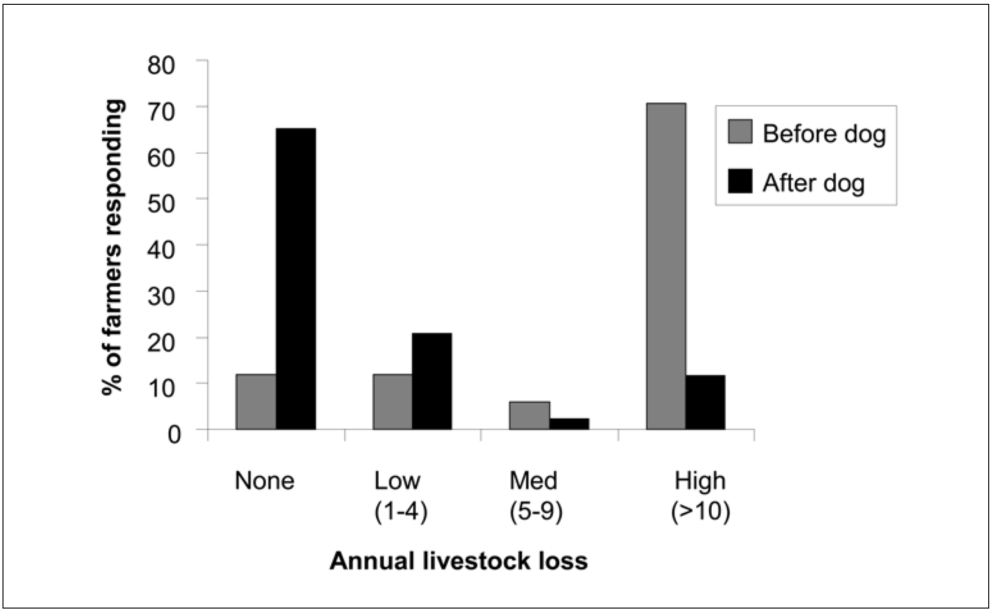

Fig. 18 Percentage of Namibian farmers reporting various levels of livestock loss before and after acquiring a livestock-guarding dog (Marker et al. 2005a).

So far, our examples have been drawn from countries in the Developing World. But what, from the perspective of a developed-country, about our own backyard biodiversity in the Developed World? Alternatives to lethal control are relevant there too, so I will mention one example – repelling badgers – before turning to English farmland as a case study of the impacts of habitat degradation, and how to mitigate it.

Mammals damage crops worldwide (Naughton-Treves 1998, Schley and Roper 2003), but killing them in an effort to curb damage can be inappropriate for all sorts of reasons (efficacy, ethical, conservation and legal) (Baker et al. 2008), and may even be counter-productive (Tuyttens and Macdonald 2000). Non-lethal control could prove more effective because the target animal is retained in its territory and social position, and population perturbation is therefore minimised (Baker et al. 2007, Tuyttens and Macdonald 2000). Understanding the biology and particularly the behaviour of problem species will in general help to achieve more effective wildlife management (Baker et al. 2006), and non-lethal methods in particular need to be developed (Baker and Macdonald 1999, Macdonald and Baker 2004). Conditioned Taste Aversions (CTA) have been proposed as a potential means of reducing wildlife feeding damage since the 1970s (Reynolds 1999). Sandra Baker et al. conducted a series of detailed behavioural experiments in which they demonstrated that wild European badgers could be conditioned to avoid target foods. They used video-surveillance initially to show that badgers could learn to avoid baits treated with a deterrent, ziram (Baker et al. 2005). However many wildlife management situations demand the protection of untreated foods (Conover 1989), and Baker et al. (2007) went on to show that badgers could be conditioned to avoid untreated baits in the presence of a benign odour cue, and that their aversion was most likely mediated by the odour. The method was successfully transferred to maize cobs, as a model crop (Baker et al. 2008). Incorporating such a cue might also facilitate using the odour to extend any protection to other areas or foods.

4. Habitat Loss

Habitat loss and degradation are perhaps the greatest threats to biodiversity of all; according to a 2008 IUCN report, this is certainly true for mammals, birds and amphibians (Hilton-Taylor et al. 2009). One definition of habitat is "the biotic and abiotic features required by a species for survival and reproduction" (Pearson 2002); it is no surprise to learn therefore that losing your habitat is losing your life-blood. Habitat is a component in almost all WildCRU's projects. For example, using satellite imagery to compare forest loss within protected areas in Gorontalo Province, Sulawesi, our team found that the park with the most active conservation intervention (largely under the UK's Darwin Initiative [http://darwin.defra.gov.uk/], Macdonald 2011), Nantu National Park, had been best protected, and went on to attribute this to a community engagement programme and, crucially, robust policing by park guards (Macdonald et al. 2011). They then explored how these findings could be used to attract international carbon-offset funding to the park (Collins et al. 2011b), although it is not straightforward to secure the hoped-for biodiversity gain (Collins et al. 2011a). But these issues and principles are not unique to the Developing World. They apply equally to degraded habitats in our own backyard, and so I will develop, as a Case Study, our work on conservation in lowland English farmland – The Upper Thames Project.

Enclosed farmland covers 60% of England, wherein the post-war agricultural miracle was delivered, at devastating cost to nature (Feber et al. 2007a, Macdonald et al. 2000a). While cereal yields have doubled (*FAO* 2008), farmland birds have declined, by two thirds even since 1970 (*Natural England* 2008). Can we modify human behaviour so that farming and biodiversity co-exist? In passing, let me play the Devil's Advocate by asking what priority conservation should give to those iconic farmland specialists that have evolved dependence on bygone agriculture – arable plants such as the cornflower (*Centaurea cyanus*) (once so common it gave its name to a colour), evolved seeds adapted to being sown with the crop, now nationally rare because of seed cleaning (Wilson and King 2003), or such as the high brown fritillary (*Argynnis adippe*), whose life-support system is the artificial re-creation of agriculturally obsolete extensive, bracken (*Pteridium aquilinum*)-rich grazing systems and freshly coppiced woodland with violets (*Viola* spp.) (Asher et al. 2001), or the corncrake (*Crex crex*) which depends on corncrake friendly mowing to avoid its chicks being diced to death (Williams et al. 1997). Is this akin to protecting steam engines as the interesting remnants of an obsolete transport system? Surely only a philistine would abandon these species, but I pose the question to provoke two points. *First*, in developed countries the detail of conservation is about consumer choices (Macdonald et al. 2007a). We may treasure the cornflower now that it's endangered, but until the mid-19th century it was, to quote, "a pernicious weed injurious to the corn and blunting the reapers' sickles" (Wilson and King 2003). Society has to decide what sort of Nature it wants, and work out how to behave so as to deliver it. *Second,* the generality of whether, and how, to secure nature in the countryside is relevant to a wider constituency than the bearded, binocular-bound few, nostalgic for Constable's haywain. Government currently considers farmland biodiversity sufficiently important that over 6 million hectares of England are now covered by agri-environment schemes seeking to modify human behaviour to conserve the landscape and its wildlife (*Natural England* 2008). Amongst many reasons why society might make this investment is the power of a hitherto-unquantified ecosystem service: human well-being. The National Health Service can save large sums of money by calling on the Natural Health Service: deaths, especially from circulatory disease, decline with access to green spaces, as does inequality in risk between rich and poor (Mitchell and Popham 2008) (Fig. 19). An important question, not yet answered, is the extent to which preserving habitats for human health can deliver benefits also for biodiversity (Hughes et al. 2013)

Globally, the big question is: can 9 billion people be fed, watered and provided with energy equitably, healthily and sustainably? How to safeguard biodiversity in the face of the spreading footprint of an already collosal, and growing, human population, is paramount amongst the 16 metaphorical elephants in the room identified by Macdonald and Willis (2013b) as challenges to conservation. Even if the current trend for human fertility to decline continues, human global population is projected to reach this figure by 2050 (May 2007). If society wants – needs – BOTH food AND a biodiverse, aesthetic and culturally rich landscape, how might farmer behaviour be changed to deliver this to the taxpayer, who, for the time-being, largely foots the bill? Variants of this question could usefully be posed almost anywhere, but I will set it in the British countryside at scales from within-fields to between landscapes. First, I turn for guidance to the Scottish poet Robbie Burns; in November, 1785, on ploughing up her nest, Burns addressed the famous "wee sleekat, cow'rin, timorous beastie" – she was probably a wood mouse (*Apodemus sylvaticus*) (Fig. 20). That poem not only anticipates the essentials of agro-ecology, but offers a lament that touches the es-

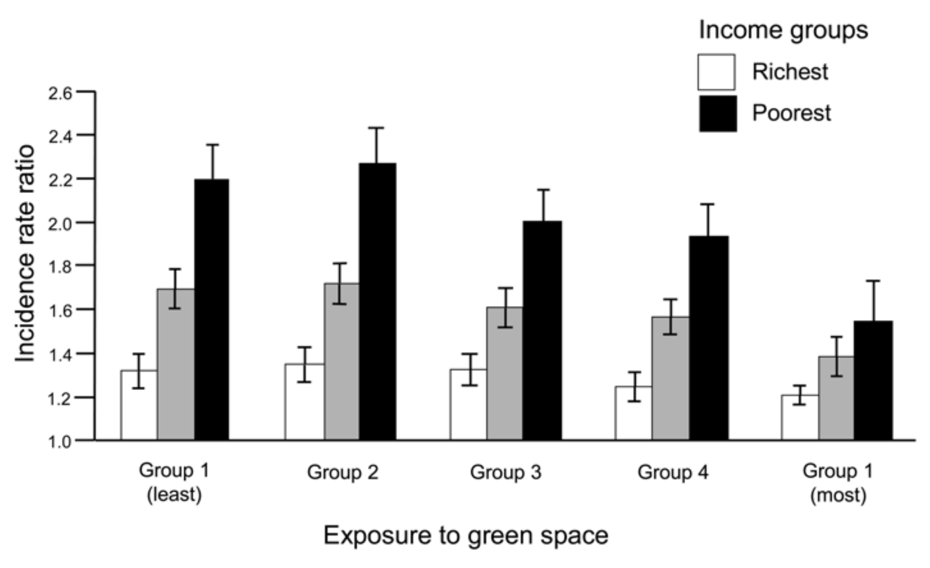

Fig. 19 Incidence rate ratios for deaths from circulatory disease in income-deprivation quartiles 2–4, relative to income deprivation quartile 1 (least deprived), stratified by exposure to green space (modified from Mitchell and Popham 2008).

Fig. 20 Wood mouse (*Apodemus sylvaticus*). (© M. Amphlett, with permission)

sence of this essay when Burns apologises to the stricken mouse: "I'm truly sorry man's dominion, has broken Nature's social union." Anyway, the point is that the wood mouse is a splendid model for exploring the effects of farming on wildlife: it is common enough to provide copious data, mobile enough to move between fields, and, perched midway in the food chain, it is a predator of seeds and invertebrates, and prey to a range of bird and mammal species (e. g. Tattersall et al. 1999a, b, 2002, 2001, Tew and Macdonald 1993).

At one four thousandth of human size, how does a wood mouse perceive the seemingly homogeneous ocean of an industrial cereal field? In total, successive WildCRU projects have gathered about 70,000 'fixes' from radio-tracking the nocturnal movements of a couple of hundred mice (Tattersall and Macdonald 2003). Examining where the mice paused to feed revealed that the crop was not, after all, homogenous: they sought out, and stayed at, weedy patches (Tew et al. 2000). Herbicides are designed to kill exactly these plants, but might some compromise mend Nature's broken social union? Tew et al. (1992) tackled this question with field experiments on "conservation headlands" – headlands being the edge of the crop where the tractor turns, and where generally lower yields offer cheaper scope for conservation intervention. As they traversed the experimental plots, radio-mice not only preferred headlands near the sanctuary of the hedge to the fully-sprayed mid-field, but while their greatest preference was for unsprayed plots, they spent almost as much time in plots sprayed with a *reduced* cocktail of herbicides that allowed some plants (and thus invertebrates) to survive: offering a compromise to farming and wildlife (Tew et al. 1992) (Fig. 21). The point is that by starting with the detail we can identify the building blocks for a policy to customise the agro-ecosystem we want (Macdonald et al. 2000b). Moving up a scale, uncropped farmland habitats can be more or less joined up. Field margins, for example, ramify, like an arterial system, through the farmscape, where they can be considered either a source of crop pests or a refuge for nature. How might farmer behaviour strike a balance? To answer this, in 1987 we created over 4 km of 2 m wide uncropped field margins at the University Farm at Wytham, and these were either sown with a grass and wildflower seed

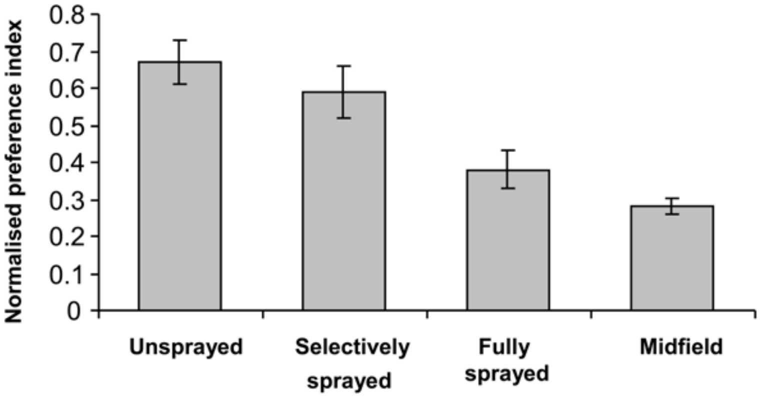

Fig. 21 Normalised preference indices (mean ±SE) for different habitat types, for 12 wood mice radio-tracked at Wytham. Values above 0.3 indicate selection, values below 0.3 indicate avoidance (Tattersall and Macdonald 2003, adapted from Tew et al. 1992).

mixture, or left to regenerate naturally. On these we imposed a range of management regimes, each replicated eight times. Each resulted in different consequences for the plant and animal communities. For example, undesirable annual weeds were suppressed three years earlier on sown margins than naturally regenerated ones, and mowing in spring and autumn led to desirably greater species richness (Smith et al. 1994). Some changes in the plant communities did not become apparent until 13 years after the margins were established (Smith et al. 2010) highlighting the importance of long-term studies. Butterflies, in turn, benefitted from the plentiful nectar supplied by sown wildflower species (Feber et al. 1996), while, for their nocturnal counterparts, Merckx et al. (2009a) showed, in a separate experiment, that double the number of widespread, but declining, moths occur on margins compared to mid-field, but even mid-field moths increase by 60 % when they adjoin wide margins, which support 40 % more moths than do narrow margins. By the way, the fundamental principles of linkage and metapopulation function (Akcakaya et al. 2007, Macdonald et al. 2000a) apply across the size range of organisms, and are writ large in the design of corridors to join up the jaguar reserves of Latin America (Rabinowitz and Zeller 2010) or tiger populations in Bhutan or throughout the Terai Arc (Seidensticker et al. 2010). Further deconstructing the management of farmland corridors revealed, for example, that the best hedgerows for birds are more than 2 m tall and contain more than 10 woody species (Macdonald and Johnson 1995), and that hedgerow trees, landscape features previously unrewarded in agri-environment schemes, are beneficial for both common (Merckx et al. 2010a, 2009b) and rare and localised (Merckx et al. 2010b) moth species. Field margins and headlands are nowadays established options in Britain's agri-environment schemes (Vickery 2009), and in 2008 hedgerow trees were recommended to join the list of funded features.

Furthermore, financial incentives *have* modified farmers' behaviour. In 1981, before payments for environmental services were even a glint in the British government's eye, we asked over 1000 English farmers: "How interested are you in wildlife on your farm?" 40 % replied "very". We also asked whether government, NGOs or farmers were principally responsible for the countryside. This question was apparently considered so silly in 1981 that quite a few farmers struck it out or wrote cynical comments across it: over 95 % of farmers answered that the countryside was primarily their responsibility. Seventeen years later, when Britain was awash with agri-environment schemes, we asked again: the percentage of farmers 'very' interested in wildlife had rocketed to 62 %, but there was almost no change in the attitude that they were primarily responsible for the countryside (Macdonald and Johnson 2000).

Attitude emerged as particularly relevant when we compared pairs of organic and conventional farms to ask which was better for biodiversity. Earlier work had shown that organic crops were weedier than their conventional counterparts and had more spiders (Feber et al. 1998), butterflies (Feber et al. 2007b, 1996) and wood mice (Macdonald et al. 2007d). A much larger-scale study of 89 pairs of organic and conventional farms confirmed these results, demonstrating positive benefits for a range of taxonomic groups across a range of scales (Fuller 2005). Organic farms differ in a number of ways from conventional farms (Norton et al. 2009) and disentangling the features which affect biodiversity is fraught with complexity. For example, both habitat extent and farm type (organic or conventional) were predictors of some bird species in the study (Chamberlain et al. 2010). Some features of organic farms are dictated by their procedures, but others, like greater likelihood of joining agri-environment schemes, suggest that the organic farmer's mindset is an asset to biodiversity, and raise the possibility that, where there's a will, there could be a way, to transplant some benefits of organic farmland into conventional practice. However, as always, there is an alternative perspective: organic cereal yields are 60–70 % those of conventional farms and so, all else being equal, need more land and, per product unit, may have higher environmental impacts (Köpke et al. 2008, Mondelaers et al. 2009, Tuomisto et al. 2012).

Moving up another scale, just as a mosaic of fields comprises a farm, so a mosaic of farms comprises a landscape. Would there be value in agri-environment policies that targeted farms to foster joined-upness? To answer this, WildCRU's Upper Thames Project established two areas where neighbouring farmers were encouraged, and assisted, to enrol in agri-environment schemes, which paid them to undertake environmentally friendly management. In two control areas, scheme uptake was *laissez faire*. While wide margins and hedgerow trees can have positive impacts on moth abundance and diversity (Merckx et al. 2009a, b, 2010a, b), this experiment showed, crucially, that the effect of hedgerow trees on widespread moth abundance and diversity was significantly stronger where farmers had been targeted (Merckx et al. 2009b) (Fig. 22). Furthermore, we found that AES aimed at increasing overall biodiversity in intensive agricultural landscapes have the potential to not only benefit common, widespread habitat generalists, but some rare and more endangered species as well (Merckx and Berwaerts 2010, Merckx et al. 2009b). So, area-specific targeting of agri-environment schemes seems to increase landscape connectivity in ways that enhance the beneficial effects of habitat features – providing the taxpayer with better returns on their environmental investment.

5. Instruments for Changing Human Behaviour

Playing the benign Dr Jekyll to the Evil Quartet's Mr Hyde is WildCRU's Conservation Quartet, which includes research to understand the problem, education to explain it, community involvement to ensure participation, and implementation of solutions (Macdonald et al. 2000c). These ingredients occur in all the projects I've reviewed in this essay, and they are relevant whether we consider species or ecosystems. On the road to sustainability there is an iterative process flowing from problem to solution (Fig. 23, a model elaborated by Macdonald and Sillero 2004).

Imagine a species in conflict. Problems can be partitioned between reducible and irreducible elements, and the balance between these will shift as currently intractable elements are rendered reducible by innovation (itself engendered by the research component of the Conservation Quartet). Mitigating reducible problems minimises current conflict, the residue being the currently irreducible problem. Depending on levels of tolerance, themselves heavily influenced by education, the problem will be either bearable or not. The unbearable component will require an interim solution. Options are either to control (often, but not necessarily, to kill) the problematic creature, or to compensate the aggrieved stakeholder. Of course, this model is grossly simplified – its purpose is to manage the messiness of the collision between Darwin's gloriously tangled bank and mankind – in reality everything interacts. Long-term solutions to conflict can be resolved by the interweaving of: education which necessitates information (ultimately from research), regulation which necessitates

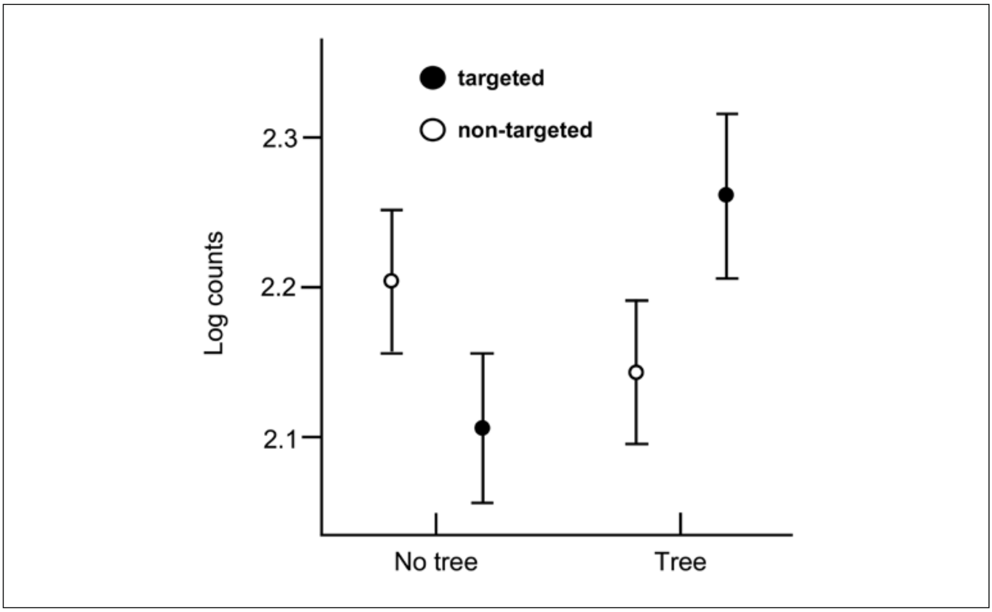

Fig. 22 Moth counts (log $N + 1$) (with SE) contrasting the effects of presence/absence of hedgerow trees on moth abundance in areas where farmers had (●) and had not been (○) targeted (Merckx et al. 2009b).

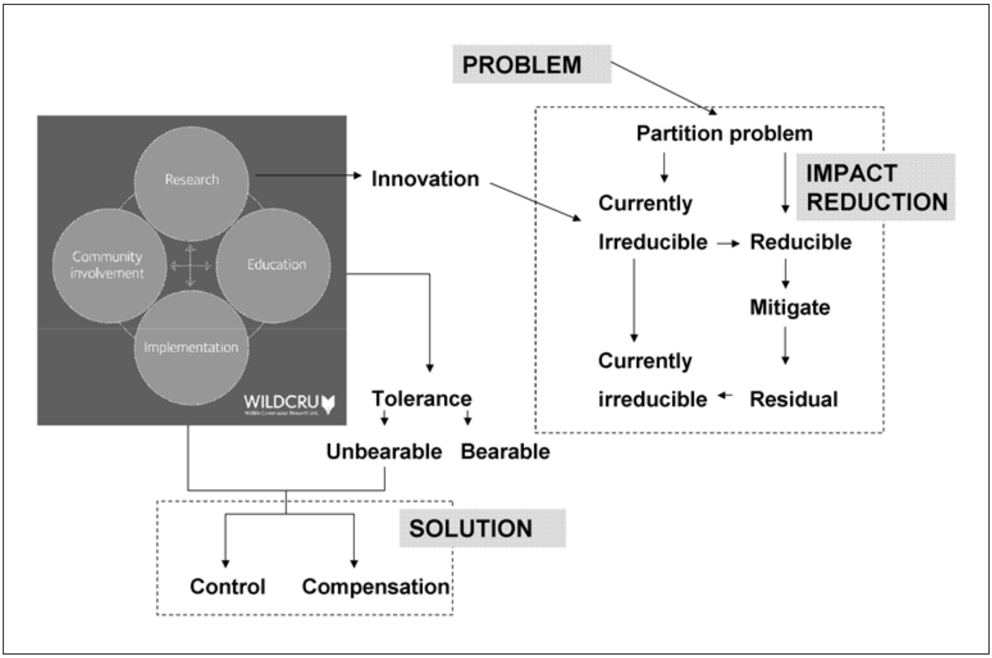

Fig. 23 Iterative process flowing from problem to solution for a species in conflict (modified from Macdonald and Sillero 2004) (Fig. 23.3 from "Biology and Conservation of Wild Canids" by Macdonald and Sillero-Zubiri 2004, by permission of Oxford University Press)

enforcement, and incentivisation, which provides a basis or need for valuation, such as a market. Glibly, "This *is* it", "It'll *cost* you to do it", and "It'll *pay* you to do it".

Hitherto, many solutions have been about stopping the rot. But I wrote this essay in 2010, the year when humanity failed to deliver the Convention on Biodiversity's target of 'significantly reducing' biodiversity loss (Sachs et al. 2009, *Secretariat of the Convention on Biological Diversity* 2010). I think the time is ripe, for conservationists too, to be more audacious in their hopes, and to turn from holding the line to repairing the environment. Repairing the environment will involve the restoration of habitats, of species that are threatened and locally or globally extinct in the wild, and of entire functioning communities; all important emerging fields in practical conservation (Macdonald 2009, Macdonald et al. 2002). Here, concepts of individual behaviour (Mathews 2005), animal health (Mathews 2006), animal welfare and stress (Gelling et al. 2010, Moorhouse et al. 2007) and disease (Gelling 2010) all play a part, as does the human dimension that is an inextricable element of 21st century conservation (Macdonald 2009). The extent of preparation and planning cannot be underestimated, as exemplified by the trial release of two beaver (*Castor fiber*) families in Scotland in 2009, which was preceded by over a decade of feasibility (Macdonald et al. 1995, 2000d) and simulation studies (South et al. 2000). There will be a need for the creative use of naturally protected areas where endangered species may be safeguarded from the negative impacts of invasives (as in the establishment of an island sanctuary for the highly endangered European mink (*Mustela lutreola*), in Estonia (Maran et al. 2009), and there will be inevitable limitations on the space available.

An exciting initiative with which my team is involved is the plan to restore the Highland ecosystem at the Alladale Wilderness Reserve (www.alladale.com) in northern Scotland, which includes as a long-term aim, the reintroduction of carnivores, omnivores and large herbivores such as wolves, wild boar (*Sus scrofa*) and elk (*Cervus canadensis*). Human interests and the potential for conflict are such that the species will be retained within a large fenced area. A small experimental release of boar into small fenced areas has already highlighted how the introduction of a native species may promote habitat restoration, in this case by re-establishing a habitat disturbance regime through the boar's rooting behaviour (Sandom et al. 2013a, b). Model simulations have been used to explore whereabouts on the scale of zoo to wilderness a fenced reserve should be in order to allow relatively natural interactions between predator and prey, while also taking into account what management options could be used to cope with potential problems such as predator extinction through over-exploitation of prey in spatially-restricted reserves (Sandom et al. 2012). Indeed, Sandom et al. (2012) explore, in the virtual reality of a GIS analysis, the options for establishing a large, fenced wilderness reserve in Scotland. In South Africa, reintroduced wild dogs are regularly moved by humans between separate fenced reserves (Davies-Mostert et al. 2009). The ideal future outcome will be the eventual restoration of wild dog populations over a much larger connected area, but the current artificially managed metapopulation is seen as a necessary interim solution (Davies-Mostert et al. 2009). Clearly there are questions about what is 'natural', and what exactly it is that we are trying to restore. Recreating conditions that are truly pristine (in the problematic sense of being devoid of human influence) is patently fantasy, and ever more so as humanity's footprint becomes heavier, and the pragmatic reality is probably that restoration is more about creating a new future than recreating the past (Macdonald 2009).

Several of the studies considered in this essay concern the building blocks of solutions; they must be assembled into an ambitious cathedral. On one hand, this will involve undertaking conservation on swathes of land that are at a seriously large scale – such as the Panthera Foundation's plans for creating those corridors for jaguars in the New World and tigers in the Old (Macdonald et al. 2010b, Rabinowitz and Zeller 2010). For example, our Zimbabwean lion study aspires to become the hub of just such a network for lions and leopards radiating from Hwange – the need is made clear by the 3,500 km wandered of one GPS-collared dispersing male (Macdonald et al. 2010b) (Fig. 24).

On the other hand, the future must involve devising markets that attach value to biodiversity and deliver payments for ecosystem services (Macdonald 2000, Barrett et al. 2013). Where values and payments are missing the environment is considered to be free and so we spend our natural capital as if it grew on trees. Global financial write-downs over the years of the banking sector crisis were estimated at $4 trillion (*International Monetary Fund* 2009). However, every year an estimated $2–5 trillion of natural assets are lost from

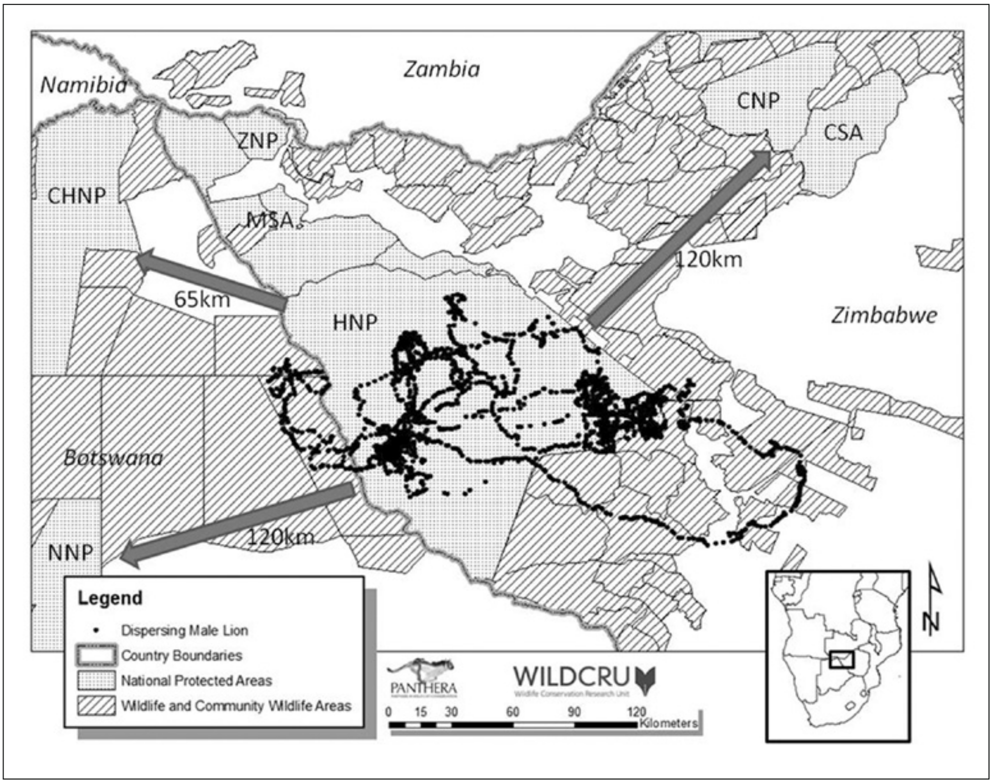

Fig. 24 Map of corridor areas leading from Hwange National Park (indicated by arrows and distances) potentially allowing dispersal of lions between protected area complexes in the region. Also shown, for context, are movements of a GPS-satellite collared 4 year old male lion between October 2007 and February 2009. CHNP = Chobe National Park, NNP = Nxai Pan National Park/ Makgadikgadi Pans National Park complex, HNP = Hwange National Park, MSA = Matetsi Safari Area, ZNP = Zambezi National Park, CNP = Chizarira National Park, CSA = Chirisa Safari Area. Inset map shows location in southern Africa. From Macdonald et al. (2010b). (Fig. 29.6 from "Biology and Conservation of Wild Felids" by Macdonald, D. W., and Loveridge, A. J., 2010, by permission of Oxford University Press)

deforestation (Black 2008) according to writers of "The Economics of Ecosystems and Biodiversity" (TEEB) project. TEEB is an impressive project but more work is required to produce figures which convince the world that they are not abstract academic dreams and are no less important than has been the banking crisis. At a fine-grained scale, a key point is to consider the marginal value to conservation of each extra unit of investment – a principle that Dutton et al. (2010) apply to restoring water vole habitat. Ask yourself how much we ought to invest to protect one hectare of a vast arboreal forest and then consider how much you might invest to protect a hectare of a relatively small biodiversity 'hot spot'. Relative scarcity ought to affect efficient spending (ecosystem prices) per unit and that is where accurate measurements of "marginal" values are vital as described by Dutton et al. Payments for Ecosystem Services already operate at scales from moths to lions (Maclennan et al. 2009, Merckx et al. 2009b), and have generated a rich literature in Environmental Economics (Macdonald et al. 2010b, Pascual et al. 2010, Barrett et al. 2013).

At a broader scale, markets in carbon offer huge potential to generate funds for wider environmental benefits – the UN's Reduced Emissions for avoided Deforestation and Degradation (REDD) mechanism is currently the trail-blazer (Parker 2009). Carbon offset payments could, for example, be used to secure the protection of pristine forest, such as Sulawesi's Nantu National Park where Clayton and Macdonald (1999) described the only known communal salt lick of endangered babirusa (*Babyrousa babyrussa*). However, currently REDD is formulated purely as a carbon management instrument, and it remains to be seen whether the conservation community's hope that it will fund biodiversity can be fulfilled (Collins et al. 2011a).

It is not surprising that the mechanism for modifying human behaviour towards nature lies in economics (Pearce et al. 2007), or that biodiversity conservation, human development and poverty alleviation are inseparable (Macdonald et al. 2007a, Sachs et al. 2009). Uncomfortably, however, delivering together biodiversity conservation and community development, a goal that trips expediently off the tongue, may often be difficult in practice (Macdonald and Willis 2013b). Implementing economic incentives to conserve presupposes a number of challenging societal functions, such as the clear allocation of property rights (Barrett 2001, 2008), facing up to opportunity costs (Norton-Griffiths 2007), and functioning regulatory systems – the inadequacy of the latter being the nub of Wasser et alia's (2010) argument that relaxing restrictions on trading ivory was uncontrollably perilous for elephant conservation. Macdonald et al. (2010b) discuss how economic instruments are central to the conservation of endangered felids, and Dickman et al. (2011) elaborate the concept of Payments to Encourage Conservation. Regions suffering biodiversity threats and poverty often overlap. Recognising the essential role that biodiversity and ecosystem goods and services play in sustainable development, the United Nations' Millennium Development Goals incorporated the CBD's '2010 Target' to halt biodiversity loss, as a stepping stone to their objective of halving extreme poverty by 2015 (Sachs et al. 2009).

Economics is clearly crucial to conservation. But economics, as Oscar Wilde did not quite say, is about value as well as price, which brings us back to education. Education is as important as the self-interest of markets in modifying peoples' behaviour. Conservationists can deliver it in forms far from a classroom: WildCRU's lion theatre group has performed to more than 5,000 village children in Zimbabwe (Telford 2006). In Ethiopia, the Ethiopian Wolf Conservation Programme opened the Ethiopian Wolf Sports Centre (www.ethiopianwolf.org), while in Oxford's Wytham Wood, rehabilitated addicts have been taught the skills of mammal monitoring (Newman et al. 2003). In some cases, however, the classroom may be the best place for conservation. Marchini and Macdonald (in prep.) have shown that school-based communication interventions based on lectures, group discussions and tailor-made resource materials can have a powerful effect on perceptions of jaguars among pupils, and that pupils can effectively transfer that effect to their fathers. By comparing the effects of conservation messages delivered *via* a conservation organization and *via* local rural schools, the authors found that landowners on the Amazon deforestation frontier were influenced not only by the information explicitly conveyed in the content of the communication materials, but also by the implicit message that jaguar conservation was supported by a community institution (the local school), and probably also therefore by other community members. The finding that pupils can influence their fathers' perceptions of jaguars suggests that conservationists can use rural schools to reach at once tens of students in a classroom, or hundreds on the school's soccer pitch, who will in turn transfer the conservation message to their fathers. Given the logistical challenge of visiting landowners one-by-one at home in rural Amazonia, this strategy might be relatively cost-effective. In short, the goal of conservation education is to inform and thus modify peoples' attitudes and thereby behaviour.

We also need to bear in mind that human behaviour is not always rational. Economists used to base many of their models on the assumption that it was. The Nobel prize-winning work of the behavioural economists Daniel Kahneman and Amos Tversky revolutionised thinking in this field (Kahneman and Tversky 1979). Their 'prospect theory' encapsulated the influence of systematic biases in human decision making based on assessments of risks and gains. These ideas have not yet been fully exploited in inter-disciplinary conservation. Stuart Sutherland documented the pervasive influence of irrationality in human behaviour (Sutherland 2007), and former WildCRU graduate, Dominic Johnson, has applied his training in animal behaviour (Johnson et al. 2002) in an evolutionary analysis of people's tendency to be over-optimistic about their chances of winning a war (Johnson 2004). We see in many of our conflict case histories that attitudes to wildlife are not based on entirely rational judgements about the damage that pests do, or the cost of dealing with it.

In undertaking a journey it is well to keep in mind the destination. What is the wider context for the Case Studies reported here, and despite all the worries is there an optimistic vision for the future and a call for positive actions to realise it? Taking the long view, where might humanity hope to reach with the biodiversity that supports it? One answer might be a human population enjoying a healthy, equitably high and sustainable standard of living, alongside functioning ecosystems populated with 'natural' levels of biodiversity. This vision for human well-being doubtless relies on advanced technology to sustain people in cleverly engineered 'green' towns, supported by sophisticated communications networks. It relies on human ingenuity and rationality, confounding Hamlet's famous caution (Hamlet, Act 1, Scene V; Shakespeare [1601] 1959). When it comes to saving the environment, and thus ourselves, we must find "more things in heaven and earth" than have so far "been dreamt of in" our "philosophy". Phrasing a scientifically-based, environmentally sensitive and humane progressive environmentalism will be the great scientific and political challenge of the immediate future. As David Orr (2003) observed: "We do not have an environmental crisis so much as we have a political crisis."

Delivering an optimistic vision will also rely on valuing the inspirational, even a feeling of the spiritual, in Nature. Optimising the solutions will require daunting cost-benefit analyses – perhaps the environmental analogue of QALYS – the Quality Adjusted Life Years used to inform tough decisions in medicine. If each person is to enjoy a satisfyingly high standard of living, then the only way this can be achieved while leaving sufficient space to deliver the associated vision for the natural world (itself a prerequisite for the desired well-being of the people), will be for the world eventually to be inhabited by fewer than the current number of people. Not everyone agrees that human population is the immediate challenge for the future. Some environmentalists rightly note that upward trends in carbon output are steepest where human population growth is slowest, and that the emphasis should be on consumption, not population (http://www.monbiot.com/archives/2009/09/29/the-population-myth/). It is true that at today's rates of consumption, slower population growth of people in poor countries would make relatively little difference to global human footprints, because shoe sizes are disproportionately large amongst the rich. However, if we look to a fairer future world – as we should urgently do – then everybody's footprint will increasingly matter. While it is obvious that it is our consumption of resources, rather than merely our numbers, that determine the environmental impact of humanity, and its sustainability, it is surely also obvious that whatever that average (and hopefully increasingly equitable) per capita impact, the likelihood that it will be sustainable alongside a fully and functionally diverse Nature decreases with the size of the human population. The pitfall within the previous, well-intentioned but almost platitudinous, sentence is that equitability is easily undefined. WWF estimates that for the world's population to live at the same standards as people in North America and China, based on their ecological footprints, would require five worlds worth of resources (*WWF* 2008). Since five worlds (or the technology to produce their resource equivalent) are currently not available, a simple approximation is that equitability today might require each human to have an environmental footprint roughly one fifth the size of a contemporary American. Worse, geopolitical, climatic and transport differences, mean that for citizens of poor, desert countries to enjoy the same standards as those in temperate developed ones would require a bigger share of resources, leaving less for those of us in currently developed countries. With such complexities in mind, and to echo Robert May's (2007) measured understatement, if we accept the ethical responsibility of bequeathing a planet rich in natural wonders to future generations, the diverse patterns of human population and consumption lead to complex challenges for human cooperation.

Whether the emphasis is consumption or human numbers, most of the alternative outcomes are unpalatable. Political compulsion and the New Testament mechanisms of famine, pestilence and strife are horrific. The only hopeful road to this goal is one of phased population reduction and concomitant curbs on consumption (along with a hope for similarly near-miraculous levels of technological innovation) over many generations. This would require an inter-generational pact for which there may be no precedent in human history or evolution. The cynical reader will understandably wonder how this pact might be reached on such an emotive subject amongst squabbling apes. By raising this question, this essay illustrates how the remit of conservation biology has, in just a few decades, expanded from its roots in classical ethology and ecology, to grapple nowadays with the greatest scientific and political challenges of the era.

6. Conclusions

To draw for a second time on Herbert Spencer: “No one can be perfectly free till all are free; no one can be perfectly moral till all are moral; no one can be perfectly happy till all are happy” (Spencer 1851). Such notions of perfection may be the province of abstract – even silly – philosophy, but at a more practical level this essay seeks to offer a small pointer en route. From foundations that include the best of ethology, the examples have spanned from mice to men, towards a journey that unites disciplines, links biodiversity conservation, sustainability and development, and makes the leap from science to practice. It’s a big jump, but there’s no choice.

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Sources of Productive Questions: Experiences of a Primatologist

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With 4 Figures

Abstract

When in the 1960s the study of primate behaviour was taken up by anthropologists it opened the way to field work, but it lost the experimental methods of ethology. The emphasis on observation of 'undisturbed behaviour' in the wild, soon coupled with sociobiology, neglected the analysis of proximate causes.

Members of primate groups interact on the basis of what they have learned about one another in their lifetime. They do not need to demonstrate this knowledge at every occasion. Intention movements suffice. Routine interactions of group members are just low key hints at these foundations. During routine interactions motivations are moderate and shift according to changing situations. Complete and intense sequences of behaviour emerge only when actors are confronted with a specific and urgent social problem, particularly with unfamiliar conspecifics. It takes specific challenges to elicit a single behavioural system in full intensity while closing down others. This paper describes my personal experience about what bred core questions in projects of my own working group. I am no longer familiar with recent primate research and therefore quote few other authors, for which I apologize.

Zusammenfassung

In den frühen 1960er Jahren eröffneten Mitarbeiter des amerikanischen Anthropologen Sherwood Washburn eine Reihe von beschreibenden Verhaltensstudien an natürlichen Gruppen freilebender Affen. Sie beschränkten sich bewusst auf die Beobachtung ‚ungestörten Verhaltens'. Ethologen hatten sich, außer dem Pionier Adriaan Kortlandt, bis dahin kaum mit freilebenden Primaten befasst. Die Primaten-Feldstudien orientierten sich bald auch an evolutionstheoretischen Voraussagen. Die proximaten Ursachen des Verhaltens, die in Niko Tinbergens vier Warum-Fragen noch enthalten waren, blieben in diesen Studien weitgehend unerforscht.

Nach meiner Erfahrung ist die Beobachtung ungestörten Verhaltens ein unerlässlicher und langer erster Schritt, aber man muss aus folgenden Gründen nicht dabei stehen bleiben. Wie ein Primat sich zu einem Gruppenmitglied verhält, wird vom Ethogramm der Art bestimmt, hängt aber auch wesentlich davon ab, was er im gemeinsamen Leben über das andere gelernt hat. Er braucht dies nicht bei jeder Interaktion mit dem anderen zu demonstrieren. Meist genügt eine Intentionsbewegung. Alltägliche Interaktionen zwischen Gruppenmitgliedern sind nur leichte Hinweise auf dieses beiderseitige Wissen. Vollständig und intensiv interagieren die Partner nur, wenn sie mit einem spezifischen, dringlichen Beziehungsproblem konfrontiert werden. Erst eine solche besondere Herausforderung löst ein motivational und funktional einheitliches Verhaltenssystem in seiner vollen Intensität aus und setzt andere Motivationen unter Hemmung. Solche Herausforderungen sind im Alltag selten, aber man kann sie nach genügender Beobachtung im Freiland gezielt stellen und damit ein bislang nur vermutetes Verhaltenssystem beobachtbar machen. So findet man Hypothesen, die man im Experiment prüfen kann, und die nach meiner Erfahrung der Wirklichkeit näher kommen als im Voraus am Schreibtisch erdachte Hypothesen darüber, wie sich Tiere in einer bestimmten Situation verhalten ‚sollten'. Dieser Artikel beschreibt, wie wir in unserer Forschungsgruppe zu zielrichtigen Fragen kamen. Ich bin mit der neuesten Primatenforschung nicht mehr in vollem Umfang vertraut und zitiere daher wenige andere Forscher.

1. Introduction

I recently attended a college lesson given to 17 year-old high school students. The topic was cognitive ethology. The teacher showed films of famous experiments on the "Theory of Mind" in primates and then asked the students to interpret the animals' behavioural responses. The students' answers were unusually sharp and imaginative and their suggestions addressed many more motivations than the one the researcher had aimed to expose. The reason was equally unusual: The teacher had not told the students the questions, which the experiments were supposed to answer. A question sets a focus, but it also narrows the horizon and channels our thinking.

At a recent scientific conference, several speakers began with the remark: "Such and such theory predicts that [...]" and then presented their data. Some data conformed to the prediction. When they did not, the speakers seemed a bit helpless. Is the theorem defective? Do the animals solve the problem with causal mechanisms other than the expected ones? Or do causal constraints prevent them from behaving according to the theory?

In the wake of sociobiology the functional aspect of behaviour has become the dominant view particularly in primate field research, at the cost of proximate causal mechanisms, which are often alien to our thinking and require complex experiments. In other words: We understand the problem to be addressed by an experiment, but have difficulties in even imagining the underlying causal mechanisms addressed by the experiment, which are possibly quite different from ours.

I was trained in the field of developmental biology of amphibians and insects. This branch of zoology investigated proximate causes in the ontogeny of an individual organism. Developmental biologists began by observing the gradual differentiation of a fertilized egg into a mature organism and got their results by experiments. Observations and experiments were my tools when, after my doctoral thesis in 1960, I turned to the study of primate social behaviour. Most fieldworkers at that time were anthropologists and had no experimental tradition. Jane Goodall had begun her observations with exemplary patience, refinement and intuition on Gombe chimpanzees she knew individually. Such careful observations had been the approach of early ethologists like Niko Tinbergen; he and others did not stop there, but explored the causal mechanisms underlying the observed behaviour experimentally.

The following example illustrates how premature questions can mislead observers in what they observe. Recently, students of decision-making in travelling primate groups have asked which group members 'lead' a group. One study found that males made more proposals, by moving ahead in front of the others, but these males were not more often followed than females. The anthropomorphic term 'leading' evokes the image of an individual that walks ahead and determines where the group will go. This is only one of several ways to direct travel. It applies to some ungulates, but not necessarily to all primates, let alone humans. In 1960 we spent months of focal observation on hamadryas baboons (*Papio hamadryas*) before they set out from their sleeping cliffs for the day's travel. We found that travel decisions were primarily made by adult males. There were two male rôles: Initiators, who set out in a given direction as if making proposals, and deciders, mostly old males, who did or did not follow. Only when these old males followed did the troop depart. These old deciders rarely initiated a departure, but when they did, the whole troop followed their direction at once; the younger males overtook the deciders and walked in front of the group in the directions the old males had indicated (Kummer 1968, Stolba 1979). In the statistical analysis, the decision making power of the few old males was swamped by the much more frequent inputs by younger prime males. Only patient observation found the counterintuitive facts that preconceived theories and questions would have missed. What I learned was: First observe, then theorize. Use your intuition alongside with your intelligence, and note down your thoughts, impressions and questions that come to your mind. The original meaning of the Greek word ‘theoria’ is ‘observation’ or ‘contemplation’, which includes the subjective powers of the observer.

One may hypothesize that a group ‘plans’ its daily route, but the far more interesting question is how the group ‘plans’. The seminal work by von Frisch (1950) on how honeybees inform stock mates about the distance and direction of a new food source is one of the most fascinating studies in animal behaviour. No theory could have predicted their way of communicating; only observations could discover the wagging dance, and only subsequent experiments could decipher the encoded messages. Animal communication systems are qualitatively so different from ours that our imagination cannot readily envisage how they work. Chimpanzees are our closest relatives, but when cognitive psychologists find that they solve a particular problem we cannot simply assume that they solve it with the same mental tools that humans use (see final section).

In most sciences, researchers begin by observations and only then develop a theory in the modern sense of the word. This is true in physiology, medicine, and psychiatry. Wondering why some branches of behavioural biology place theory first and only then observe I suspect the following: We are conscious of some of our own behaviour. We can mentally compare alternatives, goals, and outcomes of our future behaviour, and we can do this even for an animal by putting ourselves in its place at the possible cost of anthropomorphism. In contrast, we have no comparable first-hand knowledge of even our own physiology that would tempt us to theorize aforehand about what erythrocytes or the liver should do. Sociobiological theories contribute an important dimension to biological thinking, but it seems wise not to predict how an organism ‘should’ behave before one has thoroughly studied it.

In my doctoral thesis I tested Pearl’s (1922) Rate of Living Theory. It had been derived from anthropomorphic reasoning and predicted that an organism should die earlier if its life was physiologically strenuous. I tested this hypothesis on two mutants of the fruit fly *Drosophila melanogaster*. The ovaries of adult females develop from primordial tissues in the larvae. This is true also for the *fes* (female sterile) mutant. I implanted primordial ovaries of female larvae of the fertile strain into larvae of the sterile mutant. During metamorphosis the implants developed into fertile ovaries so that the genetically sterile flies became capable of laying eggs. According to Pearl’s theory this should have shortened their life span. It did the contrary; the production of eggs *extended* the life span of the operated flies. In contrast, larvae into which I had implanted additional fatty tissue that gave them additional nutritional reserves did not live longer than controls. Longevity was apparently promoted not by fat, but by cell divisions in additional active primordia (Kummer 1960). The result did not conform to the prediction of Pearl’s anthropomorphic theory.

In my time, ethologists observed before they experimented on preset hypotheses. Nowadays granting agencies demand that applicants submit specific questions at the outset, but initial behavioral observations or pilot studies are normally not financed. I was more lucky. At the beginning of my field research on hamadryas baboons the Swiss National Science Foundation granted a year of observation based on only the most general questions. In the following chapters 2 – 5, I will outline four methods that generated productive questions.

2. Observation of 'Undisturbed Behaviour' in the Wild

The observation of 'undisturbed behaviour' was the credo of the first field primatologists. It is the indispensable beginning, but it must not be the only and final method. We want to identify the adaptive behavioural systems evolved for coping with specific social or ecological problems. Most of the time, the motivations of animals in the wild are moderate, and no single motivation dominates all others. For example, social relationships once established do not demand constant explicit actions. From the viewpoint of a researcher interested in specific behavioural systems 'undisturbed behaviour' is in fact disturbed by frequent changes between different low motivations. Sometimes, certain actions nevertheless suggest a problem or solution we have not so far thought of. One should therefore not design quantitative data collections demanding so much attention that the observer has no time to notice tell-tale scenes. I stipulated that all team members noted such qualitative hints and guesses after every observation period or experiment. These qualitative notes were sometimes crucial in interpreting the quantitative data.

Observing is more than recording. When focusing on an individual for some time one cannot help putting oneself in its place and ask: Why does it do that? One conceives the animal as a subject, somewhat strange, but nevertheless a fellow primate, not an object. Together with long objective recording such empathy feeds our intuition, which stores and analyses thousands of scenes in subconscious form. Of course, our empathy and intuition are also anthropo*morphic* like everything we do and think, but they are not anthropo*centric*, not narrowed and patterned by our intellect. Experience taught me the conditions that I must fulfil before the store of intuitions contributes good questions. I first had to think on the data and a problem for several consecutive days with high concentration. When I then went for a walk the store spontaneously produced a half-forgotten scene or an idea that could explain the problem at hand, sometimes surprising the intellect, but most often confirmed by further research.

3. Anecdotes

An anecdote is a sequence of behaviour that strongly suggests an interesting interpretation outside of our usual expectations. De Waal (2005, p. 143) discovered reconciliation in a single observation when one of his male chimpanzees had attacked a female. The attack caused a great commotion. Other males came to the female's defence. Then a long, unusual silence followed until the attacker approached the victim. The two kissed and embraced. The term 'reconciliation' came to de Waal's mind. In subsequent years, many researchers found that a quarrel between two primates is often followed by a friendly exchange among the same actors above chance. Cords (1992) has shown by experiments on long-tailed macaques (*Macaca fascicularis*) that friendly acts after a quarrel do re-establish good relationships. She tested 10 pairs of females. For each test, one pair was released into a large cage where two drinking bottles with sweet liquid hung above a sitting perch. The shortest distance at which a given pair of females readily drank simultaneously was chosen as the measure of their tolerance. At shorter distances, the dominant female would not tolerate her partner to drink at the same time. In subsequent tests, Cords provoked an aggressive conflict in a separate room by giving a titbit to the subordinate while the dominant watched. After the conflict, the pair was admitted to the room with the bottles. The distance tolerated while co-drinking was now significantly greater than before. If, however, the pair was allowed a friendly reunion after the conflict, tolerance was restored to baseline levels.

Unfortunately, good anecdotes are rare. Several primatologists reported rare observations suggesting that a primate deceived another to his own advantage as if he knew that the victim was ignorant of the real situation. Byrne and Whiten (1990) invited a large number of primatologists to contribute their respective anecdotes. The collection was impressive and suggested that at least chimpanzees and baboons use tactics that are analogous to human deception.

4. The Method of Challenge

If one wishes to assess the performance of a high jumper one will not observe his ‘undisturbed behaviour’, but challenge him by the specific situation, say, of a contest. Generally, wild animals do not deploy their full potential of coping with an urgent situation unless they are challenged by an intense situation aimed exactly at the response system in question. After sufficient observation, a researcher can make a good guess of how his animals might cope with a critical situation, and he can devise a challenge that evokes an intense coping reaction. I shall give two examples.

In the first example, a challenge revealed an unexpected deep order of building social structures in several cercopithecine species. At the Delta Primate Center (Covington, Louisiana, USA) we had a colony of gelada baboons (*Theropithecus gelada*). They had been captured as adults in the wild. Thus they had acquired the full social competence of their species, unlike many lab-born chimpanzees that are presently tested for their cognitive abilities. The challenge for the geladas was to establish social relationships with unknown conspecifics. They had to use their innate and learned social programs for building new relationships with these strangers.

We convened groups of two and three individuals (Kummer 1975). Coworkers recorded the sequences of the geladas’ interactions while I focussed on the large-scale developments. It soon emerged that the *frequencies* of interactions were unimportant. The strictest order was the *sequence of the first occurrences* of behaviours in each dyad: The first aggression, if it occurred, always preceded the first presenting, followed by the first mounting, followed by the first grooming, and, rarely, by the first embrace. This sequence was the same in female-female, male-male and female-male dyads, regardless who of the pair members was first to introduce the next behaviour of the sequence. There were almost no exceptions. The challenge had revealed an order never seen in the ‘undisturbed behaviour’ of established groups.

My interpretation was: Each first occurrence of a new behaviour marks a step in the development of the relationship from the original antagonism to the stage of confidence and friendly behaviour. Male-male dyads always began with the agonistic stage and at best reached the intermediate sexual interactions, often taking hours. Female-female dyads were more compatible. Some started also with antagonisms, but most reached the grooming stage. Female-male dyads were the most compatible, skipped fighting and reached grooming within minutes.

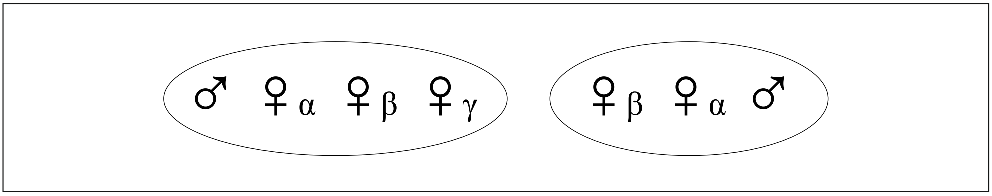

Fig. 1 Spatial arrangement of newly built one-male units of gelada baboons. The thin lines encircle the two units each consisting of a male and his females. See text for explanation.

In the wild, geladas live in one-male units. We now convened two males and several females. While building the two one-male units, the geladas began to arrange themselves in a straight line with one male at each distant end and the females strung out between them, each alpha female nearest to her male, and the two lowest ranking females at the centre (Fig. 1).

Thus, every female could and did physically prevent interactions between her superior and her inferior group members. This spatial arrangement gradually disappeared as the groups became stable in the following two weeks. The geladas now grazed in a free scatter as they do in the wild. We then reintroduced uncertainty by removing one female from each of the two groups from the enclosure for 30 min, and then readmitted her. As expected, the line formation reappeared. Confidence about established relationships seemed to make spatial order needless. The challenge exposed the problems that were important to

Fig. 2 Males of the same band compete in a rare conflict over the possession of their females.

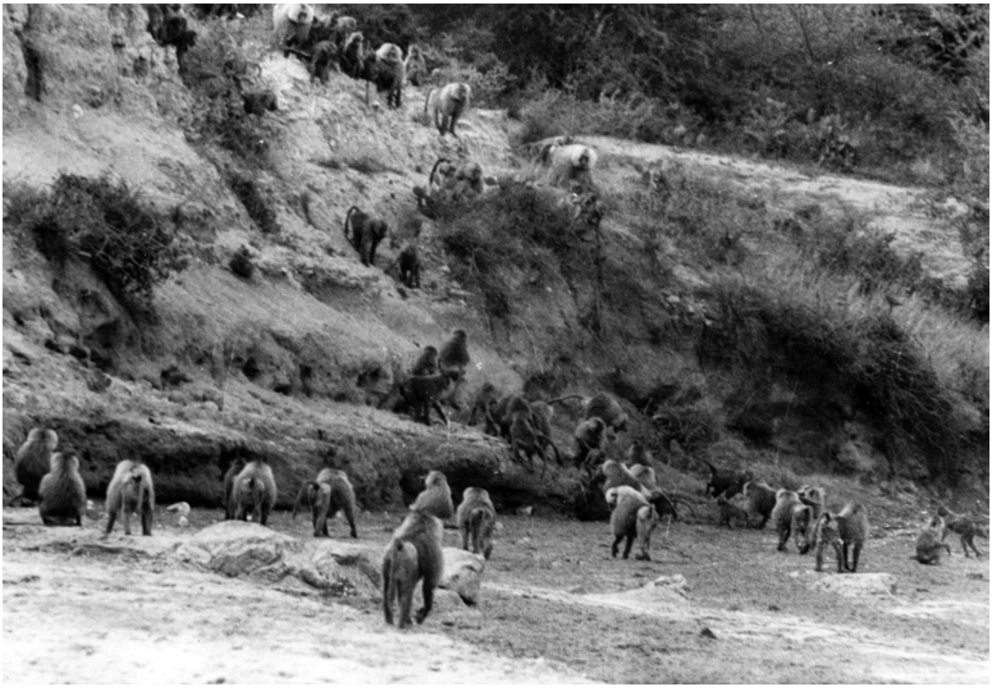

Fig. 3 However, if a conflict *between* bands arises, males of the same band cooperate in defence of their females. The males in the foreground form a front against the band on the slope in the rear.

the baboons and their solutions. It is unlikely that 'undisturbed behaviour' would have revealed these deep orders.

The second example comes from hamadryas baboons. Their social system is organized into four levels (Kummer 1995). The lowest level consists of one-male units; in each of them one adult male guards several females and prevents them from interacting with other males. Fights between males of the same band over females occur, but are generally no more than wild noisy chases (Fig. 2). Yet, males of the same band cooperate in defending their females against males of other bands (Fig. 3).

The social system critically depends on this ability of male competitors to cooperate. One day we challenged this system. We placed a female, unknown to the local baboons, in a cage below a sleeping cliff occupied by several bands. Three males immediately began to climb down. After a few meters, however, the two in the rear stopped and withdrew. The front male approached the cage and eagerly tried to lead the female back to his other females on the cliff. None of the many watching males intervened. After the challenge we returned the female to her own band.

The restraint of the two rear males was unexpected. If their withdrawal was not a coincidence, it meant one of two things: Either the approaching male was dominant over those who withdrew, or the latter were inhibited by seeing the first one closer to the female. The challenges were repeated with other females on other cliffs with the same results. Later, formal experiments rejected the dominance hypothesis and agreed with the inhibition hypothesis (see next section).

5. Experiments

Like a challenge, an experiment increases one motivation, but in addition, it excludes stimuli that would activate other motivations. It gives the most decisive answer to a question, but only a good question is worth the considerable intellectual and technical effort. Control tests must be devised that exclude other hypotheses than the one we have derived from observations, anecdotes, and challenges. Finally, the animals should have acquired the relevant competence from their life in a natural group, a requirement generally disregarded by Cognitive Psychologists who have not taken the pains of observing their animals in the wild.

The challenge in which we presented a caged hamadryas female to bands suggested the hypothesis that a male hamadryas baboon who has seen another male with a new female may be inhibited from interacting with her. Inhibitory effects have been amply demonstrated in behavioural physiology, e.g. of rats. We did the experiments in enclosures at our field station in the Awash National Park (Ethiopia) on baboons trapped in the wild. After the experiments all baboons were released into their original troops.

In each test, a female and a male, termed the ‘owner’, unknown to each other, were released into a large enclosure in our camp. After 15 min, a second male, termed the ‘rival’, was allowed to observe the pair for another 15 min and was then admitted to the pair into the enclosure (Kummer et al. 1974). The possible effects of dominance among the males were controlled in the following way: Each dyad of males was tested twice. In one test, we made A the owner and B the rival; in the second test, with a different female, B was made the owner and A the rival. If dominance were the decisive factor, the same male would acquire the female in both tests, regardless of his initial role.

The results seemed to favour the inhibition hypothesis: The rival attacked the owner and conquered the female in only 2 of 31 tests. The pair mated and groomed while the rival kept his distance and avoided even to look at the pair (Fig. 4). Every few minutes the owner went over to the rival and presented, probably as a reconciliation. This was the behaviour among owners and interested rivals we knew from the wild troops, but it was now performed at a higher rate. However, the males also behaved in ways we had never seen in the wild: The *rivals* consistently turned their back to the pair and avoided looking at the female even when she passed in front of them. They scratched excessively, which is a displacement behaviour in ethological terms. Some rivals gently fiddled with a forefinger at little pebbles, a redirected behaviour in ethological terms. Others gazed straight up at the empty sky – an extreme form of redirected attention.

Owners as well were not aggressive but appeased the rivals. They approached the rival every few minutes, presented and returned to the female. One exceptional owner sat close to the inhibited rival and slowly moved his open palm 5 cm above the rival’s back without touching him, a gesture never seen in the wild and probably an intention movement to groom him. In the wild, leaders of one-male units do not groom one another. One could discard such behaviour as unnatural and, therefore, irrelevant. However, science has gained some of its most important results from producing decisive unnatural situations.

Inhibition is the absence of a behaviour. It is not easy to convince someone that something should be there even though it is not. We, nevertheless, accepted the inhibition hy-

Fig. 4 Testing the “inhibition hypothesis” in wild hamadryas baboons. In the back, the “owner” is groomed by the female. In the front, the “rival” who obviously avoids looking at the pair. See text for further explanation.

pothesis, *first* because the dominance hypothesis was rejected, and we could not think of a third one, and *second* because the exceptional behaviours of males during experiments corresponded with behaviours ethologists had observed in animals under the influence of a motivation suppressed by a more powerful one. We had not seen these behaviours in the field where a rival can keep a distance from a pair and interact with other baboons. However, similar behaviour had occurred in the zoo study on hamadryas (Kummer 1957). Here, the challenge was that the baboons activities were entirely focussed on the social domain. In addition the group included only one fully adult male. Young sub-adult females did not dare to groom the adult male’s mantle but merely sat behind his back and touched the tips of his hair with one forefinger. Sub-adult males did not risk even that; they closely watched the adult male’s mantle for a while, then stepped back and wildly swept the ground with one hand.

The rivals’ inhibition as well as the owners’ appeasement behaviour are likely to be the crucial mechanisms permitting many hamadryas one-male units to coexist and even cooperate in bands of many one-male groups. It is interesting that this inhibition has not found the attention of other researchers on hamadryas baboons.

The experiment led to the new question whether primates also respect *material* possessions. The answer was: Hamadryas and long-tailed macaques do, but only if the owner is able to carry the object (Sigg and Falett 1985, Kummer and Cords 1991).This seems to explain why hamadryas males are careful to keep their females close by making them follow. In human terms, they respect possession but not property.

6. A Problem with Terms: Homology *versus* Convergence

Debates sometimes arise as to whether terms like role, possession or deception are appropriate for animal behaviour. Terms like deception are only anthropomorphic labels for realities we hardly ever fully understand. A label is not identical with the content of the bottle; the common tendency to reify them even in scientific discourse must be resisted. Whether animals ‘really’ deceive, respect, or attribute knowledge to others are meaningless questions. A major source of the problem, particularly in cognition, is that human language in general and even researchers do not distinguish between homology and convergence. The difference is crucial in evolutionary biology, but is not often addressed by behavioural and cognitive psychologists. The public, therefore, understands that their experiments suggest human abilities in animals. As long as the causal physiological mechanisms are not analysed it seems wise to assume that a baboon or chimpanzee brain may produce a human-like behaviour with convergent, not homologous mechanisms. To say that a bird ‘deceives’ predators by the broken-wing display invokes only one parallel with human deception: Its effect. It would be much more interesting to understand *how* a chimpanzee brain represents the knowledge of another than *that* it does.

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Auf die „Grenzen des Wachstums“ hatte bereits 1972 der *Club of Rome* aufmerksam gemacht. Seitdem sind die gesellschaftlichen Dimensionen und Folgen eines ungebremsten wirtschaftlichen Wachstums national und international ein zentrales Thema öffentlicher Diskussionen, aber auch politischen Handelns. Auf der Gaterslebener Begegnung 2011 wurde dem quantitativen Parameter „Wachstum“ das qualitative Pendant „Reifung“ zur Seite gestellt und die Thematik in zwei Problemkomplexen „Wachstum in der unbelebten und belebten Natur“ und „Quantitatives und qualitatives Wachstum in der Gesellschaft“ behandelt. Am Anfang stehen „Kritische Anfragen“ an Wissenschaftler, gefolgt von einer sozialwissenschaftlich orientierten Darstellung zu „Wachstum und Nachhaltigkeit“. Die an Natur- und Geisteswissenschaftler, Publizisten, politisch Verantwortliche und interessierte Laien gleichermaßen gerichteten Beiträge umfassen Wachstum und Reifung als grundlegende Eigenschaften organismischen Lebens, aber auch in der Bevölkerungsentwicklung, in der Ökonomie („Wachstum in einer globalisierten Welt“, „Wirtschaftswachstum und Klimawandel“) und sogar im Weltall einerseits sowie in Literatur und Kunst andererseits.

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The Evolution of Surface and Deep Structure in Primate Communication

Klaus Zuberbühler (St. Andrews, UK)

With 7 Figures

Abstract

Primates communicate not only because they are biologically hardwired to do so but also because they pursue specific social goals. Yet, non-human primates are constrained by weak control over their vocal apparatus, resulting in small call repertoires with listeners needing to infer meaning from pragmatic cues. Human infants initially differ little from other primates in their vocal behaviour, but soon gain increasing control over their vocal products. Possible precursors to this ability are seen in primates modifying elements of their vocal repertoire and in combining calls into sequences. Why humans have evolved greater vocal control compared to other primates is a largely unresolved problem. One explanation has to do with cooperative breeding, which has been linked with advanced communication demands. Flexible vocal signalling may be particularly useful in facilitating cooperative tasks.

Zusammenfassung

Tierprimaten kommunizieren nicht nur, weil sie biologisch so veranlagt sind, sondern auch weil sie spezifische soziale Ziele verfolgen. Trotzdem sind Tierprimaten stark eingeschränkt in der Kontrolle ihres Stimmapparates. Infolgedessen steht ihnen nur ein kleines Lautrepertoire zur Verfügung, und Zuhörer sind bei der Rufinterpretation deswegen oft auf pragmatische Information angewiesen. Kleinkinder unterscheiden sich anfänglich wenig von Tierprimaten in ihrem Rufverhalten, entwickeln aber schon bald zunehmende Kontrolle über ihren Vokaltrakt. Die evolutionäre Ursache dieser ontogenetischen Eigenschaft ist noch unklar. Eine Erklärung hat mit der kooperativen Kinderbetreuung der Menschen zu tun, eine Verhaltensanpassung, die eine leistungsfähigere Kommunikation braucht. Flexible vokale Kontrolle scheint besonders nützlich zu sein in der Ermöglichung von kooperativem Verhalten.

1. Goal-directness and Intention in Primate Communication

A key problem in research on primate communication is how much voluntary control individuals have over signal production. Volition is difficult to operationalise so the focus has typically been on indicators of flexibility, such as awareness of an audience, ability to produce signal sequences and combinations, or release from basic biological functions (“means-end dissociation”; Bruner 1981, Call and Tomasello 2007).

Studies on gestural communication have perhaps shown most convincingly that non-human primates can perceive others as goal-directed agents, with their own intentions and motivations, and that these can be influenced by communication signals. For instance, chimpanzees use visual gestures primarily when a recipient is looking at them, and auditory and tactile ones in other circumstances. Similarly, chimpanzees may position themselves in the visual field of a receiver before producing a visual gesture (e. g. Poss et al. 2006, Russell et al. 2005, Call and Tomasello 2007). If a human experimenter is oriented so that there is no visual contact, then chimpanzees are likely to produce vocalisations as their first communication signals (Hostetter et al. 2001).

Another line of evidence for intentional signalling comes from studies on apes' altering gestures to direct non-attentive experimenters to a desired object (Povinelli et al. 2003). Similarly, captive orang-utans modify gestures depending on how well they have been understood (Cartmill and Byrne 2007). Such means-end dissociation is unusual in animal communication where signals usually are strongly linked to a narrow range of biological functions (Pollick and de Waal 2007). Ape gestures, in contrast, are adjusted and controlled by individuals, an indication of communicative intent rather than a hardwired response to external stimuli or a mere expression of mood (Call and Tomasello 2007).

However, it is also the case that not all primate gestural communication is so highly flexible. Facial gestures, common to all higher primates, play an important role in social communication in a way that is beneficial to both signaller and receiver (Andrew 1963, van Hooff 1962, Eibl-Eibesfeldt 1972, Chevalier-Skolnikoff 1973). They develop under strong genetic influences with individuals experiencing comparably little executive control over production. Equally important are some phylogenetic effects in the more flexible body gestures. For example, Asian apes do not produce auditory gestures, such as chest beating or buttress drumming, but many tactile ones. African apes gesture mainly during play, travel or feeding; Asian apes mainly during agonistic and affiliative interactions (Call and Tomasello 2007). A parsimonious preliminary conclusion thus is that primate gestures are the result of an interaction between biological predisposition and acquired flexible use.

In the vocal domain, evidence for goal-directedness and intentional signalling in primates is somewhat weaker. One way to address the problem has been to subject individuals to operant conditioning procedures, with the goal of getting them to vocalise in response to arbitrary stimuli (Adret 1993, Myers et al. 1965, Sutton et al. 1973, Wilson 1975, Aitken and Wilson 1979). Humans are easily capable of producing both speech and non-speech signals (laughter, cries, screams) volitionally and intentionally. For non-human primates, one of the earliest documented attempts was by Furness (1916) who home-reared orang-utan and chimpanzee infants removed from the wild: "The orang in one respect does use the lips, to make a sound indicating warning or apprehension; this sound is made with the lips pursed up and the air sucked through them – an exaggerated and prolonged kissing sound, followed by a grunting expiration and inspiration. [...] My oldest orang would make this sound on command (I had merely to say 'What is the funny sound you make when you are frightened?')."

In a later study with their home-raised infant chimpanzee 'Viki' Hayes and Hayes (1951) report: "The first step was aimed at teaching her merely to vocalize on command, in order to obtain a reward. [...] The task was surprisingly difficult. Although she seemed to learn what was required quickly, she had serious trouble with the motor skill of voluntary vocalization. It took her five months to learn to produce a hoarse, staccato grunt, quite unlike her normal spontaneous sounds."

A number of more systematic studies were subsequently conducted with various monkey species, and usually with substantial the training efforts. In one case it was possible to condition macaques to produce “coo” calls in response to light cues (Sutton et al. 1981). More complicated designs required individuals to either emit or withhold vocalisations on command. Rhesus macaques were able to learn this, but only if conditioned with electric shock, not with food rewards (Aitken and Wilson 1979). A puzzling finding was that the types of vocalisations produced by the monkeys to avoid shock were ‘food barks’ (typically given in response to valuable foods) and ‘clear calls’ (typically given during movement and separation; Rowell and Hinde 1962) but not calls normally given in aversive situations, such as distress or alarm calls. The fact that the monkeys were tested in isolation and the fact that the previous interaction history typically involved food, reveals something about how the monkeys assessed the situation.

Another way of addressing the problem of intentional signalling is to investigate the degree to which signallers are aware of the consequences of their vocalisations, by studying audience effects (Zuberbühler 2008). For example, vervet monkeys do not produce alarm calls when alone or if in company of an unsuitable audience (Cheney and Seyfarth 1985). Free-ranging male Thomas langurs, exposed to a predator model, also produce alarm calls when in the company of other group members. The intriguing finding here was that males continued to alarm call until all other group members had responded with at least one alarm call as if they kept track of which group members had and had not responded to the predator (Wich and de Vries 2006). In another example, blue monkey groups heard a play-

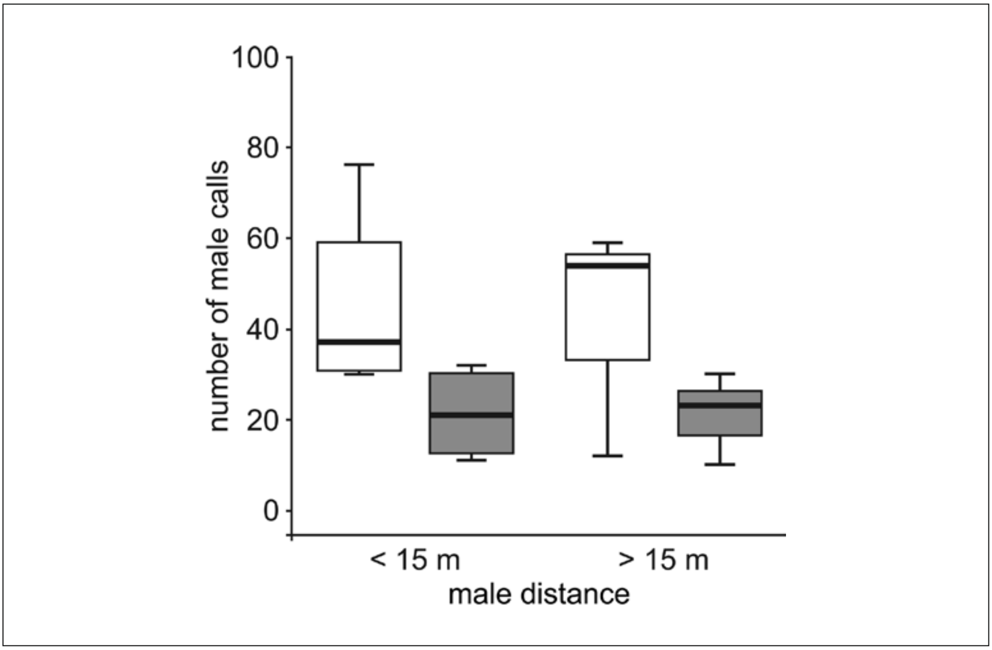

Fig. 1 Male blue monkeys take audience into account when producing eagle alarm calls. Male calling effort in response to a playback of a neighbouring male’s eagle alarm calls is a function of the females’ distance to the speaker. White boxes represent cases when the females were close (less than 15 m) and grey boxes when they were far from the stimulus (greater than 15 m). Printed with permission from Papworth et al. 2008.

back of a neighbouring male's eagle alarm calls. The single males of different groups reliably responded with their own eagle alarm calls, but their call rates depended significantly on the position of their group members relative to the presumed eagle. Males gave significantly more alarm calls if group members were close to the suspected eagle than if they were far away, regardless of their own position (Papworth et al. 2008, Fig. 1). Although there are alternative explanations, it is possible that the callers took into account the degree of danger experienced by others.

In wild chimpanzees, oestrous females have been observed to adjust the production of copulation calls depending on who is nearby. In general, females are reluctant to produce these vocalisations, unless they mate with a high-ranking male and other high-ranking males are in the audience. Most likely, this is part of a female strategy aimed at spreading the likelihood of paternity widely amongst the socially relevant males (Townsend et al. 2008). Chimpanzee females often depend on male support, especially when with vulnerable offspring. For instance, in the Sonso community of Budongo Forest, an established adult mother of dependent offspring was fatally wounded, most likely by some male of her own group, a highly unusual event in chimpanzees (Townsend and Zuberbühler, personal observation). The event happened shortly after the female returned to the group, following a period of prolonged absence. A subsequent autopsy revealed that she was several months pregnant, suggesting that she was not with the group at the time of conception. Furtive mating has already been suspected for one of her current offspring (Reynolds 2005).

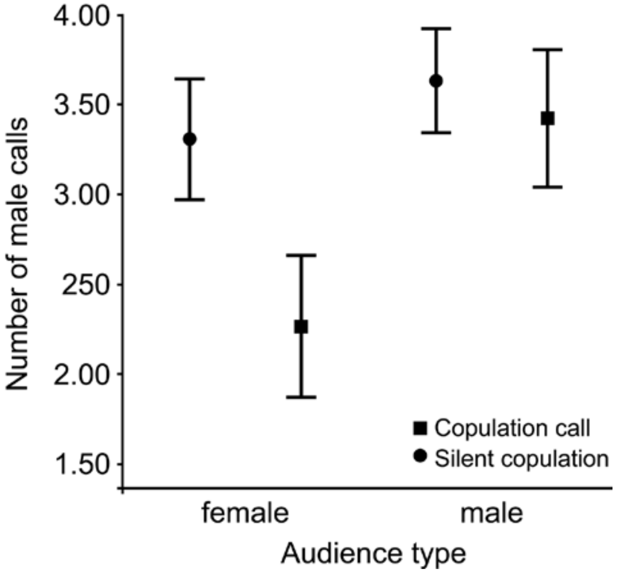

Fig. 2 Female chimpanzees suppress copulation calls in the presence of other females. Mean number of individuals in the audience in the presence or absence of copulation calls. Audience type refers to the average number of females or males present (± standard errors). Printed with permission from Townsend et al. (2008).

A second more intriguing type of audience effect in chimpanzee copulation calls was due to other females, whose presence significantly lowered the likelihood of a female giving copulation calls during mating (Townsend et al. 2008). One interpretation is that this cryptic behaviour has to do with their awareness of the potential social consequences of female-female competition (Townsend et al. 2007, Fig. 2).

Audience effects have also been found in other contexts and with other vocalisations. For instance, chimpanzees produce one acoustically distinct grunt variant when finding food ("rough grunts") and another variant when encountering higher-ranking group members ("pant grunts"). Male chimpanzees are more likely to give rough grunts to foods if they are with group members with whom they maintain good relations (as assessed in terms of grooming behaviour), compared to other group members, suggesting that call production is not just an immediate response to finding food but a signal directed to benefit specific receivers (Slocombe et al. 2010).

In another related study, female chimpanzees were observed in how they allocated their pant-grunt based greeting behaviour to other group members. They were more likely to produce pant grunts to adult males, and especially the alpha male, than to other higher-ranking group members. If females were already in the presence of the alpha male, however, then they generally refrained from producing pant-grunts to other high-ranking males (who would normally obtain such calls), suggesting that the alpha male had inhibitory effects on the females' social relations with others (Laporte and Zuberbühler 2010). One way of interpreting such results is that chimpanzees produce their calls strategically by taking into account the potential impact of their signals on the audience, an indicator of a high degree of social awareness.

2. Causes and Consequences of Articulatory Control

2.1 Primate Limitations

A recurrent theme in essays on primate vocal communication is how profoundly constrained individuals are in the number of acoustic signals they can produce. Non-human primates, including apes, do not appear to have nearly as much motor control over their vocal tracts as even very young human infants (e. g. Jürgens 1998, Owren and Goldstein 2008). In contrast, human vocal behaviour is characterised by the ability to generate a large range of acoustically distinct sounds ('phonemes'), mechanically achieved by changing the spatial configurations of the vocal tract precisely, rapidly, voluntarily, and with considerable ease, the result of unprecedented oro-facial, laryngeal, and breathing control. In contrast, all attempts to home-rear great apes have noted a striking absence in producing human vocal sounds and lack of interest in trying to imitate speech patterns (Kellogg 1968).

This failure was particularly striking in contrast to these individuals' high-levels of imitation of other human behaviour. Hayes and Hayes (1951) observed: „An especially interesting feature of human social play is imitation; and here, again, Viki shows no great difference. Just as a human child copies its parents' routine chores, so Viki dusts; washes dishes; sharpens pencils; saws, hammers, and sandpapers furniture; paints woodwork; and presses photographs in books. [...] On the other hand, she is less vocal: while the human child commonly keeps up an almost continual stream of chatter-with or without meaning, Viki is silent. She babbled a little during her first year, and at present she occasionally devotes a few minutes to rather stereotyped vocal play; but she gets only a small fraction of the practice which provides background for the human child's most distinctive accomplishment – language."

More active teaching of human sound patterns was also tried several times, with equally little success. In one of the earliest studies, Furness (1916) writes: "In the case of the orang-utan it took at least six months of daily training to teach her to say 'Papa.' [...] At the end of about six months, one day of her own accord, out of lesson time, she said 'Papa' quite distinctly and repeated it on command. Of course, I praised and petted her enthusiastically; she never forgot it after that and finally recognized it as my name. When asked 'Where is Papa?' she would at once point to me or pat me on the shoulder. One warm summer's day I carried her in my arms into a swimming pool; she was alarmed at first but when the water came up to her legs she was panic stricken; she clung with her arms about my neck; kissed me again and again and kept saying 'Papa! Papa! Papa!' Of course, I went no further after that pathetic appeal."

The orang-utan subsequently also learned the word "cup" and appeared to use it in appropriate contexts, before she died of illness a few months later. Several decades later, Hayes and Hayes (1951) reported on the same issue: "By manipulating Viki's lips, as she vocalized, we were able to make her say 'mama.' She soon learned to make the proper mouth movements herself, and could then say 'mama' unaided – softly, and hoarsely, but quite acceptably. Viki's later words were learned more easily, and by a different procedure. Like many other chimpanzees, she has developed a type of play, which is superficially similar to babbling. It differs in that the sounds are produced entirely by mouth vibrations, without use of the larynx. Some of these sounds are roughly similar to certain human consonants, and since Viki readily imitates our production of them, we attempted to teach her to use them in words. By the time she was two-and-one-half years old she had learned to pronounce satisfactory approximations of the whispered words 'papa' and 'cup.' We did not manipulate her mouth in teaching these words, but simply insisted that she copy our example of a certain combination of play sounds."

Why exactly it is so difficult to train apes to produce human-like vocal signals is, in some sense, one of the central problems in the origins of language debate. This lack of ability is even more surprising in light of the fact that the human vocal tract is anatomically not profoundly different from most other terrestrial mammals, including apes (Fitch 2006). It has been argued that the permanently descended larynx, an anatomi-

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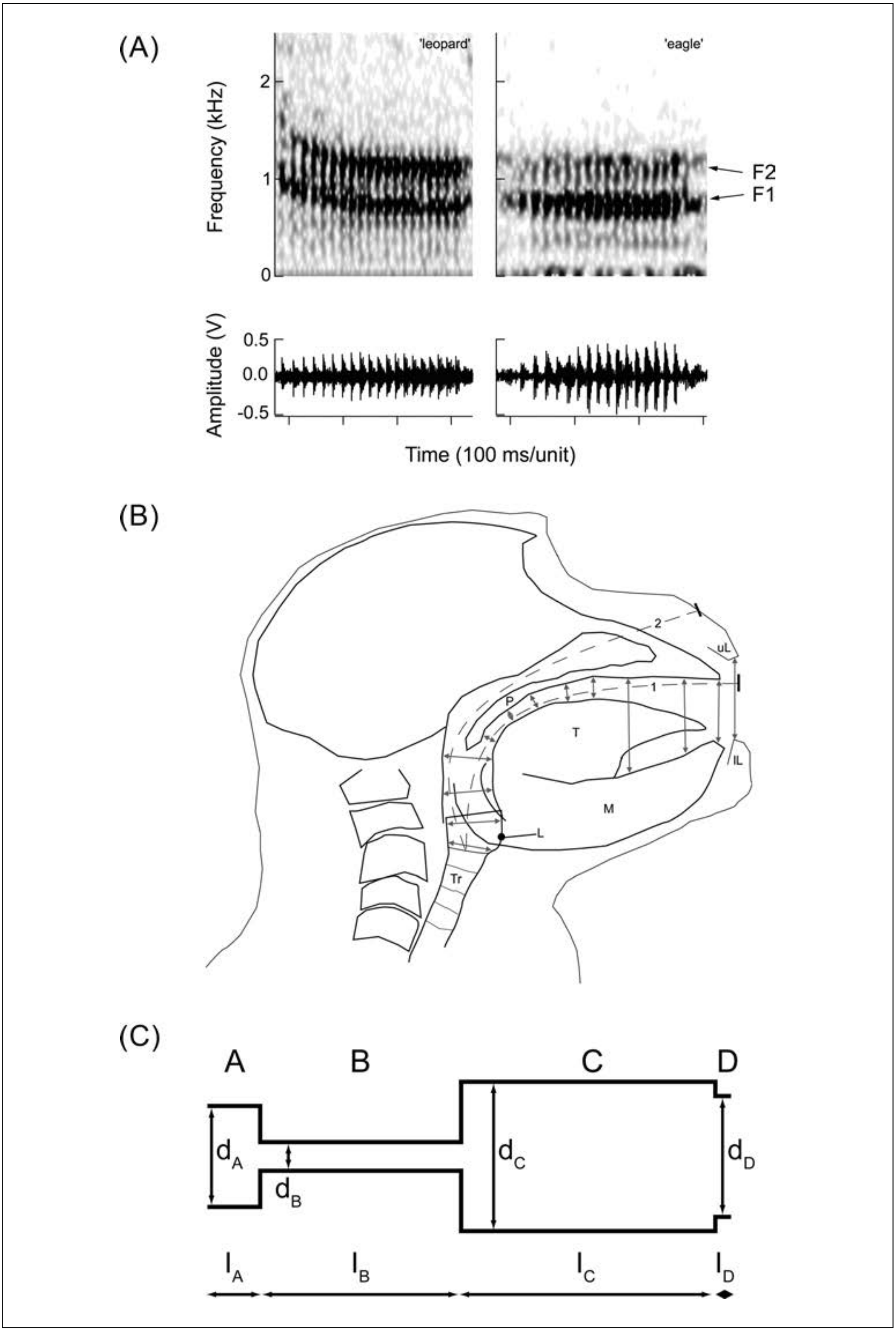
Fig. 3 The relationship between vocal tract anatomy and formant frequencies in Diana monkeys. (*A*) Spectrogram and time series of a leopard and an eagle alarm call uttered by a male Diana monkey illustrating the downward modulation at the beginning of the leopard call but not in the eagle alarm call. (*B*) Schematic drawing of the head-neck region of a Diana monkey based on lateral x-ray dissections (T – tongue, Tr – trachea, uL – upper lip, lL – lower lip, L – larynx, P – palate) (*C*) Schematic 3-tube-approximation of a Diana monkey's vocal tract used for a computational model to simulate the formant structure of Diana monkey eagle or leopard alarm calls. Calculations were based on lengths (l_A, 1_B, 1_C, 1_D) and diameter dimensions (d_A, d_B, d_C, d_D). Tube D represents the mouth opening to simulate the closing of the lip aperture (from Riede et al. 2005, printed with permission). ►


(A)
'leopard'
'eagle'
Frequency (kHz)
2
1
0
F2
F1
Amplitude (V)
0.5
0.0
-0.5
Time (100 ms/unit)
(B)
2
uL
1
P
T
lL
M
L
Tr
(C)
A
B
C
D
d_A
d_B
d_C
d_D
l_A
l_B
l_C
l_D

cal peculiarity of humans, is causally responsible for the speech ability (e.g. Lieberman 1975, 2007), but this argument rests on weak empirical grounds and has been challenged from the start (Andrew 1976, Riede et al. 2006, Fitch 2010). For example, when responding to their natural predators, crowned eagles and leopards, Diana monkeys produce two distinct types of alarm calls, which differ mainly in the shape of their formant transitions (Riede and Zuberbühler 2003a, b). Morphological measurements of the Diana monkey vocal tract, based on radiography and dissection, suggested that these transitions are accomplished by altering the configuration of the vocal tract, manoeuvres that could also be simulated with a multi-tube computational model (Riede et al. 2005, Fig. 3).

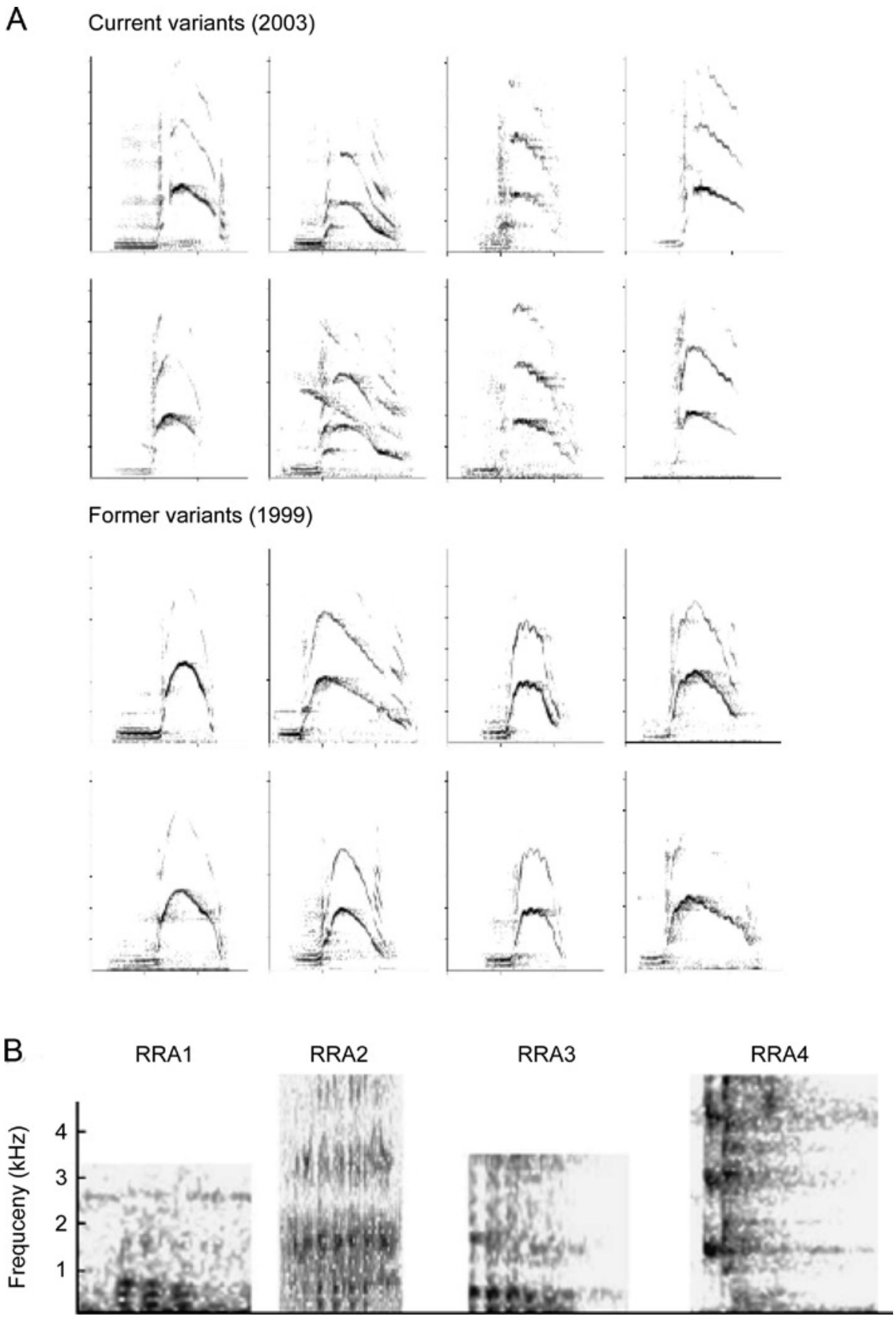
In sum, one profound difference between human and non-human primates concerns the degree of articulatory control individuals experience during sound production. Overall, the current empirical state-of-the-art is more consistent with the notion that neural control, rather than anatomical specialisation, lies at the heart of this human specialisation. Non-human primates are unable to play with sounds, to imitate each other vocally, or to combine existing elements in creative ways. This is not because their larynges and vocal tracts are different, but because they do not have adequate control over these body parts.

2.2 Variable Call Morphology

Much has been speculated about the causes for the human-primate difference in vocal control. One line of argument is of a genetic nature. It has been known that the sequence of the FoxP2 gene, a DNA region important during brain development in a wide range of animals, is unique in humans (Enard et al. 2002, 2009). Since damage to this region in humans can lead to severe speech defects (Lai et al. 2003), it has been suggested that the gene plays an important role during the development of oro-facial motor control in humans. It is also the case that individuals with defects in the FoxP2 region are still able to produce intelligible speech, albeit much more effort is required (Vargha-Khadem et al. 2005), suggesting that vocal control is the result of multiple factors.

Primate call repertoires are generally small, with repertoire sizes positively correlated with social complexity (McComb and Semple 2005). However, this relationship is not always so clear, because the appropriate level of analysis is sometimes uncertain. Some call types are characterised by considerable acoustic variation, and in some cases this can be meaningful to recipients (e.g. Fischer 1998, Crockford and Boesch 2003). A recent series of studies with Campbell's monkeys (*Cercopithecus campbelli*), for instance, has revealed surprising levels of acoustic variability such as in female contact calls (Lemasson et al. 2005) and female alarm calls (Ouattara et al. 2009b, Fig. 4).

Fig. 4 Acoustic variants in two call types produced by female Campbell's monkeys, the CH6 and RRA calls. (*A*) Spectrographic illustrations of contact call (CH 6) variants produced by female Campbell's monkeys during relaxed and friendly social interactions, recorded 4 years apart. (*B*) Spectrographic representations of different acoustic variants of female alarm calls (RRA). Printed with permission from Lemasson et al. 2005 and Ouattara et al. 2009c. ►


A
Current variants (2003)
Former variants (1999)
B
RRA1
RRA2
RRA3
RRA4
Frequceny (kHz)
4
3
2
1

Acoustic variation at the level of the individual call type appears to have different functions. *First*, as illustrated repeatedly, it enables callers to expand their signal range in response to external events. For instance, chimpanzees produce screams in response to aggression by other group members, the victim screams (Slocombe and Zuberbuhler 2005a). The acoustic structure of these screams varies and reflects relatively reliably the severity of the attack experienced by the caller (Slocombe and Zuberbühler 2007). These subtle acoustic differences are discriminated by uninvolved bystanders, suggesting that they are meaningful to them (Slocombe et al. 2009). In addition, victims also take into account the composition of the nearby audience when producing these screams. If high-ranking individuals are nearby, victims tend to produce scream variants that indicate a more severe attack than has actually taken place, probably as an attempt to recruit nearby high-ranking group members to intervene on their behalf (Slocombe and Zuberbühler 2007, Fig. 5). One intriguing possibility, which requires further testing, is that chimpanzees are socially aware of the impact of their

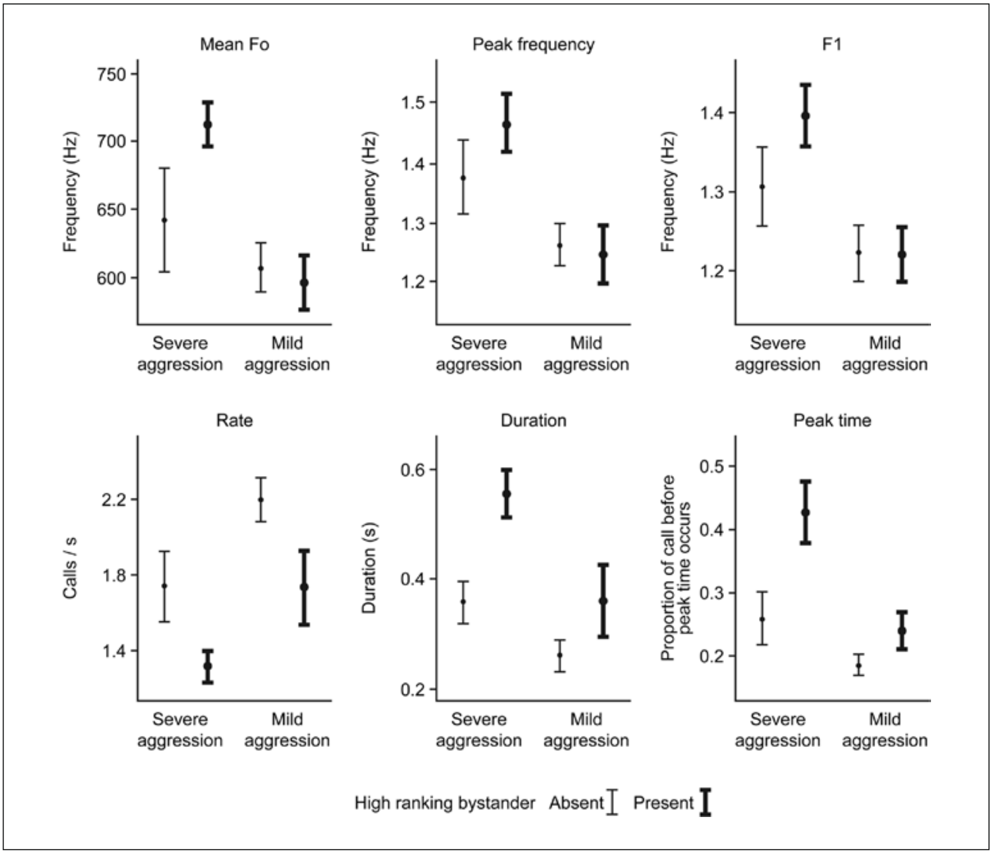


Fig. 5 Chimpanzees modify the acoustic structure of recruitment screams as a function of audience composition. The vocal structure of victim screams differs both as a function of the level of aggression experienced by the caller and whether or not an individual equal to or outranking the aggressor is in the audience (mean and standard errors). Sample sizes were: cases of severe aggression with (N = 12) and without (N = 9) a high-ranking bystander; cases of mild aggression with (N = 9) and without (N = 10) a high-ranking bystander. Printed with permission from Slocombe and Zuberbühler 2007.

screams and strategically modify the acoustic structure in order to influence the audience to their own advantage, essentially by producing inaccurate information.

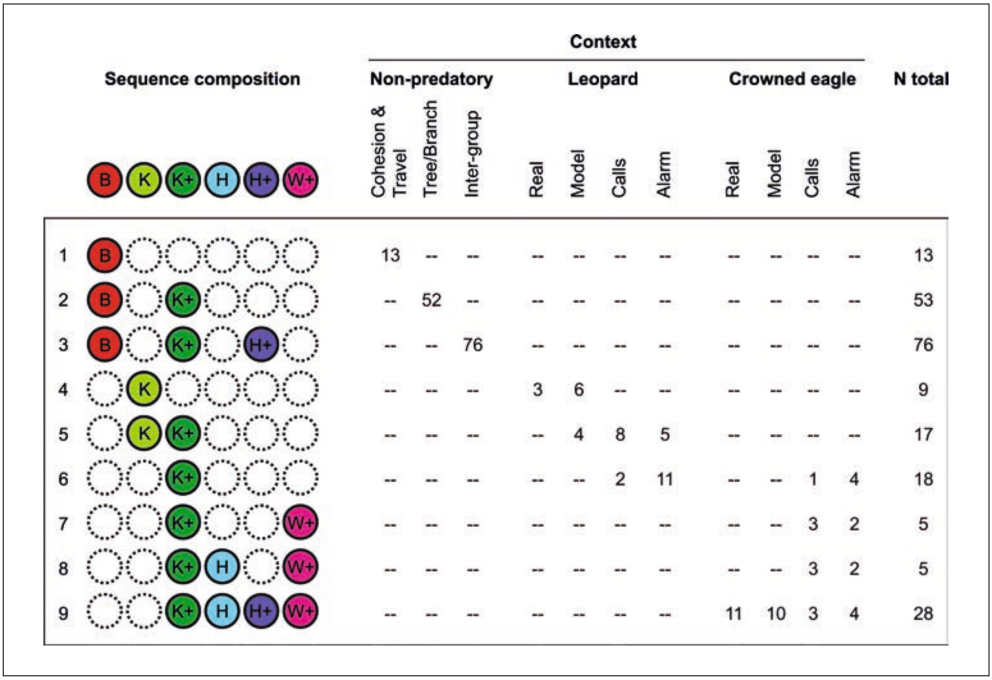
Second, another possible function of within call acoustic variation is that it can lead to group-specific vocal signatures, as for instance observed in Campbell's monkeys contact calls. Here, some pairs of adult females produce contact calls that appear acoustically more similar than others, and this has been linked with the quality of their social relations (Lemasson et al. 2003, 2005). Socially-derived acoustic similarity also appears to lie at the heart of vocal dialects, a well-known phenomenon in songbirds (Marler and Tamura 1962), with some isolated examples in non-human primates, such as in free-ranging pygmy marmosets (de la Torre and Snowdon 2009). In great apes, there is some evidence for dialects in chimpanzee pant-hoot vocalisations, a compositional vocal signal that occurs in group-specific call variants (Crockford et al. 2004, Marshall et al. 1999, Mitani et al. 1999).

Taken together, non-human primates can acoustically modify some of their calls, usually in response to social variables or aspects of their environment. Further research will have to address how widespread this is in primates and how much active volitional control callers have. It is also unclear which call types of a species' repertoire are most prone to acoustic variability or rigidity and whether there are general phylogenetic trends. Another unresolved problem concerns the phylogenetic history of the different call types. In some cases, phylogenetic reconstructions have been made, most recently for laughter (Davila Ross 2009), but generally only little systematic empirical work has been done (e. g. Gautier and Gautier 1977, Gautier 1989). The relationship between form and function is also not well understood, although some theoretical points have been made regarding this relationship (Owren and Rendall 2001).

2.3 Call Sequencing

A relatively recent finding is that primates can combine different call types into more complex sequences in context-specific ways, possibly in response to the constraints of their limited vocal plasticity. Examples include *Cebus* monkeys (Robinson 1984), Campbell's monkeys (Zuberbühler 2002, Ouattara et al. 2009c), Diana monkeys (Stephan and Zuberbühler 2008), putty-nosed monkeys (Arnold et al. 2008), black-and-white Colobus monkeys (Schel et al. 2009), gibbons (Clarke et al. 2006), chimpanzees (Crockford and Boesch 2005), and bonobos (Clay and Zuberbühler 2009). In putty-nosed monkeys, adult males combine two calls, 'pyows' and 'hacks', into multi-call sequences in context-specific ways (Arnold and Zuberbühler 2006a, b). Series of 'pyows' tend to be associated with events on the ground, while series of 'hacks' are reliable indicators of crowned eagles. In addition, males produce a peculiar call combination consisting of a few 'pyows' followed by a few 'hacks'. This combination can be produced alone, or it is inserted into another sequence. Regardless of context, 'pyow'–'hack' combinations reliably predict group movement, a fact that has been verified with field experiments (Arnold et al. 2008, Arnold and Zuberbühler 2008). In Campbell's monkeys, males combine six different calls in context-specific ways and functions include induction of group travel, as well as referring to various predatory and non-predatory events (Ouattara et al. 2009c, Fig. 6).

A largely unresolved issue is how non-human primates learn to use calls in contexts-specific ways, especially acoustic modifications and call combinations. Research on vervet monkeys



		Context											
	Sequence composition	Non-predatory			Leopard				Crowned eagle				N total
	B K K+ H H+ W+	Cohesion & Travel	Tree/Branch	Inter-group	Real	Model	Calls	Alarm	Real	Model	Calls	Alarm	
1	B ◌ ◌ ◌ ◌ ◌	13	–	–	–	–	–	–	–	–	–	–	13
2	B ◌ K+ ◌ ◌ ◌	–	52	–	–	–	–	–	–	–	–	–	53
3	B ◌ K+ ◌ H+ ◌	–	–	76	–	–	–	–	–	–	–	–	76
4	◌ K ◌ ◌ ◌ ◌	–	–	–	3	6	–	–	–	–	–	–	9
5	◌ K K+ ◌ ◌ ◌	–	–	–	–	4	8	5	–	–	–	–	17
6	◌ ◌ K+ ◌ ◌ ◌	–	–	–	–	–	2	11	–	–	1	4	18
7	◌ ◌ K+ ◌ ◌ W+	–	–	–	–	–	–	–	–	–	3	2	5
8	◌ ◌ K+ H ◌ W+	–	–	–	–	–	–	–	–	–	3	2	5
9	◌ ◌ K+ H H+ W+	–	–	–	–	–	–	–	11	10	3	4	28

Fig. 6 The composition of male Campbell's monkey call sequences in different behavioural contexts. B – boom call, K – Krak call, K+ – krak-oo call; H+ – hok call; H+ – hok-oo call; W+ – wak-oo call. "Alarm" indicates leopard or eagle alarm calls given by sympatric Diana monkeys. Printed with permission from Ouattara et al. 2009b.

has shown that infants initially produce alarm calls to a broad range of events (e.g. any startling event from above) and only with experience learn to narrow call production to the biologically relevant predators (Seyfarth and Cheney 1980). Whether this mechanism is representative of primate vocal learning in general is currently unknown. After having taught Viki three words, Hayes and Hayes (1951) observed: "She did not use her three words meaningfully at first; but when we required her to employ them appropriately, she soon learned to address the proper experimenter as 'mama' or 'papa,' and to say 'cup' when she wanted something to drink."

This anecdote suggests a more active process of aligning vocal structures and proper contextual use, based on social learning, but in general the ontogeny of call production is a largely unexplored area of research.

3. Meaning as an Inferential Process

3.1 Context-specific Acoustic Variation

A key consequence of restricted vocal flexibility and small vocal repertoires is that call – context relations are often only vague. Alarm calls appear to be somewhat of an exception. The classic case is the East African vervet monkeys with individuals giving acoustically distinct alarm calls to eagles, leopards, pythons, and other types of dangers. The content of these calls is demonstrated by experiments showing that the calls alone can elicit adequate anti-predator behaviour in listeners, in the absence of any predators (Seyfarth et al. 1980). This basic finding has been replicated, suggesting that predator-specific alarm calls are a general feature of primate communication (Zuberbühler 2009). Other call types (e. g. copulation calls, screams, food calls) may also carry relatively specific meaning in the sense that receivers are able to infer the type of event the caller is engaged in. Field experiments with baboons, for instance, have demonstrated the complexity of call processing and the kinds of inferences these primates are capable of doing when hearing each other's calls (Cheney and Seyfarth 2007).

In apes, the same basic comprehension mechanisms appear to be at work, despite the fact that many of their calls are acoustically highly graded. In one study, chimpanzees housed at Edinburgh Zoo were taught to find preferred food ("bread") in one corner of their enclosure and not so preferred food ("apples") in another. Both foods reliably triggered specific food

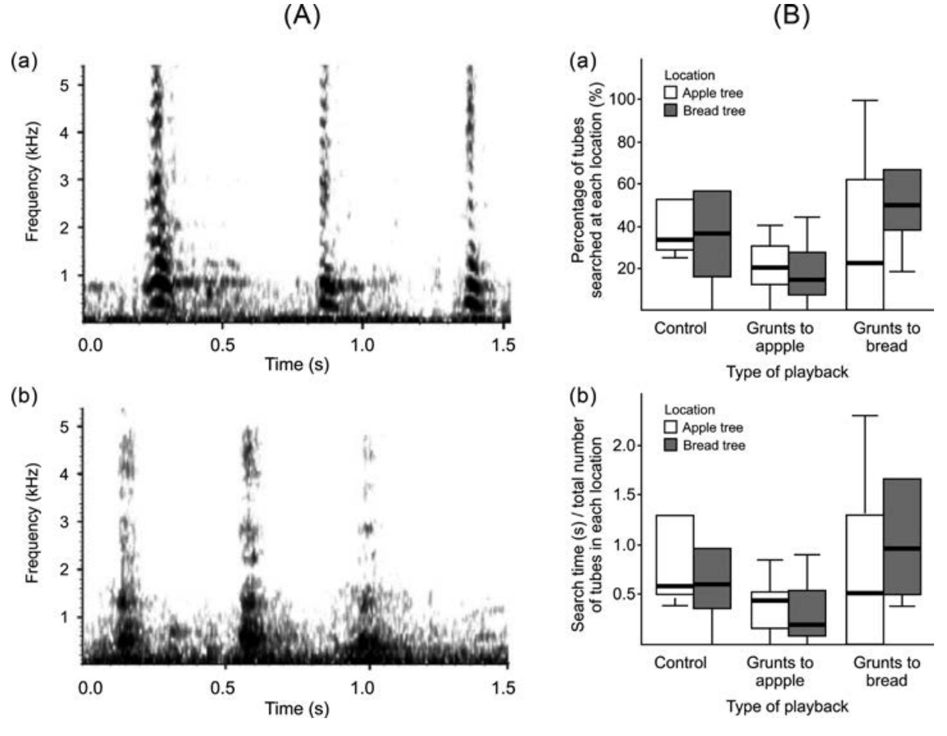


Fig. 7 Chimpanzees extract semantic information from an acoustically graded signal, the 'rough grunts'. (*A*) Time-frequency spectrograms of rough-grunt calling bouts given by the adult male Louis. Grunts given to bread (a) have more energy (depicted by the darkness of the image) at higher frequencies and have a clear harmonic structure, in comparison to the lower-pitched, noisy grunts given to apples (b). (*B*) Results of a playback experiments involving recordings of "apple" and "bread grunts". Box plots illustrate the percent of tubes searched and the time spent searching in each location after hearing playbacks of grunts given to apples or bread (Slocombe and Zuberbühler 2005b, reprinted with permission).

grunts upon encounter, but their acoustic fine structure differed in reliable ways (Slocombe and Zuberbühler 2006). Subsequent playbacks of "bread grunts" and "apple grunts" triggered significantly different foraging behaviour, suggesting that the subtle acoustic variants in their food grunts were semantically relevant (Slocombe and Zuberbühler 2005b, 2006 Fig. 7).

3.2 Mechanisms of Comprehension

Although there is generally very good evidence that primates attend to each other's vocalisations to make predictions about the event encountered by the caller, it is not clear whether this requires specialist comprehension skills beyond what is handled by general cognition. According to one view, a listener has simply learned that one thing predicts another, or even causes another, in the same basic way as many other everyday phenomena (Tomasello 2008). Whether all empirical evidence is sufficiently explained by this associative account – and how human language comprehension fits into this model – is not clear. On apes' understanding of human communication Furness (1916) writes: "As to a comprehension of the connection of spoken words with objects and actions both the orang-utan and chimpanzee, I think, exceed any of our domestic animals; both of my anthropoids have been able to understand what is said to them, more intelligently than any professionally trained animals I have ever seen."

Some experimental evidence from the field is consistent with the notion that primates do not merely attend to the peripheral acoustic features of calls but generate some kind of mental representations from the different calls they hear (Zuberbühler et al. 1999, Zuberbühler 2000a). In many cases, however, call – context relations are only very vague, ambiguous, or in other ways inconsistent. For example, the monkeys of Tai Forest, Ivory Coast, share their habitat with a range of other species, which are often hunted by the same predators. For instance, crested guinea fowls are exposed to leopard predation due to their terrestrial foraging. When Diana monkeys hear Guinea fowl alarm calls they respond with their own leopard alarm calls and other leopard-specific anti-predator behaviour. However, the birds' alarm calls are not so specific because they also produce them when chased by humans, suggesting that the calls indicate little more than the presence of a ground predator. In one field experiment, Diana monkeys were first led to believe that the guinea fowls' alarm calls were caused by either a leopard or by a human poacher. This experience had a significant effect on how the birds responded to subsequent playback of guinea fowl alarm calls, suggesting that primates take the wider pragmatic features into account when producing vocalisations, rather than responding to the calls themselves (Zuberbühler 2000b). As listeners cannot always rely on simple stimulus-response associations, meaning can only be retrieved through some basic inferential processes. Whether such inference-based comprehension is similar to the one used by humans has to be investigated in more detail.

4. Transitions to Speech

4.1 Babbling

From early on, humans and non-human primates rely heavily on their species-specific vocal repertoire as primary mode of communication in a range of social situations. Like those of non-human primates, the human call repertoire consists of a few basic call types, such as grunts, cries, screams, or laughter (McCune et al. 1996, Wolff 1969). Calls are acoustically variable and can carry meaning if listeners can infer something about the event the caller has experienced (Zeskind et al. 1985). The obvious difference in vocal behaviour between humans and the rest of the primates concerns the production of speech sounds. Although non-human primates do not show this feature, the basic vocal tract structures and mechanisms of articulation are the same, as outlined earlier. In human infants, increasing motor control results in the production of consonant- and vowel-like sound sequences: babbling, a peculiar vocal behaviour that emerges in the first 12 months of life.

This is not observed in infant chimpanzees, as confirmed by Hayes and Hayes (1951): "Viki babbled much less than human babies do, and even this disappeared by five months of age. However, the variety of sounds observed in her babbling, and in her vocal expressions of emotion, left no doubt that her vocal mechanisms were adequate for producing satisfactory approximations of most of the elements of human speech."

In humans, babbling generally triggers very positive social responses in listeners, regardless of kin relations, suggesting that the behaviour has evolved on a pre-existing receiver predisposition (Locke 2006). By producing signals that receivers find attractive as well as easy to detect, discriminate, and remember, human infants have evolved a communication tool that aids them with their daily social challenges (e.g. Guilford and Dawkins 1991).

Nevertheless, babbling is not a uniquely human vocal behaviour. The behaviour is also found in some non-human animals, particularly songbirds (e.g. Goldstein et al. 2003, Aronov et al. 2008) but also in greater sac-winged bats (Knornschild et al. 2006). An interesting primate example is the pygmy marmosets, a facultative cooperative breeder with bi-parental care (Elowson et al. 1998a, b, Snowdon and Elowson 2001). As infants, pygmy marmosets are highly vocal, and they produce over a dozen different call types at high rates. Some are specific to infants, others resemble the adult calls or are acoustic variants thereof, and they are generally assembled into long sequences. As in humans, babbling enhances social bonding by increasing interactions between parents and offspring (Elowson et al. 1998a). The behaviour is observed until puberty, before rates decline and eventually disappear during adulthood (Snowdon and Elowson 2001). The degree to which babbling is crucial for vocal development is currently unknown, but it is interesting that pygmy marmosets are one of a small number species for which vocal dialects have been reported.

4.2 Cooperation and Communication

One difficult-to-understand transition in language evolution concerns the one from vocally-inflexible to vocally-flexible systems, i.e. the origins of vocal control. A second difficult-to-understand transition concerns the willingness of individuals to share information, as opposed to trying to influence each other's behaviours, or merely responding to external events.

One explanation for why humans have evolved such an elaborate communication system probably has to do with cooperative behaviour, which is particularly manifest during foraging and childcare (Tomasello 2008). Collaborative behaviours require a high degree of mutual understanding and an ability to share intentions, and this in turn may favour a special kind of communication. Humans can be classified as specialised cooperative breeders, in which non-breeding helpers are essential, while most other cooperatively breeding primates are mere group breeders with several females breeding together (Clutton-Brock 2006). Amongst all primates, humans are unmatched in the amounts of childcare undertaken by individuals other than the mother (Hrdy 1999, 2009). Humans often entrust non-relatives with looking after their offspring in both modern and traditional hunter-gatherer societies (Hewlett and Lamb 2007), and children may grow up in peer-groups looked after by a non-relative, while their mothers are away foraging (Henry et al. 2007).

Allocare is also found in New World primates, usually in the form of fathers helping with infant carrying. In Old World primates, allocare is rare and infants typically avoid the proximity of other adult females and prefer to play with other infants or juveniles (e.g. Forster and Cords 2005). Great apes, in particular, provide conspicuously little allocare. In chimpanzees, infant caretaking is almost exclusively done by the mother, although cases of adoption by older siblings have been reported occasionally (Goodall 1989). As a consequence young chimpanzees stay uninterruptedly with their mother and form small family units with her, who travel, forage, rest, and nest together. A basic vocal repertoire and some ritualised gestural conventions may be fully sufficient to regulate the social interactions that emerge in this setting.

The potential for conflict and negotiation are probably much greater in cooperative care systems. Especially for the infants, competition over resources and caregiver attention is likely to be a common problem. Infants will compete with one another over non-maternal caregivers, who may be reluctant to provide care. Natural selection may thus favour communication skills that help individuals to overcome such obstacles. If allo-mothering is essential, infants will require mechanisms to attract the attention of allo-parental caregivers. Interestingly, high degrees of allocare have been linked with other types of elaborated infant signalling especially in the visual domain (Alley 1980). Across primates, Ross and Regan (2000) found that species with high degrees of allocare have more brightly or conspicuously coloured infants than species with little or no allocare. High degrees of allocare could also select for more acoustic conspicuousness compared to single parent care systems. Increased vocal control may be one way to achieve this effect. If this enables infants to secure care more effectively, perhaps in response to pre-existing receiver biases, then natural selection is likely to favour it. Hrdy (2009) similarly argues that human infants are equipped with especially powerful tools to solicit and secure care, not just from their mothers but potentially any involved bystander. Vocal control may have been the crucial component of this tool kit, paving the way to the elaborate and unique speech abilities of modern humans.

The other key ingredient on the route to language has to do with perceiving the receiver as someone whose knowledge and motivation can be actively influenced with communication signals. Chimpanzees and other primates show some indication that they are moderately aware of how others view the world, but this psychological ability is much more advanced in humans (Tomasello 2008). These two key transitions – increased vocal control and increased social awareness – may be sufficient to establish an intentionally-based symbolic communication system that is based on arbitrary sound patterns.

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Der Begriff der Natur
Wandlungen unseres Naturverständnisses und seine Folgen

Gaterslebener Begegnung 2009

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Das Verhältnis des Menschen zur „Natur“ ist in seiner Geschichte durch unterschiedliche Beziehungen geprägt. Seit der Aufklärung wird die Natur dem Menschen zu seiner Nutzung untergeordnet und zunehmend ausgebeutet. Natur wurde zum Objekt technischen, ökonomischen und politischen Handelns. Spätestens seit Mitte des vorigen Jahrhunderts wissen wir um die akute Gefährdung natürlicher Lebensräume.

Die Gaterslebener Begegnung 2009 widmete sich daher dem Thema „Der Begriff der Natur“ und untersuchte Wandlungen des Naturverständnisses sowie die Folgen der gegenwärtigen Auffassungen von Natur. Behandelt werden unser Bild vom Leben, die Frage „Was ist Natur?“ aus verschiedenen Perspektiven und die philosophische Analyse der Stellung des Menschen in der Natur. Beiträge zum Naturverständnis in der Gegenwartskunst und zum Problemkomplex Naturrecht und Bioethik sowie eine Diskussion „Frieden mit der Natur“ ergänzen den Band.

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Selectivity in Stone Tool Use by Wild Bearded Capuchin Monkeys – Field Observations and Experimental Evidence

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With 5 Figures

Abstract

Visalberghi (1987) predicted that wild capuchins monkeys with terrestrial habits would be likely to show tool use for cracking nuts. Expectations built on the basis of scientific considerations are often fulfilled, but rarely do they overcome the most optimistic expectations. When we found a population of capuchin monkeys living in an area where nuts, stones, and anvils were available we did not anticipate that their stone tool use skills would be quite so amazing. This chapter provides (*1.*) a brief historical summary of tool use reports in wild capuchin monkeys (*Cebus* spp.), and (*2.*) an overview of our field observations and experiments on tool selectivity on wild bearded capuchins (*Sapajus libidinosus*) cracking nuts with stone hammers and anvils.

Zusammenfassung

Visalberghi sagte 1987 voraus, dass wilde, bodenlebende Kapuzineraffen wahrscheinlich Werkzeuggebrauch beim Knacken von Nüssen zeigen würden. Voraussagen, getroffen auf der Basis von wissenschaftlichen Überlegungen, werden zwar des Öfteren erfüllt, selten jedoch übertreffen sie die optimistischsten Erwartungen. Als wir eine Population von Kapuzineraffen fanden, die in einem Gebiet lebt, in dem Nüsse, Steine und Ambosse vorhanden sind, konnten wir nicht ahnen, dass ihre Fertigkeiten in der Benutzung von Steinwerkzeugen so erstaunlich sind. Dieser Beitrag gibt (*1.*) eine kurze historischen Zusammenfassung der Berichte von Werkzeugbenutzung bei freilebenden Kapuzineraffen (*Cebus* spp.) und (*2.*) einen Überblick über unsere Feldbeobachtungen und Experimente zur Werkzeugselektion von Rückenstreifen-Kapuzinern (*Sapajus libidinosus*) beim Knacken von Nüssen mit Steinhämmern.

> "The relative lack of observations of tool-use by capuchins for cracking nuts in the wild contrasts with its presence in captivity. In this respect, the arboreal habits of capuchins, especially when compared to chimpanzees, can be of some relevance. […] For arboreal monkeys the chances of manipulating stones or other percussors and finding horizontal surfaces on which to pound them are scarce. Therefore, the absence of observations of tool use to crack open nuts can be tentatively explained by the scarcity of appropriate conditions for innovative behaviors to arise (Kummer and Goodall 1985). Both cognitive abilities (Parker and Gibson 1977) and motor skills of tufted capuchin monkeys permit the prediction that this species, […] if observed in field sites with nuts, stones and anvils, would be likely to show innovative behavior and tool-use for cracking nuts."
>
> Visalberghi 1987, p. 179

1. Historical Overview of Tool Use in Capuchin Monkeys

Observations of tool use in captive capuchins date back about 500 years. The Spanish naturalist Gonzalo Fernández de Oviedo y Valdés (de Oviedo 1526/1996, cited by Urbani 1998) was the first to describe a capuchin monkey cracking open a nut with a tool. About 250 years later, Erasmus Darwin, the grandfather of Charles Darwin, observed this same behaviour in a park in London (Darwin 1794). A century after that, naturalists and psychologists began to report serendipitous observations as well as systematic studies of captive capuchins using tools (e.g., Romanes 1883/1977, Watson 1908, Klüver 1933, 1937, Nolte 1958, for further details, see Beck 1980, Fragaszy et al. 2004b). In the last two decades of the last century, research on captive capuchin tool use grew tremendously, providing insight into how behaviour, morphology, and cognition contribute to the emergence of tool use, the range of tool use by capuchins, the extent to which social influences are important in learning to use objects as tools, the flexibility of tool use with different objects and surfaces, and what this flexibility means in terms of comprehension of the task. Naturalistic observations of tool use by capuchins living in semi-free conditions were also carried out (e.g., Jalles-Filho et al. 2001, Ottoni and Mannu 2001, Rocha et al. 1998, for reviews see Fragaszy et al. 2004b, Visalberghi and Fragaszy 2006). At this point, it became clear that these South American monkeys were capable of using many different tools to reach many different goals (sticks to rake/push/insert, hard objects to crack open nuts, etc.).

Until very recently the impressive achievements by captive capuchins in using tools sharply contrasted with the extreme scarcity of reports of tool use by wild capuchins (see Fragaszy et al. 2004b), and only recently observations of capuchins using tools have been reported. Boinski (1988) carefully documented how a male wild white-faced capuchin (*C. capucinus*) killed a snake by hitting it with a branch obtained from nearby vegetation, and Fernandes (1991) reported the first direct observation of a wild capuchin using a broken oyster shell to strike oysters still attached to the substrate, successfully opening them.

This state of affairs changed in 2004, when two research teams reported repeated use of tools in two populations of wild bearded capuchin monkeys (*Cebus libidinosus*, now *S. libidinosus*[1]) in Fazenda Boa Vista (Fragaszy et al. 2004a) and in the Serra da Capivara National Park (Moura and Lee 2004), both located in north-eastern Brazil, State of Piauí. Fragaszy et al. (2004a) observed several individuals cracking open palm nuts using stones and anvils in Fazenda Boa Vista (Fragaszy et al. 2004a; see Fig. 1). Four hundred kilometres away, in the Serra da Capivara National Park, capuchins were observed using stones to access embedded food by percussion and by scraping, and sticks to probe for honey and to flush vertebrate prey (Mannu and Ottoni 2009). The capuchins observed by Mannu and Ottoni (2009) sometimes exhibited sequential use of tools and seemed to have a broader tool-kit (i.e., a set of objects used as tools) than wild capuchin monkeys elsewhere.

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[1] Recent molecular analysis has revealed that capuchin monkeys, formerly identified as the single genus *Cebus*, are two genera, with the robust (tufted) forms (including *libidinosus*, *xanthosternos*, *apella* and several other species) now recognized as the genus *Sapajus*, and the gracile forms retained as the genus *Cebus* (Lynch Alfaro et al. 2012a, b). The nomenclature for *Sapajus* is registered with ZooBank (urn:lsid:zoobank.org:act:3AAFD645–6B09–4C88-B243–652316B55918). To date, tool use has been observed in some species of wild *Sapajus*, but no species of wild *Cebus*.

Fig. 1 An adult male uses a stone hammer to crack a palm nut (*A*) on a wooden anvil (the nut is not in view), and (*B*) on a sandstone anvil (Photographs by Elisabetta VISALBERGHI).

Reports of percussive tool use in other populations of capuchin monkeys followed soon after (for review see Ottoni and Izar 2008). In the Brasilia National Park, a preserved area of the *Cerrado* Biome of Central Brazil, Waga and co-workers (2006) observed several instances of tool use performed by a few *C. libidinosus* (now *S. libidinosus*) belonging to two neighbouring groups. To exploit the encased fruits of the jatoba fruit (*Hymenaea courbaril*) and macauba nut (*Acrocomia aculeata*), the capuchins used stones weighing on average 654 g; both pounding stones and anvils were weathered pieces of cement from the nearby pavement.

Further data were obtained through surveys and interviews. Canale et al. (2009) surveyed the dry forest and thorn scrub (*Caatinga*), the Brazilian bush savannah (*Cerrado*) and the wet Atlantic forest in the States of Alagoas, Bahia, and Minas Gerais. They conducted 250 interviews in which the presence of capuchins was confirmed. One hundred and seventy-seven of these were done in the wet Atlantic forest and 73 in dry forest (20 in *Cerrado* and 53 in *Caatinga* habitat). Nut-cracking behaviour was reported by local residents in 26 localities, all in dry forests (20 in *Caatinga* and 6 in *Cerrado*). On the basis of visits to anvil sites (likely to be used by capuchins) and information obtained from local residents they found evidence of stone tool use for both wild yellow-breasted capuchins (*C. xanthosternos*) and bearded capuchins. Overall, all the anvil sites found and the reports of nut cracking obtained from local residents were in dry environments described as highly seasonal *Caatinga* or transitional areas between *Caatinga* and *Cerrado*. Canale and co-workers also surveyed a number of places in wet Atlantic forest and carried out more than 160 interviews in these areas. Although nuts from palm trees and stones were sometimes available, no evidence of nut cracking was found in these wet areas.

Ferreira et al. (2010) carried out a survey in the State of Rio Grande do Norte (*Caatinga* habitat). They systematically noted the weight of hammer stones found on anvils (presumably used for nut-cracking by individuals of two groups of bearded capuchins not yet habituated to human presence) and identified the species of the broken nut shells found on the anvils. The finding that hammer weight differed according to nut size indicates a certain degree of selectivity in the use of hammers.

2. Tool Use in Wild Capuchins and Terrestriality

As mentioned in the prologue, the chances of manipulating stones and finding horizontal surfaces on which to pound them are higher for terrestrial monkeys than for arboreal ones. Visalberghi et al. (2005) predicted that in sites with nuts, stones, and anvils, the chances to discover tool use for cracking nuts would be higher in capuchin populations that spend more time on the ground than in more arboreal populations. This prediction is supported by the recent review of Ottoni and Izar (2008) showing that in wild capuchin populations, the use of tools to access encased food is limited to those living in the *Cerrado* and *Caatinga* habitats, and by the systematic survey carried out by Canale et al. (2009) showing that tool use routinely occurs in more terrestrial populations inhabiting dry forest environments but not in more arboreal populations living in wet environments.

However, an accurate comparison of the time spent on the ground by capuchins living in dry and wet habitats would require quantitative data systematically collected on many populations. Unfortunately, few field studies report the percent of time spent on the ground (possibly because capuchins rarely do so in wet habitats where they have been well-studied). However, the available data indicate that the capuchins living in *Cerrado* and *Caatinga* habitats spend more time on the ground than those living in more wet environments (Spagnoletti 2009). Therefore, the distribution of stone tool use in capuchins supports the hypothesis that terrestriality favours the discovery of nut cracking.

3. An Overview of Nut Cracking in Wild Capuchin Monkeys at Fazenda Boa Vista

Our study area is located at Fazenda Boa Vista (9°39' S, 45°25" W; hereafter FBV), a privately owned land 21 km northwest of the town of Gilbués (Piauí, Brazil). FBV is located in the transition area between the *Cerrado* and the *Caatinga*. It is a sandy plain at approximately 420 m above sea level, punctuated by sandstone ridges, pinnacles and plateaus surrounded by cliffs composed of heavily-eroded sedimentary rock. The climate is seasonally dry (annual rainfall 1,156.00 mm, total rainfall during dry season, April to September 230.00 mm, data from 1971 – 1990, source: Embrapa).

Behavioural observations were carried out on two groups of wild capuchins: the Chicao group and the Zangado group. Research began in 2005, but systematic observations of the behaviour of the two groups started in June 2006. Tool use occurred year-round and its monthly frequencies did not differ between groups or between wet and dry seasons (Spagnoletti et al. 2012). Infants start to practice nut cracking when about 6 months old but do not become proficient until the end of the second year of age or during the third year (Visalberghi and Fragaszy 2012). Of the 23 healthy capuchins old enough to use tools, only two females were never seen to crack nuts with stones. Among adults, males use tools to crack open palm nuts about three times more often than do females (Spagnoletti et al. 2011).

In the open woodland of FBV, palms are abundant and produce fruit at ground level. FBV capuchins exploit four species of palm nuts: tucum (*Astrocaryum campestre*), catulè (*Attalea barreirensis*), piassava (*Orbignya* sp.), and catulí (*Attalea* sp.). Typically, the capuchins collect the palm nuts by plucking one nut from the cluster, pulling and turning it until it comes loose. The mesocarp of catulè, catulí and piassava (but not of tucum) is thick, and capuchins usually eat it until the woody endocarp of the nut is exposed. At this point, they can either immediately look for an anvil provided with a hammer stone (anvil site) to crack the nut, or leave the nut on the ground. In the latter case, they may recover the nut some time later and, then, look for an anvil site.

The resistance of the structure of the nuts varies across nut species (Visalberghi et al. 2008). The mean peak-force-at-failure values were 5.15 kN for catulè, 5.57 kN for tucum, 8.19 kN for catulí, and 11.50 kN for piassava. All four species of palm nuts exploited by capuchins are 13 times more resistant than walnuts (*Juglans regia*), and the piassava nuts are approximately as resistant as the panda nuts cracked open by chimpanzees.

Whereas chimpanzees are seated when cracking nuts, wild capuchins most often adopt a bipedal stance, raising and rapidly lowering the hammer by flexing the lower extremities and the hip. Proficiency in cracking nuts with tools varies widely among wild capuchins, even when the same hammer stone and the same anvil are used to crack open nuts of the same palm species (Fragaszy et al. 2010a, b). In Fragaszy et alia's sample, the most efficient monkey opened on average 15 nuts per 100 strikes (6.6 strikes per nut) whereas the least efficient monkey opened on average 1.32 nuts per 100 strikes (more than 75 strikes per nut). They also report that the efficiency of one physically fit adult human male (20 years, 185 cm, 78 kg) striking the same species of nuts with the same stone, was 16.1 nuts per 100 strikes (6.2 strikes per nut).

Body weight and diameter of the nut best predicted whether a monkey would crack a nut on a given strike: increasing body weight improved the likelihood of cracking the nut; increasing diameter of the nut decreased the likelihood. In fact, smaller capuchins (such as females and youngsters) often fail to crack whole nuts even after numerous strikes with a stone that weighs more than 50% of their body weight (FRAGASZY et al. 2010a, b).

4. Selectivity of Hammer Stones: Behavioral Observations

In the wild, tool selection has been inferred in chimpanzees by comparing the features of hammers and anvils used to crack open different species of nuts. BOESCH and BOESCH (1983) examined the characteristics of anvils and hammers present in the tool sites (ateliers, in their terminology) used by the Taï chimpanzees to crack open nuts and showed that (*a*) the high-resistance Panda nuts (*Panda oleosa*) were more often cracked open on stone anvils than on wood anvils and (*b*) with stone hammers more than with wooden hammers, and that (*c*) chimpanzees used heavier stone hammers to crack open Panda nuts than the less-resistant Coula nuts (*Coula edulis*). These findings indirectly demonstrate that chimpanzees use functional tools, by taking into account the properties of the different nut species. Subsequent observations confirmed this pattern of tool use in Taï (BOESCH and BOESCH-ACHERMANN 2000) as well as in Bossou (MATSUZAWA 1994). On the basis of detailed behavioural observation, MATSUZAWA wrote that Bossou chimpanzees “can recognize the functions of the tools and which stone or combination of stones function best” (MATSUZAWA 1994, p. 361).

To efficiently crack nuts, FBV capuchins need to be selective in their tool choices. In the home range of our two capuchin groups, surfaces suitable as anvils and palms are relatively common; in contrast, stones that are large enough and hard enough to serve as hammers are rare (VISALBERGHI et al. 2009b). Sandstone – the most common stone in the area of FBV – is not suited to crack open high resistant nuts since it breaks during use. Other types of stones, like quartzite and siltstone, which are quite rare in the area, are needed. Furthermore, the elements indispensable for tool use (i.e., hammer stones, anvils and nuts) co-occur only in the cliff-plateau and in the talus (the transition area between the cliff and the plain). Thus, when these elements are not in the vicinity of one another, capuchins have to transport the nuts and/or the stones to the anvil. Since stones are transported for some distance (VISALBERGHI et al. 2009b) and transport involves a cost, selectivity in tool choice is extremely important (Fig. 2).

Field observations indicated that adult capuchins take into account the resistance of the food item to be cracked when transporting and using a stone as hammer. Capuchins use hard and heavy stones, suitable to overcome nut resistance (such as quartzites and siltstones) more often than unsuitable ones (such as weathered sandstones). Conversely when exploiting encased foods less resistant than the nuts, they transport and use soft stones (SPAGNOLETTI et al. 2011, VISALBERGHI et al. 2009b).

Fig. 2 (*A*–*H*) Chicao, an adult male weighing 4.4 kg, transports two palm nuts (in its left hand) and a hammer stone weighing 1.8 kg to a wooden anvil (Photographs by Noemi Spagnoletti).

However, observation of spontaneous behaviour is insufficient to demonstrate active selection of tools on the basis of their functional characteristics. Other processes may increase the chance of encountering functional tools in proximity to anvils and lead to the use of functional tools without active tool selection by the individual. For example, an individual may repeatedly use the same tool sites and therefore encounter tools already selected by others, and/or it may keep using the same tool that has been successful ("tool fidelity", Biro et al. 2006). Therefore, tool selectivity should be tested by providing individuals with functional and non-functional tools and observing their choice and use patterns.

So far, tool selectivity has been investigated almost exclusively in captive settings, mainly by requiring subjects to choose between functional and non-functional sticks to retrieve food, or to dip for it (e. g., New Caledonian crows, *Corvus moneduloides*: Chappell and Kacelnik 2002, 2004; Woodpecker finches, *Cactospiza pallida*: Tebbich and Bshary 2004; capuchin monkeys: Fujita et al. 2003, Cummins-Sebree and Fragaszy 2005; chimpanzees: Hirata 2006; orang-utans, *Pongo pygmaeus*, and gorillas, *Gorilla gorilla*: Mulcahy et al. 2005). Especially in the last years great attention has been paid to tool use in birds often comparing their achievements with those of nonhuman primates. Naturally tool using species, as New Caledonian crows and woodpecker finches (*Cactospiza pallida*), show some understanding of the requirements of tasks in which they had to select stick tools of the appropriate length or diameter to retrieve a piece of food (Chappell and Kacelnik 2002, 2004, see also Bluff et al. 2010, Tebbich and Bshary 2004). Tool selectivity has also been investigated at length in naturally and non-naturally tool using primate species, such as cotton-top tamarins (*Saguinus oedipus*) (Hauser 1997), capuchins (Cummins-Sebree and Fragaszy 1995), lemurs (*Lemur catta* and *Eulemur fulvus*, Santos et al. 2005) and apes (Herrmann et al. 2008). All these species can take into account tool functional features and solve the task more or less efficiently; apes, however, usually outperform monkeys.

Only a few studies have investigated selectivity in the context of stone tool use. Aumann (1990) reported that one captive black-breasted buzzard (*Hamirostra melanosternon*) that dropped stones on domestic hens' eggs preferred a 40-g stone from a range of stones weighing 15–65 g. Similarly, wild and captive Egyptian vultures (*Neophron percnopterus*) provided with models of ostrich eggs and a range of stone sizes (27–232 g) preferred 46-g stones (Thouless et al. 1989). In an early study of hammer tool selection by captive capuchins, subjects were presented with a choice of three potential tools of different weight (a stone, a wooden block, and a plastic container) to crack open coated nuts (Antinucci and Visalberghi 1986). Although the functional stone was preferred over the other two non-functional objects, this paradigm did not allow for assessment of which features of the objects (e. g. their visual appearance or their weight) guided the capuchins' choices. More recently, captive capuchins were presented with choices among three visually identical objects of different weight and two out of three subjects learned to select the heaviest tool. In a subsequent condition, when capuchins were required to choose between a small heavy object and a large light object, only one subject learned to select the small heavy object (Schrauf et al. 2008).

However, no study has yet experimentally addressed the issue of stone-tool selectivity in wild non-human primates. To this purpose, we repeatedly provided FBV capuchins with sets of tools varying in specific properties (Visalberghi et al. 2009a; Fig. 3). Specifically, we aimed to assess whether capuchins select stones typically available in their habitat according to their functional characteristics, and whether they use stone weight as a prominent feature guiding their tool selection.

Fig. 3 The setting in which the experiment was carried out. Here, the experimenter has placed two artificial stones of the same visual appearance but different weight (Same Size–Different Weight condition), as seen on the left side of the image. The subject was provided with a nut (not in view) and is moving towards the artificial stones. After choosing a hammer stone, the subject can move to the wooden anvil (on the right), to the sandstone anvil (on the upper left), or to other anvils present in the area (not shown) (Photograph by Elisabetta Visalberghi).

As shown in Figure 3, capuchins were tested opportunistically in a familiar area. We individually presented eight capuchins with stones differing in functional features (material, size, and/or weight, according to condition). In each trial, subjects were given a nut and required to choose between (or among) functional and non-functional stones, and to transport the selected stone to one of the two anvils located 4 m away, or to other anvils farther away. In the first two conditions, when no other stones were available in the area, subjects were required to choose between natural stones, similar to those they usually encounter in their habitat, differing in friability and in size and weight, respectively. In the next three conditions, subjects chose between novel artificial stones, made with the purpose of controlling the variables of interest (size and weight). Here, in all conditions subjects should choose the stone heavy enough to crack open the nut. Furthermore, in one condition, to select the most functional tool capuchins had to disregard stone size since the heavier stone was the smaller one.

The capuchins were thus presented with various choices depending on the test condition: (*1.*) a sandstone *versus* a siltstone (*Friability* condition), (*2.*) a small *versus* a large quartzite (*Size and Weight* condition), (*3.*) two stones of the same size but different weight (*Same Size-Different Weight* condition), (*4.*) a light and large stone *versus* a heavy and small stone (*Conflicting Size and Weight* condition, in which weight did not correlate with size, as it is usually the case for natural objects of the same material), or (*5.*) a light and large stone, a light and small stone, and a heavy and large stone (*Three Stones Size and Weight* condition). Video clips of these experiments can be viewed at http://www.cell.com/current-biology/supplemental/S0960–9822%2808%2901624–2.

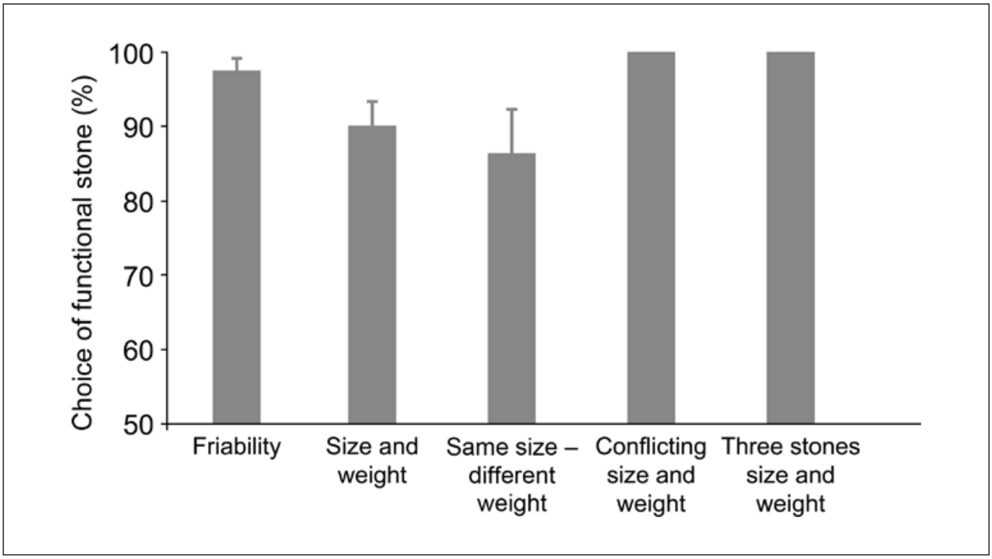

Fig. 4 Average percent (and SE) of trials in which the functional stone was chosen in the five experimental conditions (from VISALBERGHI et al. 2009a).

Overall, choosing the functional instead of the non-functional stone was mandatory for success. Already in trial 1, subjects touched first, transported and used the functional stone significantly more often than expected by chance (except one subject in the *Same Size-Different Weight* condition). Moreover, they always used the stone they transported to the anvil and never modified their initial choice (Fig. 4).

Interestingly, whenever visual cues were available and reliable, as with the natural stones, capuchins always touched the functional stone first, suggesting that they discriminated between stones by sight. In contrast, when visual cues were not predictive or conflicting, as with the artificial stones, individuals gained information about the weight of the experimental stones by moving, lifting and/or tapping them. Conversely, in the conditions with natural stones, where visual cues were available, no subject performed tapping behaviour on either stone. Capuchins tapped the artificial stones to generate acoustic or haptic information (Fig. 5). We argue that by tapping they could infer the weight of the stones based on their previous knowledge of the different sounds or haptic sensations that objects of different densities produce (see also SCHRAUF et al. 2008, FRAGASZY et al. 2010a, b, VISALBERGHI and NÉEL 2003). In sum, wild capuchins faced with stones differing in functional features (friability and weight), choose, transport and use the most effective stone to crack open nuts. Moreover, when weight cannot be judged by visual attributes alone, capuchins act to gain additional information to guide their selection.

In conclusion, when experimentally tested, FBV capuchins consistently and immediately selected among novel functional tools, regardless of the condition intricacies. Furthermore, systematic field observations showed that they habitually use stone tools and select them according to the resistance of the nuts they exploit (SPAGNOLETTI et al. 2011). Capuchin nut cracking behaviour therefore surpassed the most optimistic expectations and proved to be fully comparable to that described in wild chimpanzees that habitually use stone tools.

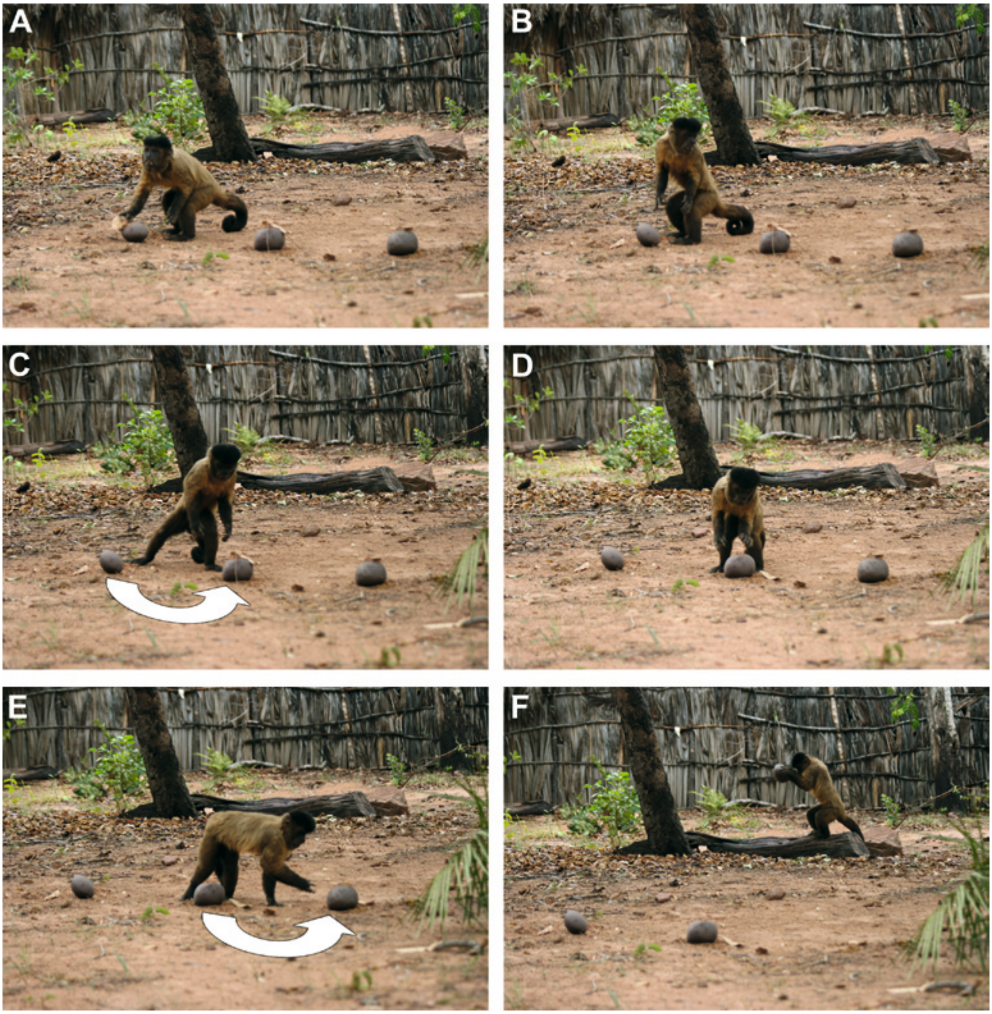

Fig. 5 *Three-Stones Size and Weight* condition. The stones are positioned as follows: left, small light stone; center, large light stone; right, large heavy stone (from the reader's point of view). Chicao, an adult male, contacts the left stone (*A*), turns his head towards the other stones (*B*), and switches (white arrow) to the middle stone (*C*). Then, he switches (white arrow) to the most functional stone (*E*), transports it to the wooden anvil (not shown), and lifts the hammer stone to crack open a tucum nut (*F*) (Photographs by Noemi Spagnoletti; from Visalberghi et al. 2009a).

Overall, FBV capuchins outperformed the captive ones tested in stone tool tasks (Antinucci and Visalberghi 1986, Schrauf et al. 2008), possibly because lifelong interactions with a wide variety of nuts and stones allow them to learn what these objects afford in a given context. This result is in agreement with the Ecological Psychology approach (Gibson 1979/1986), which argues that embodied perceptual knowledge gained through action supports flexible behaviour, and recognition of the affordances of objects develops in parallel with use and feedback from use. Thus, because experience strongly affects cognitive development, a more accurate appreciation of intelligence in nonhuman species requires carefully designed field experiments (Boesch 2007).

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Human Uniqueness – Constructions of Ourselves and Our Sibling Species: *Pan troglodytes* and *Pan paniscus*

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Abstract

Scientists interested in the origin of human mind are attempting to redefine the mental abilities which differentiate humans from chimpanzees. These exercises, being of relatively recent origin, represent a reaction to three discoveries: (*a*.) the ability of bonobos to acquire language through observation, in a manner equivalent to human children, (*b*.) the finding that chimpanzees and humans are sibling species, sharing approximately 99.4 % of their genome and (*c*.) the discovery that simple changes in early rearing variables effectively reorganize the brain in dramatically different ways. Before these findings emerged, scientists rarely attempted to define the characteristics of human mind. Language was the signature of humanity and it was to be only a matter of time till unique neurological and genetic structures would be found to account for its presence in human beings. But language capacities (and most other complex cognitive behaviours) proved difficult to locate in genes that were specifically human. The seemingly infinite plasticity of the human nervous system is evident. Similarly obvious is the brain's requirement for incessant feedback from a world of action, which it employs to self-organize in order to adapt to that world. As the brain self-organizes, through cultural feedback, the body begins to produce the patterns we have heretofore considered synonymous with 'human mind.' These discoveries have thus placed our definitions of 'humanness' under a new level of scrutiny. Scientists have become engaged in an illusive quest to find some simple means by which they may separate all humans from all apes – under all conditions. The most recent candidates are those offered by Hauser (2009). He posits the existence of four uniquely human traits: generative computation, promiscuous combination of ideas, mental symbols and abstract thought. He declares that the search for origins of human mind "will require explaining how these properties came about" (Hauser 2009, p. 46). Yet, each of these properties are continually manifest whenever language is employed in real life settings, to solve real world problems of behavioural co-ordination between individuals. Therefore any entity, human or ape, shown to be capable of acquiring a human language to coordinate behaviour, possesses Hauser's four faculties by default, and is human. Similarly, according to Hauser's logic, any human who does not possess language would not have a human mind.

Zusammenfassung

An der Entstehung des menschlichen Geistes interessierte Wissenschaftler versuchen derzeit, die geistigen Fähigkeiten neu zu definieren, welche Menschen von Schimpansen unterscheiden. Diese Bemühungen sind relativ neuen Ursprungs und eine Reaktion auf drei Entdeckungen: (*a*.) der Fähigkeit von Bonobos, sich Sprache durch Beobachtung in einer Weise anzueignen, die der von Kindern entspricht, (*b*.) die Erkenntnis, dass Schimpansen und Menschen Schwesterarten sind und etwa 99,4 % ihres Genoms teilen, (*c*.) die Entdeckung, dass durch einfache Änderungen in den Variablen der Aufzuchtbedingungen im frühen Alter das Hirn in grundlegend verschiedener Weise wirksam reorganisiert werden kann. Bevor sich diese Erkenntnisse herausbildeten, haben Wissenschaftler nur selten versucht, die Eigenschaften des menschlichen Geistes zu definieren. Sprache war das authentifizierende Merkmal des Menschseins, und es war nur eine Frage der Zeit, bis einzigartige neurologische und genetische Strukturen gefunden worden wären, die für ihr Vorhandensein beim Menschen verantwortlich sind. Jedoch erwies es sich als schwierig, die Sprachkompetenz (und auch die meisten anderen komplexen kognitiven Verhaltensweisen) in spezifisch menschlichen Genen zu lokalisieren. Die scheinbar unendliche Plastizität des menschlichen Nervensystems ist offenkundig. Ebenso offensichtlich ist der Bedarf des Gehirns nach konstanten Rückmeldungen aus der Wirkwelt (*world of action*), welche es einsetzt, um sich in einem Prozess der Selbstorganisation an diese Welt anzupassen. Während dieser Selbstorganisation beginnt der Körper, durch kulturelles Feedback, das Muster zu erzeugen, welches wir bisher als gleichbedeutend mit dem „menschlichen Geist" angesehen haben. Diese Entdeckungen erfordern daher eine strengere Prüfung unserer Definitionen von „Menschsein". Wissenschaftler haben sich auf eine illusorische Suche nach einfachen Wegen und Mitteln begeben, um alle Menschen von allen Affen abgrenzen zu können – und dies unter allen Verhältnissen. Die jüngsten Kandidaten dafür hat Hauser (2009) angeboten. Er postuliert die Existenz von vier einmaligen menschlichen Eigenschaften: generatives Errechnen bzw. Hervorbringen (von Worten, Ideen etc.) (*generative computation*), das Kombinieren von Ideen aus verschiedenen/vermischten Bereichen (*promiscuous combination of ideas*), mentale Symbole und abstraktes Denken. Er erklärt, dass die Suche nach den Ursprüngen des menschlichen Geistes „die Erklärung erfordert, wie diese Eigenschaften zustande kamen" (Hauser 2009, S. 46). Diese Eigenschaften manifestieren sich jedoch immer, so oft Sprache unter realen Bedingungen eingesetzt wird, um reale Probleme der Verhaltenskoordinierung zwischen Individuen zu lösen. Jedes Wesen, ob Mensch oder Menschenaffe, von dem gezeigt werden konnte, dass es im Stande ist, sich die menschliche Sprache zur Verhaltenskoordination anzueignen, besitzt daher von vornherein Hausers vier Fähigkeiten und ist menschlich. In gleicher Weise besäße ein Mensch, der keiner Sprache mächtig ist, nach Hausers Logik, keinen menschlichen Geist.

1. The Concept of Human Uniqueness

If we are to follow Hauser's behavioural definition, or any behavioural definition, then being human is about more than being born *Homo sapiens*, it is about being able to behave in certain ways typically attributed to human beings. All behaviourally based definitions are at odds with the legal perspective of humanness – which holds that any being manifesting a human form (and able to live outside the womb) is 'human,' regardless of the mental abilities that person might, or might not, possess. Similarly, any being bearing the physical appearance of an ape, is classified as an ape, regardless of the mental abilities that being might, or might not, possess. Under the law, all apes are property and automatically deemed incapable of possessing rights or personhood. Cultural regulations regarding how they must be housed and treated are designed to maintain this assumed difference. This assumed difference is now at odds with the extent scientific evidence. Thus scientists, such as Hauser, are searching for new ways of bringing 14th century legal concepts into more satisfactory alignment with scientific evidence. To accomplish this, they must seek acceptable means of carving a firm and deep divide between sibling species.

It is tempting to conclude that this legal concept makes sense, even if there are some humans who don't have language and some apes who do, because most apes do not seem to have language and most humans do. The problem with this approach is that it is not just few human beings who lack language, all of us initially lack language. Each human must go through a process of human socialization, which is inextricably tied to language acquisition. This process changes the human from a nonlinguistic being into an entity capable of negotiating the human social world. Language and personhood are simply not coincident with the human form. They are coincident with all known extant human societies, but the acquisition of these capacities is not a given feature of being born human. They appear through a development process which is culturally instantiated, relatively fragile, and becoming increasingly more so.

Autism (the failure to achieve normal human socialization and/or language) is on the rise in all modern countries (Dade 2009). A myriad of subtle events during ontogeny can disrupt the appearance of linguistic behaviour, its accompanying personal narrative, and the development of a concept of self-identity (Greenspan and Shanker 2004). The most celebrated example of this is the children reared by wolves in India (Gesell 1941). These children never self-identified as human, nor did they acquire language. Even with many years of human care and much deliberate instruction, they moved, thought and behaved as do captive wolves. They steadfastly resisted the imposition of humanity that their caretakers attempted to inculcate within them.

The great plasticity of the genome and the human nervous system permits the infant human to acquire behaviours and thought patterns we would typically associate with nonhuman species (Doidge 2007, Raymont and Grafman 2006). It thus seems eminently logical to conclude that our sibling species (bonobos and chimpanzees) should manifest a similar degree of plasticity, and likewise display an ability to become human if immersed in human culture from birth. Of course, it would be essential that such an infant was intentionally reared to become human – rather than to become an intriguing pet or research subject – by those around them. Not all human rearing is equivalent. Human rearing can fail to produce linguistically competent children as well as linguistically competent apes. It is the *expectancy of becoming human*, not simply being with humans, that moulds the developing consciousness. The importance of rearing is revealed in the finding that apes not reared in the wild have as much difficulty learning how to survive in a forest, as do human children reared in cities. One must learn how to *become* an ape, just as one must learn how to *become* a human being (Laland 2008, Whiten 2000). It is in the process of this *becoming* that the seeming human/ape differences are generated.

2. Ape–Human Differences

The differences between humans and apes are illusive to define at the individual level, but this is not true at the species level. All non-captive chimpanzees live in the forest and are nomadic, while most humans live in city states under the rule of law, and have some form of written symboling skills. No chimpanzee groups have constructed city states, developed trading routes for material goods, raised armies, built monuments to deities, or flagellated themselves for breaking God's commandments. Indigenous human tribes still remain who, like chimpanzees, live in the forest and are nomadic. Such tribes, like chimpanzee nomads, have also failed to create city states or trading routes for material goods. They have not taught themselves to read and write, nor built monuments to deities. As recently as the last century there were aborigines in Australia whose tool kits were arguably only minimally advanced over those which chimpanzees produce today. Thus the mandate to create what we have come to call 'civilization,' does not exist in every human society, but it nonetheless exists only in human societies. Being 'human' appears to be a necessary condition for passing beyond the tribal state, but not a sufficient condition.

This implies that there is something humans are able to do together, but which they do not necessarily do together. This 'thing' enables our species to congregate in very large groups whose members remain essentially anonymous to one another. In these large groups humans find ways to collaborate and communicate which require no directly shared history or friendships. They are able to do so across vast spans of time and space. The ability to do this requires not only language, but a particular kind of language, which we shall call human language (to allow for the possibility that apes, in the wild, possess language, but one that is structurally unlike ours). All known human languages (with the possible exception of the Peridot language) possess an internal grammatical structure which bifurcates the self into an I and a me, thereby allowing its user to take on a persona, to internalize a personal self-narrative, and to thus become an agent who is enabled to perceive the self as having freewill. (The perception of freewill, as opposed to the concept of 'ultimate freewill,' exists in every human being who has acquired language.) The perception of freewill leads, inevitably, to the tendency of all human groups to hold individuals responsible for their actions, and eventually to the rule of law. These capacities define the essence of the human world, and science assumes they do not exist in the animal world. Because they are structurally embedded in every human language (some to greater degree than others), they appear to reside at the core of our being. As human beings, we cannot learn to speak our language, or become 'persons' in our culture, without adopting, and manifesting these concepts.

Hum*an language* enables us to construct worlds that are entirely mental, relationships that are entirely mental and objects that exist only in the mind. Once constructed, *via* language, these mental entities, rules, obligations and expectancies govern human action in its entirety. Consequently, different human beings in different cultures behave in dramatically different ways. It is not simply that different cultures employ different tools, different handshakes and different styles of dress and food. They construct their mental worlds, obligations, expectancies, and relationships in radically different ways; *so sufficiently different that even causality, time, and sexuality are not the same kinds of things from one culture to the next*. Therefore, to understand the origin of human mind then, we must ask how *human language* and human culture arose initially? If there were no human beings present who already had these skills to pass on to babies, what bootstrapped human language and human culture toward that which we know it to be today?

3. Human Language

The commonalities that exist across human cultures are few, but they include bipedalism, infant carriage, and human language. Human language has the embedded structural property of forcing the user to bifurcate the self into a doer and a viewer. Each human language user must eventually become both the impassioned ego-involved doer of all things and the more detached and reflective viewer of the same actions (that is one's own actions). Human language embodies the doer – who acts effectively in the moment – and the viewer – who constructs the internalized self and thereby contemplates past and future actions. The viewer eventually becomes (as linguistic skill increases) able to judge the appropriateness of the actions of the doer, according to linguistically instantiated behavioural norms. The viewer also begins to judge other individuals according to these same norms.

The viewer is typically associated with left-hemispheric function and language. The doer is typically associated with practiced patterned reactions, which can become governed and instituted by the cerebellum and rapidly executed. In between the viewer and the doer, exists the experiencer, which neither acts, nor judges. The experiencer is presumed to reside in the right hemisphere and to be responsible for the perception of the now, the constant awareness that one simply exists in the present, apart from ones actions and apart from ones judgements. As the child grows and acquires language, the doer (the I) and the viewer (the me) become integrated through the constant perception of the experienced self. It is the connection between these different but ever-active forms of consciousness that produces beings we think of as human. The ever present experienced self recognizes the body as an agent of freewill but does not itself take action. It is the ever present experienced self of which DESCARTES speaks when he states, “I think, therefore I am.” Human language lacks a structural grammatical role for the experienced self. That is, there is no linguistic counter-part to the roles assigned to doer and the viewer. Yet the experienced self is omnipresent in our lives, from our earliest memories until our death. Even in cases of amnesia, when the personality is lost, the ever present experienced self exists. It is a kind of silent watcher.

It is human language that drives the appearance and integration of these different conscious processing systems, or selves. The ever present need of the child to become human, in order to share the world of those around it, makes it seem as though something ‘innate’ is emerging from the child. Yet, it is not the inner mind that is structuring language acquisition, it is the outer language that is structuring the development of inner mind. The components appear to be ‘innate’ only because they are already lodged in the outer structure of human language. To be able to acquire a human language, the inner mind of the child must structure itself in a specific way, or he or she will fail. This skill enables each new user to participate in the social dynamic that surrounds him or her from birth by permitting the new user to ‘make sense’ of the world in the same manner as those around him ‘make sense’ of their world. To speak and to understand human language is to become human. To fail to do so is to fail to become human.

Were humanity to create a fundamentally different kind of language, one which, for example made no grammatical distinction between the terms I, me, you or we, this language would also create a different kind of human. It would result in dramatically new and different potentials for how humans would co-construct their joined interactions. We have believed that anything other than human language as we encounter it today to be impossible and thus searched inside the mind, rather than outside for the fundamental governing and binding structures of all human language. Perhaps we should ask instead, why (or how) did humanity come to design a language that constantly enables us to move back and forth between being engaged as a *doer*, who also has the property of being evaluated by the self who is a *viewer* of these same actions. Might the languages of other species lack this basic bifurcation at the level of the grammatical agent, and thus be unrecognizable to us as language? Bifurcated agency is the primary domain of our consciousness of language. From our earliest moments of existence our behaviours are described of those bifurcated agents acting upon objects and persons.

4. Human–Ape Divergence

With the discovery that chimpanzees and humans share 99.4 % of all non-synonymous DNA and 98.4 % of all known functioning DNA, the estimated date of the human/ape divergence leapt forward from 25 million years ago to 5 to 6 million years ago (*The Chimpanzee Sequencing and Analysis Consortium* 2005, WILDMAN et al. 2003). The 25 million year date was based upon the fossil record, coupled with assumptions regarding the amount of time presumed necessary to accumulate the required genetic changes for producing the human form. These estimates reflected our human biases, leading biologists to conclude that the number of genes in the human and chimpanzee genome would be far larger than proved to be the case. The degree to which biologists and palaeontologists were in error is a sobering reminder of how anthropocentric perceptions lead us astray when we consider our own origins.

The degree of DNA similarity and the more recent data of divergence (now well established) support the behavioural finding that bonobos and chimpanzees can acquire a human language. They support the finding that bonobos can intentionally produce, and fluently manipulate, complex vowel consonant patterns at a range and pitch that exceeds that of the human ear and the human temporal capacity. They legitimize the link between ape and man, that behavioural data began to manifest, when rearing parameters were equated between sibling species, in the 1970s, and languaged apes began to first appear.

The new dates of divergence remain a partial guess because of different methods of calibrating the molecular clock. When the rate of mutation is kept the same for all mammals (rather than being calculated exclusively for the human/ape divergence based on the interpretations of the current fossil record) the clock then suggests an even more recent date of divergence – 3.6 million years ago (Easteal and Herbert 1997). If this date is accurate it becomes possible that *Australopithecus africanus* (as well as *Australopithecus ramidus*) are ancestral to both humans and apes. This would also account for why there are no fossil apes in the record. In addition this date suggest that bipedalism predates knuckle walking and that knuckle walking is a specific adaption to carrying infants in a forest environment where long-distance travel in dense underbrush requires such an adaptation (Easteal and Herbert 1997). Chimpanzee and bonobo infants are frequently bipedal, and their knuckles lack the calluses that form later in response to habitual knuckle posture.

The greatest value of the genetic data lies not in its ability to estimate time, but in its capacity to precisely define the degree of relatedness, and the specific genetic differences, which separate chimpanzees and humans. When branching patterns for individual gene segments are compared between living chimpanzees, humans and gorillas; a far more complex branching picture has been found than was ever anticipated. There is evidence for a *Pan*/*Homo* clade, a *Pan*/*Gorilla* clade and a *Homo*/*Gorilla* clade. Such data have been difficult to integrate with the traditional paleontological drawings which depict a linear transition ape to human transition (Chen and Li 2001). Wider, and more complete, genomic comparisons reveal that whenever the human/bonobo/chimpanzee split occurred, it took more than four million years to accomplish and that the differences range over the entire genome (Patterson et al. 2006). In addition, the changes on the X chromosome are much more recent than those in the rest of the genome. This could happen only if hybridization continued beyond speciation itself. Thus, proto-humans and proto-chimpanzees were a ‘mixed species’ for three million years. They interbred for at least an additional million years following speciation. It is likely that chimpanzees, bonobos and gorillas continue to hybridize as well even today. There are sporadic reports of young apes being captured in Africa that appear to be gorilla/chimpanzee hybrids and bonobo/chimpanzee hybrids. Such findings bring into question evolutionary scenarios that depend upon strong evolutionary pressures for a large brain, bipedalism, vocal speech, etc. If such pressures were driving human evolution during speciation, it is unlikely that four million years of common genetic inter-change could have taken place.

Before the emergence of DNA sequence data, palaeontologists universally assumed that modern day apes had changed little from the common ancestral form. Humans, however, were thought to have undergone rapid change, as a result of inhabiting new climatic niches. This hypothesis also proved to be incorrect. The truth is that apes changed far more rapidly than humans since the divergence (Shi et al. 2006). Moreover, it was not the genes that code for anatomical structure that altered. The majority of changes have been in genes that code for inflammatory cell response and cell proliferation (Perry et al. 2008). While apes have improved their immunity profile, humans have accumulated oncogenes and pseudogenes, and lost a few functional genes. One of those functional genes codes for larger jaw muscles, chemoreceptivity and some aspects of keratin in the hair. Thus, our species has become, if anything, a reduced version of the chimpanzee genome, while the chimpanzee has become a kind of super-human genome. Chimpanzees accumulated large segments of replicated DNA, in some cases more than 100 copies of the human version of some genes. Most of the differences between human and chimpanzee DNA are due to expansions of the common genome, rather than to base pair substitutions that encode different proteins (Cheng et al. 2005). The highest number of duplications (> 400) map to the location of chromosomal fusion (or alternatively, chromosomal fission) on chromosome number two. They all lie very close to the centromere. Most of the remaining duplications occur exclusively on subterminal portions of the chimpanzee chromosome. Thus, the locations of human/chimpanzee genetic differentiation are not randomly scattered over the genome.

On the bases of a genome wide comparison of human and chimpanzee DNA, Cheng et al. (2005) propose that most of the asymmetrical increase of duplicated DNA in the chimpanzee lineage has emerged as a mechanistic consequence of changes in chromosome structure and is not due to selection. It is possible that chromosome number two fused or fissioned more than once during interbreeding, resulting in sudden morphological change and genetic loss in the line leading to Homo sapiens. Until we better understand what is happening to chromatic structure during mitoses and to epigenetic markers during embryogenesis, speculation about our large brain, our bipedal stride, etc. will continue to play a role in traditional palaeontology. However, the story told by the genetic data is already clear. Humanity is either an accident, or evolutionary theory, as currently understood, is insufficient to explain humanity's existence. Chromatin rearrangements are not consistent features of reproduction. Thus, they are not amenable to the slow selective forces – which act upon differential rates of reproduction, the staple of evolutionary theory.

As noted earlier, it is human behaviour in groups that is unique, not our behaviour as individuals. When human groups become so large as to prevent individual knowledge of relationships, they can only be maintained through human language and human culture. Since it is now accepted that culture, not just genes, is driving evolutionary outcomes; it has become clear that culture can select for changes in population traits such as the transport of serotonin, which dramatically affects mood. The rapidity with seeming innocuous cultural changes can alter genes and behaviour is only beginning to be realized (Chiao and Blizinsky 2009).

If we wish to understand the origin of this salient aspect of human uniqueness, we must try to understand what it is about the properties of *human language* that enable us to construct complex societies of individuals who do not know one another. Our language fosters the development of mental constructs that enable us to communicate with individuals we have not previously met – on the basis of a shared world view that has been instantiated by the common mental constructs of a common language. No chimpanzee society is able to accomplish such a feat. Should chimpanzees possess a language it will surely lack the kind of bifurcated agency present in human language. A bifurcated agency is required for the common construction of symbolic mental worlds, symbolic mental time travel, and the personal narratives that guide our lives, enabled us to represent ourselves and our intentions to one another… even if we have just met.

5. Cultural Humanness

Modern molecular phylogenetics enables us to trace the biological origin of *Homo sapiens* sapiens to Central Africa between 150,000 and 200,000 years ago. We also know the approximate dates and times that our ancestors moved out of Africa and into China and Europe (Liu et al. 2006, Mancia et al. 2007). However, there is a notable gap (of more than 80,000 years) between the anatomical appearance of the species we call *Homo sapiens sapien*s and the appearance of behaviours which are clearly associated with linguistic and symbolic processes, such as fire, beadwork, ochre, or stone tools flaked to precise patterns and dimensions (Lock 2000, Mithen 1996, Yellen et al. 1995). If we trust the archaeological record and assume that this gap is real, rather than the result of inadequate preservation (or current lack of discovery of appropriate remains) then human language and symbolic behaviour arose somewhere between 40,000 and 70,000 years ago. Prior to that time, there are no examples of representational art, fossilized forms of bodily decoration, hearths for cooked food, or indications of widespread trading. Therefore, we must assume that humans lived in Central African forest conditions similar to those inhabited by modern day bonobos, for a significant period of time prior to developing lifestyles that included fire, villages, trading, beadwork, weaving and other skills associated with all known living societies. The apparent absence of these skills before 40,000 years ago has been attributed to a lack of language ability. Consequently, the term *Homo symbolicus* is now employed to signal the arrival of a unique kind of human on the scene, one which differed behaviourally in important ways from all human beings who preceded them, but who retained essentially the same anatomy.

The current scientific evidence for human origins is converging in the direction of the oral legends of Longondo people who inhabit the Central African rainforest of the Democratic Republic of Congo. These people continue to share the resources provided by the forest with bonobos and to live in direct association with them. Because human and animal remains do not fossilize in the wet climate and acidic soil, no archaeological records exist for this part of the world. Here, humans depend completely upon the forest for survival, just as do bonobos, though humans access the forest resources in a slightly different manner. Their activities focus around village home bases with semi-permanent dwellings, fire, food gathering, food preparation and food storage activities that depend on fire (such as the smoking of meat, the production of alcoholic beverages, and the cooking and fermentation of food). Bonobos have no permanent dwellings (though they do return to the same nesting sites over and over), no fire, no food storage and no food preservation activities. They do practice some primitive forms of agriculture, and they make small dams in which to trap little fish. Most of the food resources consumed are common to both populations and are gathered daily from the forest. The exception is manioc, which bonobos are not reported to consume. Manioc requires special soaking in streams, to remove toxins, before it is edible by human beings.

The oral legends of this region say that bonobos and humans once lived as sibling species in the forest, both inhabiting trees and leading a nomadic life existence. During this period humans and bonobos purportedly shared a sufficiently common vocabulary as to make communication between the species possible. Today approximately 20 words are held to remain in common, including attack, electric eel, die, fire, and water. Bonobos are believed to hold religious practices and to maintain a knowledge of their kinship to humans. There are reports, for example, of bonobos assisting humans to the ground, when humans have become stranded in trees. There are also reports of bonobos retaliating against any specific human that kills one of them. The retaliation is not directed toward all humans, only toward the one that committed what is considered to be an act of murder. Additionally, bonobos are believed to engage in religious practices which involve ritual objects.

When bonobo and humans lived together in the forest, humans did not build huts, nor plant crops nor make fires. According to legend, it was the control of fire that caused humans to adopt a different mode of life, one that led to the need for huts on the ground. Huts enabled fires to keep burning, even during the rainy season. The desire to control fire and the building of huts led humans to abandon daily nomadic life and to construct semi-permanent villages. The bonobos are said to have understood fire and even to have learned to make fire, but they had no desire to keep their fires going. Instead they chose to move on and to allow their fires to die. According to legend, humans began to orient their lives around fire; for warmth, to keep predators at bay and later for food preparation. The Longondo people never let their fires go out. Even today there is always a small fire in the centre of every hut. There is also a religious component to the myth. It states that when the Creator placed men and bonobos on the face of the Earth, each one came to him for a face. The bonobos were late in arriving, and God had given out all the beautiful faces. The bonobos received the ones that were left. The Longondo people view bonobos as beings similar to themselves, who long ago decided upon an alternate path of life. Bonobos are not thought of animals, but as beings who possess the capacity, like themselves, to make rational decisions with knowledge and intent. They are believed to hold other bonobos (and human beings) liable for decisions that are not in accord with the norms and wishes of the group.

The overlap between oral legends and modern anthropological theory and data is intriguing. While oral legends can be easily invented, what would have led the Longondo people to such a story? Where they concerned with the degree of similarity between bonobos and human beings? Living in the same region and sharing the same forest does not necessarily lead the people of that region to invent stories about a common past with bonobos. These legends exist only in areas where people of Longondo origin live. It is only in those areas that bonobos are not hunted for meat, because they are considered to be ‘brothers’ to human beings. When hunters break this taboo, it is believed bad luck will befall them. In one village, there was a child who had been born with bowed legs. The people explained that the child’s mother had broken the taboo against eating the meat of bonobos while she was pregnant and that this caused the deformity experienced by her child. While this sounds outlandish by the current standards of science, these beliefs are real and powerful for those hold them, and they serve as strong deterrents to the consumption of bonobo flesh.

6. Language and Standard Genetics

No serious student of genetics continues to subscribe to the idea that a gene for language exists. However, certain productive skills associated with speech fluency may have begun with a point mutation in a single gene, the FOXP2 (Enard et al. 2002, Varga-Khadem et al. 2005). When the FOXP2 gene undergoes mutation in modern humans, affected individuals manifest a language deficit known as developmental verbal dyspraxia (Varga-Khadem et al. 2005). This is a disruption of the motor co-ordination and control required for *fluent human speech*. Interestingly, neither cognition, nor the ability to vocalize voluntarily are strongly affected. To study the general mammalian effects of this point mutation, mice were genetically engineered to contain a copy of the human version of FOXP2. The FOXP2 mice were more vocal than normal mice and they displayed increased synaptic plasticity and dendrite length in the basal ganglia (Enard et al. 2009, Lieberman 2009). Should early *Homo sapiens* have lacked the FOXP2 mutation, their ability to produce fluent speech would have been compromised. When the mutation appeared, the cognitive substrate for language (already in existence) would have allowed for rapid changes in the vocal system, rendering it free from the constraints on fluent sound production that characterize many mammals who are subject to predation.

The proposal that this gene acts, in a general way, to increase the tendency to vocalize is supported by the discovery that its up-regulation is also related to song acquisition in birds (Haesler et al. 2004). It is again supported by the observation that the chimpanzee version of the FOXP2 gene differs from the human version by only two amino acids. This lends credence to the view that the onset of *fluent speech* could have been a sudden, and recent, event with the incorporation of a single point mutation (Enard et al. 2002). Another gene has also been found which enables the human vocal cords to remain limber. When the human version of this gene (dubbed the ‘to speak’ gene) is compared with the chimpanzee version, it can be seen that the human version has a higher number of duplications (Clarke 2009).

Might Kanzi, a bonobo who is already attempting to emulate human sounds and who is vocally fluent, carry a different form of FOXP2 gene, the ‘to speak’ gene, than chimpanzees? The discovery of FOXP2 suggests that the intelligence of chimpanzees might currently be underestimated. They may possess the cognitive substrate for language, but lack the capacity for *fluent human-like speech*. Would a chimpanzee with the human FOXP2 inserted into their genome, be able to produce fluent sound and thus more readily attempt to emulate language?

7. Epigenetics, Embryogenesis and the New Genetics

The *standard theory* of evolution portrays the genetic code as being passed, relatively unchanged, from any given parent to any given child. Genetic variations that accrue across time had been thought to arise from four factors: (*a*.) sexual recombination, (*b*.) genetic drift, (*c*.) selection toward reproductive success (or fecundity), and (*d*.) random mutation. The standard theory is incorrect. A vast array of factors effects not only how the DNA is passed from one generation to another, but how the DNA is activated once it has been passed on. Defining how DNA is activated, and the profile of its activation, has spawned an entirely new field – epigenetics. This term *epi* refers to the phenomenon that certain kinds of events cause the genome to be activated in a specific manner and, once activated, to pass along markers of that activation, to offspring. This field was first defined in December of 2008 when Shilatifard offered the following account in *Genes and Development:* “an epigenetic trait is a stably heritable phenotype resulting from changes in a chromosome without alterations in the DNA sequence.” (See Berger et al. 2009, p. 781.)

Beyond epigenetic traits as defined by Shilatifard, there are additional factors affecting gene activation that do not seem to be inherited in a stable way, but rather in something like a dynamic way. For example, farm salmon have, across generations, come to display a different gene activation profile from that of their wild relatives, yet they retain the same genes. When wild and farm raised salmon mate, the gene activation profile of their offspring differs more from either parent, *more than* the parents differ from each other. Such is not predicted by natural selection. It suggests that the genome of the offspring is able to respond with a pattern of its own, a pattern that is unlike that of either the wild parent or the farm raised parent. This is the case even though the mating takes place in the wild and all the environmental factors acting upon the offspring are the same as those acting upon offspring from two wild parents. This suggests that the environment may be shaping the organism, not by random selection or differential mating, but through direct action upon the genome itself.

The field of epigenetics has rapidly expanded to encompass gene activation profiles, methylation events, parental imprinting, environmental stimuli (and many more phenomena which were relatively obscure prior to the ability to rapidly sequence the genome) and is beginning to provide an entirely new picture of how biological forms change across time. Many scientists struggle to interpret their work within the confines of evolutionary theory. The genetic sequencing techniques appear to be leading biology into free-fall through a whole new door of understanding with regard to the transmission of life. Surprisingly, it was the arrival of mammalian cloning that drove many new explorations into how life passes from one generation to another.

Cloning is a not natural process for animals that reproduce by sexual selection. The discovery that mammals could be cloned from a single adult cell, by reprogramming it to a state pluripotency, seemed to open up the striking possibility that each person, if they wished, could simply create a copy of themselves to carry on, when their body wore out. But once science proceeded beyond its initial fascination with the potential of cloning; it began to try to resolve an often overlooked fact regarding all clones; *most of them do not make it through embryogenesis*. Each successful clone requires a large number of *in vitro* fertilization trials to produce a single viable embryo. Initially, it was thought that once the techniques of obtaining and working with cloned cells became more advanced, the rate of successful clones would rapidly increase. Instead, it was found that embryos typically require epigenetic markers from both parents to make it through embryogenesis (Janis and Bird 2003). This led to attempts to better understand what happened to epigenetic markers during embryogenesis. Much to the amazement of the scientist doing the research, the epigenetic markers from both parents were found to be stripped off during embryogenesis and reintegrated such that each stage of embryonic development has its own characteristic epigenetic profile. According to Shi and Wu (2009): “Preimplantation embryo development involves four stages: fertilization, cell cleavage, morula and blastocyst formation. During these stages, maternal and zygotic epigenetic factors play crucial roles. The gene expression profile is changed dramatically, chromatin is modified and core histone elements undergo significant changes. Each preimplantation embryo stage has its own characteristic epigenetic profile, consistent with the acquisition of the capacity to support development. Moreover, histone modifications such as methylation and acetylation as well as other epigenetic events can act as regulatory switches of gene transcription. Because the epigenetic profile is largely related to differentiation, epigenetic dysfunction can give rise to developmental abnormalities."

This raises the following question. If the genes are determining the process of embryogenesis, why are epigenetic markers stripped away and why does each stage of embryogenesis have its own gene activation profile as determined by those markers? To make matters more complex, Shi and Wu (2009) also note that different mammalian lines have different patterns of removing and replacing epigenetic markers during embryogenesis. The embryogenic process observed in the mouse has no direct relevance to embryogenic process in human beings. Perhaps it is because each mammalian line has its own means of responding to the presence of epigenetic markers during embryogenesis (Fulka et al. 2004), that breeders of domestic animals find it possible to quickly produce extreme phenotypic variation in a given line, such as the domestic dog, but essentially impossible to move from "dogness" toward "catness" through artificial selection. This raises the question of "how does natural selection (a far slower process) do it?"

Not only do the stages of embryogenesis have different gene activation profiles, each cell is expressing its own unique activation profile during development. This profile is constantly changing in relation to all the other cells which are doing the same thing. While a mechanistic explanation of the genesis of life during embryogenesis may be attainable at some point, the number of variables that are co-acting in a constant state of change will make this extremely difficult and not readily attainable in the foreseeable future. The embryonic changes taking place can be effected by genes, by epigenetic markers and by the inter-uterine environment itself (which can be affected by activities of the mother). The degree to which external factors are acting upon the developing embryo during embryogenesis remains unknown. However, the fact that the epigenetic markers are stripped away provides an opportunity for nongenetic events to affect how the markers are reintegrated into the DNA. The markers added to the DNA while an adult was experiencing some external or internal event are not transmitted directly to the infant. They are stripped away and added in a new context. Perhaps they are able to somehow code for both environmental contexts that affected the parent and ones that are present during embryogenesis. Obviously, the greater the ability of the environment to affect embryogenesis directly, the less the need for a large genome equipped with genes that define how the phenotype of the offspring will construct itself.

It appears that something is going on during embryogenesis that is not easily reducible to genetic transmission, to epigenetic transmission, or to any currently known mechanistic process. Once epigenetic markers are stripped away, how does the embryo know where to attach them at a later stage in development? Such questions mandated a new definition of epigenetics a year after the first one was offered. In the new definition –"Epigenetics refers to a collection of mechanisms that can cause a change in the phenotype of a cell or an organism without altering its DNA sequence [...] these epigenetic events constitute a particular signal for each cell. Early studies focused largely on the effects of DNA methylation and the regulation of histone modifications on preimplantation embryo development.

Further studies have added chromatic organization (core histone variants) to this epigenetic regulation network, making it more complex, intriguing and – more importantly – making the start of life more mysterious and beautiful."

Linear evolutionary theory has been effectively challenged at the level of the single cell organism. Bacteria pass genes back and forth in a horizontal manner – which means that bacteria are constantly co-evolving as a population in and of themselves (Vetsigian et al. 2006). Bacteria are not competing against one another in the body, rather they are co-operating with one another in a constant dance of co-survival. It is no longer really appropriate to think of them as "good bacteria" and "bad bacteria" – or in many cases perhaps even as "different species" of bacteria. Rather, they are more appropriately characterized as different instantiations of form, each of which is designed to help promote the flow of life. With the development of multi-celled organisms and sexual reproduction, horizontal gene transfer is not directly accomplished. However, the principle that organisms are co-operating to ensure a kind of co-survival may emerge in a different manner. Since epigenetic markers are stripped away during embryogenesis and then returned, the developing embryo is undergoing a period during which magnetic fields, light, fluids within the mother's body, etc. have the potential to act upon it and perhaps upon how the epigenetic markers are reattached as well as to add new epigenetic markers that could dramatically affect development from embryogenesis forward. Restriction enzymes present in bacteria and archaea react to light and are able to cut DNA at specific points in response to light (Schierling et al. 2010). During embryogenesis then the possibility exists that gene segments could be moved around and/or duplicated. Bacteria utilize epigenetic markers as kind of immunological system, thus they might pass their immunity on to their hosts as well in some way. Expression of certain genes in bacteria, are regulated by the methylation of GATC sites. The cells' environment conditions just seconds after DNA replication determine if a methyltransferase is blocked from methylating certain regions.

Since the biggest change between chimpanzees and humans has to do with immunological systems (not anatomical systems), we should not let our former ideas about evolutionary theory and vertical evolution prevent us from seeing what the new data is unfolding to us. Surely, if humans and chimpanzees required 4 million years to speciate, they faced similar immunological challenges. Additionally, when humans and chimpanzees live together today in bicultural communities they face immunological challenges that are again converging, instead of diverging as in the recent past. The effect of bicultural rearing upon the bacteria, archaea and epigenetic profiles, and the effect of immunological profiles upon neurological development await future understanding.

8. The Biology of Mind

The dance between biology and behaviour, to the degree that it includes 'mind' – must come to grips with the differences between minds that lack language and minds that possess language. To the extent that human minds affect deep biological processes, through the vehicle of human language, the standard practices of studying disease, which depend upon animal models designed so as to ignore the role of the mind. Yet, data continue to indicate that the mind can affect the body, and the degree to which it does and/or can do so is only beginning to be understood. Essentially, any aspect of bodily function that is not normally conscious can be affected by conscious thought as long as the individual's attention is drawn to the role of thought, through the provisioning of feedback that can be seen and interpreted by the conscious mind.

Moreover, diseases long thought to be a function of specific genes, such as lupus, have now been found to affect identical twins in different ways, depending upon the degree of ontogenetically produced DNA methylation. Those twins with a greater number of DNA methylation events do not manifest lupus, while their common genetic partners, with less DNA methylation event do. Is lupus a genetic disease or an epigenetic disease? If it is an epigenetic disease, are the markers passed from parent to child or are they laid down by the environment, or by the embryo itself during embryogenesis?

Aging is another aspect of biology that has been attributed to genetics. During the normal aging process the telomeres begin to shorten, and the chromosome loses its protection from fusion, fission or rearrangements with other chromosomes, resulting in abnormalities which can lead to cancer and/or other infirmities associated with age. However, stress can also cause telomeres to grow shorter in young individuals. Since the number of stress events anyone experiences naturally increases with age – it is possible that aging itself is a function of stress. In a study by EPEL, young mothers caring for severely ill children were found to have telomeres that were significantly shortened compared to mothers caring for healthy children, thus increasing the likelihood that during cell reproduction some anomalies would arise (EPEL et al. 2004). Obviously, caring for severely ill children is a stressful event. But the most intriguing aspect of this study was the finding that mothers of healthy children, who self-identified as feeling under stress due to childcare burdens, also experienced telomeric shortening. Thus, overt stress and perceived stress had the same capacity to penetrate to the heart of the molecular machinery within the body's cells and to effect changes that have been shown to be associated with aging, through the action of the mind.

The standard medical model has inadvertently overlooked the role of the human mind, because of a conviction that the body has, shall we say, "a mind of its own." That body-mind is thought to be the same for animals and humans. But lacking language, animals are unable to form a concept of perceived stress, apart from experienced stress. Lacking language and the capacity to self-reflect, they must experience a world without constructed time, linear cause-effect thought, moral judgement, criticism, episodic memory, mental time travel and/or moral responsibility (SUDDENDORF and CORBALLIS 2010). The phenomenon of perceived stress, or feared future stress requires the ability to engage in mental time travel and this capacity is the largest contributor to human health issues. Humans constantly ignore the present in order to worry about the future. Concern and worry naturally arises in a human mother when her child is ill. However, it can also arise when the child is fine, because even healthy children can become ill. The stress of the mother is then conveyed to the child through expressions, intonation, gesture and hormonal cues and the child shares the perceived stress.

A moments' reflection upon such facts is sufficient to realize a medical model which treats the bodily as a mechanical repository of bacteria, organs, vessels, pumps and electrical energy eliminates any responsibility, or opportunity, the patient might bring to their own control of bodily processes. It is well known that humans can control most unconscious bodily processes (for example brain waves), if given sufficient external feedback.

Possibly, if patients were provided feedback regarding the activation and deactivation of genetic code, they might be able to exert similar control.

The placebo effect is the classic example of the power of the mind. Some placebo effects can be attributed to conditioned responses, but these are minimal and extinguish rapidly. The long-lasting powerful *placebo effects are generated by conscious expectations*, which arise upon hearing the comments of the physicians (Breidert and Hofbauer 2009). Even statements such as "This medication has ***no*** active agent but it has helped a lot of people," will produce a strong placebo effect. Thus, the knowledge that a drug contains no active agent is easily over-ridden by faith in the recommendation of the doctor. Such studies reveal that the power of the drug lies as much within the belief of the physicians as in the drug itself. Doctors, like shaman, hold control over life and death and by placing their belief in the doctor, rather than in themselves, the patient may be dismissing important internal capacities. While medical procedures clearly stitch together wounds, remove tumours and set bones, it is the body that does the healing. The lack of awareness of conscious participation in this process has led the patient to attribute healing to outside factors.

Equally important for the practice of modern medicine is the existence of the nocebo effect (i. e. telling the patient that their conditions are likely to become much worse). The nocebo effect is probably more potent than physicians realize, because most nocebo tests are deemed unethical (Benedetti et al. 2007). That is, one cannot tell patients that they are about to become ill, or die, when such is not the case. In one approved nocebo study patients were given a drug which they were told would cause some pain. The patients not only experienced pain but displayed fMRI changes identical to those known to be produced in patients who were given noxious stimuli (Kong et al. 2008).

Apes who have acquired language and self-reflective thought *could* serve as appropriate animal models, although it would be unethical to use them in that way. Apes are very sensitive to the effects of language and show placebo effects. For example, if Kanzi is given a shot, along with the spoken information that the injection contains ketamine, he will soon begin stumbling about as though his co-ordination is failing him and then he must lie down and rest. The behaviour is exactly like that he displays upon receiving an actual injection. The 'loss of co-ordination' which one experiences under ketamine cannot be faked. Under a normal injection, the ape's body fights to move in a very clumsy way as the ketamine takes effect and to imitate that progressive lack of co-ordination is not possible. Kanzi appeared to experience the brain events that accompany a true injection just as did the human patients in the Kong et al. (2008) study.

Kanzi also feels anticipatory stress when told of events that will happen, and/or when he himself invents events that could happen. For example, the large beaver that demolishes trees is perceived by Kanzi as potentially able to chew through his door at night and attack him, should it want to do so. Kanzi has constructed this belief, even though there is no basis for it in reality. He will maintain its potential in the face of assertions by others to the contrary. Kanzi and Panbanisha display cause-effect reasoning, moral judgement, mental time travel, episodic memory, criticism, moral responsibility and self-reflection. Should they become permitted to assume responsibility for their own actions, they would be sensitive to expressed potential contingencies and behave accordingly. These abilities may or may not be properties pluripotent for all apes and all humans, but they are pluripotent in users of *human language.*

9. The Emergence of the Self as Active, Reflective Intentional Agent

The *languaged human mind* begins its development prenatally, forming a special sensitivity to the sounds and rhythms of the human mother even as it constructs itself. As soon as the infant emerges, it is imperative that the mother supports it and keeps it warm or it will die quickly. Unlike all other primates, it cannot cling and thus the human mother cannot treat the infant as an extension of her own body as she moves through space. Ape infants become extensions of the mothers body within minutes after birth. From its very entrance into the world, the human infant undergoes a radically different *self-other* embodied experience. It is an object that is swaddled, carried, passed around, rocked, spoken to, picked up, put down, attended to – and sometimes not attended to, but left to cry. It has little input to, or responsibility for, any of the adult activities directed toward it. Unlike ape infants, it does not attend to the maintenance of contact with the mother by holding tight and paying attention to her slightest movement to prepare itself for travel. Indeed, the only means available to it for maintaining parental contact is to signal by crying. Human parents are far more likely to ignore loudly crying babies than bonobo mothers are to ignore the soft whimpers of their babies. If a human baby is inside a hut and relatives are watching outside, predators who hear the cry, will not gain access to the baby.

A bonobo infant, within hours or days after birth, must begin to take some responsibility for its own survival by clinging to its mother. This has been characterized as a simple 'innate response,' – but such is far from the truth. Clinging requires skilful co-ordination with the bonobo mother, who must be constantly monitored by the infant (Bolser and Savage-Rumbaugh 1989). Human infants are too heavy to cling at birth and, unlike bonobo infants, they continue to gain weight quickly, making it impossible for them to cling even when they become strong enough to do so. In addition, their feet and the size of their heads relative to the strength of their necks renders clinging hopeless. Human mothers must support the large head, weak neck and mobile spine in careful manner. The human baby is not 'helpless' as often stated, but it is not designed to cling. It is designed to be sat down from time to time and to be swaddled. It is designed to observe the activities of those around it, without forever being immersed within them as a direct extension of the mother.

When a human infant is placed on a substrate other than the mother's body, a very different visual, auditory, tactile and kinesthetic world impinges upon it. The bonobo baby is, during this same time, looking at a sea of hair and trying to stay with the mother. The human baby is looking at the mother's face while observing her mouth move in synchrony with the sound that is coming to its ears as she speaks. Babies neurologically entrain to the mouth-movements, facial expressions and sounds of others and they engage in facial-vocal dialogues with caretakers by two to three months (Stern 1971, 1977, Trevarthen and Hubley 1978, Trevarthen 1998). These entrainment periods evoke rhythmic similarities to later 'true conversations' that emerge between one and two years. New born infants also 'imitate' facial expressions such as tongue protrusion and smiles from a few days after birth (Meltzoff 1996, Myowa-Yamakosi et al. 2004). The early onset of such behaviours, suggests that they are being guided by the mirror neuron system, and that the inter-individual neurological mirroring is intimately tying them to their caregiver from birth (Rizzolatti et al. 2001).

When a human mother sets the baby down, even for a moment, if she is attending only to her own tasks, something can happen to the child. The bonobo mother, by contrast, needs only to watch out for her own welfare, as by so doing the welfare of the baby holding tightly to her assured. As a human baby is put down; it is exposed to the sun, rain, smoke, insects, wind or predators that could harm it quickly. Thus, the human mother must create in her mind, a constant scenario of the baby's needs, which are different from her own. This is demanding for most new human mothers. Their feelings about such efforts and the baby's receptivity to her own feelings, affect the content and style of the linguistic dialogue which accompanies the mother's actions toward the baby (Oh, you're all wet, You are getting sleepy, Now smile, don't be fussy, What is bothering you?, Stop crying, Why don't you smile at me, etc?). The dialogue carries a quality of *aboutness* with it, towards the baby. The degree of and tone of the *aboutness* expressed corresponds directly to the degree of differentiation taking place between mother and infant (BRIGAUDIOT et al. 1996, SAVAGE-RUMBAUGH 1990).

These different styles of caregiving are molded within the first two years of life and give rise to adult social-structure. All infants raised by either pattern eventually develop some degree of self-awareness and reflective thought. But the objectification of the self is fostered far earlier by human rearing and human language patterns. Thus the bifurcation of self agency becomes far more elaborate in the human adult. By the time the bonobo infant has begun to develop its sense of self-agency, its primary focus of attention has already been unalterably fixated upon group cohesion and group movement through the terrain. It has formed a formidable spatial/temporal map of its world and it has become inextricably embedded within its landscape and its social group. Thus, time spent in self-reflection is minimized by a culture which places a much higher priority on group survival and shared knowledge than individual survival or private knowledge.

These differences in maternal care patterns, which human and bonobo infants experience from the moment of birth forward, are responsible for the majority of the behavioral distinction that later emerge between the species. They are culturally instantiated and are open to change at any time. From these caregiver patterns emerge the different styles of human/ape consciousness which have captivated philosophers and psychologists (KITCHER 2006, LOCKE 1690/1959, SAVAGE-RUMBAUGH et al. 2005). The key issues to be understood are that (*a*) *it is possible for ape mothers to exhibit human patterns (which they do when they have an infant that cannot cling)* and (*b*) *it possible for human mothers to rear ape infants who do not cling because they are carried and treated precisely as human infants would be treated.* Therefore, the apparent differences between humans and apes are not biologically fixed but they are biologically and culturally facilitated.

When apes experience human-rearing and are exposed to a *human language* which they can produce they begin to display the human patterns of self-awareness and self-reflection by 6 months of age. An obvious index of self-awareness is the use of a mirror to view the self as the self is being intentionally altered (or immediately after it has been altered). Many apes explore their image by seeking out a mirror to look at their teeth, their tongue, their ears, their eyes and other portions of their body that could be observed only in a reflected image. But linguistically competent apes paint their faces, put on wigs, shawls and monster masks, and rush to the mirror to see how they look. They try to blow bubbles with bubble gum while using mirrors to watch their cheeks. They practice displays by adding fur capes as they swagger in front the mirror. They seek out live video images to see things that even a mirror would not reveal. Only a live camera image can reveal their epiglottis and allow them to learn to vibrate in real time (MENZEL et al. 1985, SAVAGE-RUMBAUGH 1986).

This concern with understanding the appearance of the self from the perspective of another arises directly from the bifurcated dualistic view of the self, whose roots lie in the I/Me distinctions embedded in the structure of the *human language* which they are acquiring. The *viewer/doer* duality of consciousness enables the youngster to think about what it is doing, the appearance of its action and/or how the action will be perceived by others, all at the same time. When this dualistic process begins to operate, there emerges, within a single brain and body, the capacity to consciously separate the imaged self into that of the *doer* of ones actions and the *viewer* of those same actions (Bates 1990). The *viewer* begins to sometimes hold an action by the *doer* in abeyance, or sometimes even reflect upon the past actions of the self as *doer* with a certain amount of chagrin and dismay. This is the formative basis of mental time travel and the mental construction of alternative world views (Suddendorf and Corballis 2010).

Every act of the *viewer* is like a tiny seed that grows and expands very slowly at first, but with increasing maturity it takes over more and more of the body's actions until the adult individual emerges with a highly self-reflective consciousness, capable of moral agency. This capacity for dual consciousness, or bifurcated thought, lies at the root of Cartesianism, but there is no need to reduce the bifurcations of consciousness to mind/body dualism. When consciousness, as an emergent property of the neural system, reaches a certain level of self-awareness or self as causal agent, it becomes able to bifurcate and, as it does so, gains the ability to self-reflect. Metaphorically speaking, it splits into two parts, like a soap bubble that becomes two halves, by the appearance of film in the middle. One half of the 'consciousness bubble' specializes in guiding the immediate actions of the organism and the other half specializes in reflecting upon those actions. Through this lens of reflected consciousness, one sees one's self as a causal agent outside one's immediate tendency to react. *Human language*, coupled with *human maternal care*, enables the consciousness to bifurcate very early and extensively. Without the self-reflective properties inherent in a reflexive agent-recipient language, and without the objectification of the human infant – a very different kind of humanity would arise.

10. Human Consciousness

Human consciousness, constructed by human language, becomes the vehicle through which the self-reflective human mind envisions time. Language enables the *viewer* to reflect upon the action so of the *doer* (and the actions of one's internal body), while projecting forward and backward – other possible bodily actions – into imagined space/time. Thus, the projected and imagined space/time increasingly becomes the conscious world and reality of the *viewer* who imagines or remembers actions mapped onto that projected plan. The body thus becomes a physical entity progressing through the imaged world of the viewer. As the body progresses through this imaged world, the *viewer* also constructs a way to mark progress from one imagined event to another. Having once marked this imagined time, into units this conscious *viewer* begins to order the anticipated actions of the body into a linear progression of events.

A personal narrative arises through language. Indeed a personal narrative is required, expected and placed upon every human being, by the very nature of human language. This personal narrative becomes organized around the anticipated bodily changes that are imagined will take place from birth to old age. Thus, the power of the bifurcated mind, through linguistically encoded expectancies, shapes and molds all of human behaviour. When these capacities are jointly executed by other similar minds – the substrate of human culture is manufactured. Human culture, because it rides upon a manufactured space/time self-reflective substrate, becomes unique. Though it shares some properties with animal culture, it is not merely a natural Darwinian extension of animal culture. It is based on constructed time/space, constructed mental relationships, constructed moral responsibilities, constructed personal narratives and individuals, must, at all times, justify their actions toward another on the basis of their co-constructed expectancies.

On planet Earth there are many organisms, and a myriad of life styles. The ability to develop a self-reflective consciousness has been demonstrated only in humans and great apes. Humans and apes are sibling species. During embryogenesis, their offspring follow a similar route of self-organization, different from other mammals. Consciousness itself is a mysterious property of the Universe. All we truly understand is that it arises as property of biological nervous system.

Whether similar conscious potential exists in other nonhuman animals such as whales and dolphins is unknown. They neither cling, nor are they carried. They must stay with the mother by swimming. They lack hands, legs and feet. Their eyes are not oriented in the frontal plane. They experience life through echo-location – a series of consecutively order click-trains, beamed on objects, a sense we lack entirely. Their world rarely stops, they are in constant motion. One half of their brain can sleep, while the other half guides their actions, suggesting that possibly they experience a bifurcated conscious of a kind we cannot know, because our brain experiences sleeping and waking states in both sides simultaneously.

What is known is that apes reared as members of a human culture – when given a workable language output mode – begin to self-reflect, to report on past events, predict future events, to worry and to respond to the invisible as depicted only through language. As they begin to develop conscious moral agency, they seek to step into the area of self-responsibility. But human cultural forces are unwilling to permit them to do so. Our societies categorize this sibling species as “animal.” The bonobos with language remain property. They remain entities incapable of being allowed any form self-control or self-determination.

Until this view changes, and at least some apes are given both the right to self-manage *and all responsibilities that co-emerge with the right to self-manage*, humanity will never know the full power of language. It will never know whether it is the only species on the planet capable of conscious moral agency, conscious self-control, and the conscious desire to forgive. It is the expression of these conscious desires which has enabled humanity to construct city-states. Without these conscious desires, the laws necessary for city-states to emerge could not materialize. All manifestation of these conscious desires depends upon *human language*.

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Numerical Abilities of Grey Parrots: Comparisons with Apes and Children

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Abstract

Do humans and nonhumans share numerical and perceptual abilities? Some researchers argue that nonhumans, lacking human language, possess exact understanding only of quantities up to about 4. Animals trained in human communication systems might, however, be more advanced. Alex, a Grey parrot, could, for example, quantify sets of ≤ 8 items (including heterogeneous subsets) using vocal English labels, comprehend these labels fully, sum small quantities, and had a zero-like concept. He understood number symbols as abstract representations of real-world collections, in ways comparing favorably to those of apes and young human children. He appeared to learn in ways more similar to humans than apes.

Zusammenfassung

Teilen menschliche und nicht-menschliche Wesen ein Verständnis und eine Wahrnehmung von Zahlen? Einige Forscher behaupten, dass nicht-menschliche Wesen, denen die menschliche Sprache fehlt, ein exaktes Verständnis nur für Quantitäten bis vier besitzen. Tiere, die in einem menschlichen Kommunikationssystem ausgebildet wurden, könnten jedoch fortgeschrittener sein. Alex, ein Graupapagei, konnte z. B. Gruppen mit bis zu acht Einheiten quantifizieren (einschließlich heterogener Untergruppen). Er verwendete dabei gesprochene englische Bezeichnungen, die er voll und ganz verstand, konnte kleinere Mengen summieren und hatte ein Verständnis für die Quantität „Null“ entwickelt (*zero-like concept*). Er begriff Nummernsymbole als abstrakte Repräsentationen für Gruppen realer Objekte, und dies in einer Art und Weise, die zu seinem Vorteil im Vergleich zu der von Menschenaffen und kleinen Kindern zu sehen ist. Seine Art zu lernen erschien der von Menschen ähnlicher als der von Menschenaffen.

1. Introduction

Studies of the development of nonhuman numerical competence remain controversial (Pepperberg 2006b). Even for humans, some researchers still disagree on what constitutes various stages of numerical competence; which are the most complex, advanced stages; what mechanisms are involved; and even what is enumerated (for a detailed review, see Carey 2009). And little agreement exists as to the role of language in numerical competence, not only for preverbal children but also for primitive human tribes and nonhumans (e. g., Gordon 2004, Watanabe and Huber 2006, Frank et al. 2008). If language and number skills require the same cognitive capacities, then animals, lacking human language, should not succeed on most number tasks; an alternate view is that humans and animals have similar simple, basic number capacities but that only humans' language skills enable development of numerical representation and thus abilities such as verbal counting, addition, etc. (reviews in Pepperberg 2006b, Carey 2009). Possibly, label acquisition simply directs attention to characteristics involved in set formation, providing preparation for dealing with number sets for children *and*, interestingly, label-trained nonhumans: Nonhumans trained on symbolic labelling can acquire exact understanding of number up to about 8 and of simple mathematical processes (e. g., addition of small numbers), much like young children (review in Pepperberg 2006b; see also Boysen and Hallberg 2000, Matsuzawa 2009).

Whatever the similarities in overall competence, human-nonhuman differences still seem to exist in acquisition patterns, at least for larger integers. Although acquisition of numerical competence – both comprehending and producing exact integer number labels appropriately – is, at least initially, a difficult process for humans and nonhumans alike, children and nonhumans eventually diverge. Specifically, both children and animals who are taught to label numerical sets learn the meaning of their first few integer labels very slowly. Each of the smaller integers (generally one through three) is learned in turn, with little savings from one number to the next (e. g., Matsuzawa 1985, Pepperberg 1987, Boysen and Berntson 1989, Wynn 1990, 1992). Even young children (less than 3.5 years of age) who recite an ordinal integer list appropriately (e. g., "one, two, three…") may not understand fully how it relates to real-world quantities (Wynn 1992, Le Corre et al. 2006, Sarenecka and Carey 2008). Soon after children reach a full understanding of the quantity four, however, at roughly 3.5–4 years, they seem to tie together various strands of numerical information: Knowing that, for example, "five" follows "four" in their number list, they fairly rapidly attach the label to the appropriate set of items (see Wynn 1992, Le Corre et al. 2006); that is, they understand that the next label in the count list is the same as adding one item (Carey 2004). In contrast, most animals trained to recognize larger quantities (i. e., who learned, symbol by symbol, to match symbols to exact sets of items up to six or nine) did not make the same intellectual leap as children. Even apes, humans' closest evolutionary relatives, showed little if any savings in time needed for acquisition of larger labels, although their eventual accuracies were impressive (Matsuzawa et al. 1991, Boysen 1993, Murofushi 1997). And, in most cases, the ordering of the numerals had to be trained subsequently (Matsuzawa et al. 1991, Boysen et al. 1993, Tomonaga et al. 1993, Tomonaga and Matsuzawa 2000).

Because no ape had been trained to produce a numeral list (i. e., a count line, count list, number or numeral line), and only a subset had undergone any form of language-like training (Matsuzawa's Ai; Boysen's Sarah), the question arose as to the effect of such training (or lack thereof) on the animals' abilities. In particular, what might be the effect of such exposure on another species that was trained in symbolic representation, a Grey parrot? Might it make the intellectual leap so far found only in children? The parrot in question, Alex, had received number training and testing that significantly differed from that of children and apes (Pepperberg 1987, 1994, 2006a,c; Pepperberg and Gordon 2005), but all elements of training, including two-way communication (Pepperberg 1999), had been acquired. Here, I provide background on Grey parrot number studies prior to mine, discuss Alex's early abilities, and then review data showing that Alex's number capacities were closer to those of children than to other nonhumans (Pepperberg and Carey 2012).

2. Early Grey Parrot Number Studies

I was not the first person to study avian number concepts, or even Grey parrots. Much earlier, Koehler (1943, 1950) and colleagues (Braun 1952, Lögler 1959) demonstrated Grey parrots' sensitivity to quantity – numerosity and numerousness. Koehler's birds learned, for example, to open boxes randomly containing 0, 1, or 2 baits until they obtained a fixed number (e. g., 4). The number of boxes to be opened to obtain the precise number of baits varied across trials; the number being sought depended upon independent visual cues: black box lids denoted two baits, green lids three, etc. Koehler claimed his birds performed four different problems of this kind simultaneously. He did not state, however, if he presented different coloured lids randomly in a single series of trials, and thus if colours indeed *represented* particular quantities (see Pepperberg 1987, 1999). He also showed that Grey parrots and jackdaws could perform match-to-sample on quantities to 8, with controls for mass, density, contour, brighness, etc. Lögler (1959) transferred such behavior to light flashes and flute notes, thus going from simultaneous visual representations to sequential visual and auditory ones. But could a parrot, like Matsuzawa's (1985) chimpanzee Ai, go beyond these tasks and use number as a symbolic, categorical label?

3. Alex's Non-Numerical Capacities

When I first began numerical work with Alex in the 1980s, he had already achieved competence on various tasks once thought limited to young children or at least nonhuman primates (Pepperberg 1999). Through the use of a modelling technique, roughly based on that of Todt (1975), Alex learned to use English speech sounds to identify large numbers of objects and their colours; at the time he could also label two shapes ("3-corner" for triangles, "4-corner" for squares; later he identified shapes from one to six corners). He understood concepts of category: that the same item could be identified with respect to material, colour, shape, and object name (e. g., "wood", "blue", "4-corner", and "block"). He had functional use of phrases such as "I want X" and "Wanna go Y", X and Y being appropriate object or location labels. He was acquiring concepts of *same, different*, and *absence* – for any object pair he could label the attribute ("colour", "shape", "matter") that was same or different, and state "none" if nothing was same or different; he was also learning to view collections of items and state the attribute of the sole object defined by two other attributes – e. g., in a set of many objects of which some were yellow and some were pentagonal, to label the material of the only one that was both yellow *and* pentagonal (Pepperberg 1999). But could he form an entirely new categorical class consisting of quantity labels?

4. Alex's Early Numerical Abilities

To succeed on number concepts, Alex would have to reorganize how he categorized objects in his world. He would have to learn that a new set of labels, "one", "two", "three", etc. represented a novel classification strategy; that is, one based on both physical similarity within a group and a group's quantity, rather than solely by physical characteristics of group members. Thus an object would not only be a piece of paper, or a red or triangular one, but also would have to be labelled with respect to its membership within a quantifiable set. Alex would also have to generalize this new class of number labels to sets of novel items, items in random arrays, heterogeneous collections, and eventually to more advanced numerical processes (Pepperberg 1999, 2006b). If successful, he would demonstrate a *symbolic* concept of number; that is, vocally designate the *exact* quantity of a given array with an appropriate numerical, referential utterance in his repertoire.

4.1 Training and Testing Methods

Alex was trained to identify small number sets with the same modelling procedure used to train labels for object, colours, and shapes; details are published elsewhere and will not be repeated (e. g., Pepperberg 1987, 1994, 1999, 2006 a, b, c). Training was limited to sets of a few familiar objects; testing involved transfer to sets of other familiar and novel exemplars. The same references describe, again in great detail, testing procedures that ensured against myriad forms of possible external cuing, both with respect to inadvertent human cuing and cues based on nonnumber issues such as mass, brightness, density, surface area, odor, item familiarity, or canonical pattern recognition (Pepperberg 1987, 1999). The following material summarizes, in a stepwise manner, the results from various studies of Alex's number concepts.

4.2 Labelling of Basic Quantities and Simple Heterogeneous Sets

The first number study demonstrated that Alex could label small sets of familiar different physical items, up to six, exactly (78.9 %, all trials; Pepperberg 1987); that is, his error patterns did not show a peak near the correct responses, which would have suggested only a general sense of quantity. Rather, his most common errors across all sets was to provide the label of the object involved – to respond, for example, "key" rather than "four key", which accounted for almost 60 % of his roughly 50 errors in ~250 trials (about 20 % of his errors involved unintelligible responses or misidentifications of the object or material). Thus Alex indeed had a concept of quantity; he was not, however, necessarily counting, as would a human child who understood, for example, "five" (Fuson 1988, Pepperberg 1999, Mix et al. 2002); that is, who understood the counting principles: that a stable symbolic list of numerals exists, numerals must be applied to individuals in a set to be enumerated in order, they must be applied in 1–1 correspondence, and the last numeral reached in a count represents the cardinal value of the set. Nevertheless, on additional tests Alex demonstrated that items did not need to be familiar, nor to be arranged in any particular pattern, such as a square or triangle; he maintained an accuracy of about 75–80 % on novel items in random arrays.

Moreover, if presented with simple heterogeneous sets – a mixture of X's and Y's – he could respond appropriately to "How many X?", "How many Y?", *or* "How many toy?" (70 %, first trials; Pepperberg 1987). Here his level was above some children, who are generally tested on only homogeneous sets and who, if asked about subsets in a heterogeneous set, usually label the total number of items if, like Alex, they have been taught to label homogeneous sets exclusively (see Siegel 1982, Greeno et al. 1984).

Because tests involved a variety of exemplars of various sizes and of both familiar and novel textures and materials (e. g., metal keys *versus* bottle corks) often presented by simply tossing them in random arrays on a tray, Alex could not, as noted above, use cues such as mass, brightness, surface area, odor, object familiarity, or canonical pattern recognition (PEPPERBERG 1987, 1999). These tests did not, however, determine if Alex had used a noncounting strategy such as subitizing for the smallest collections – a perceptual mechanism that enables humans to quickly quantify sets up to ~4 without counting – or "clumping" or "chunking" – a form of subitizing (e. g., perception of six as two groups of three; for a review, see VON GLASERSFELD 1982) – to correctly quantify larger collections, again without counting. Thus many other tests would be needed to determine the mechanisms that Alex was indeed using.

4.3 Complex Heterogeneous Sets

The next study involved adapting a task initially presented to humans in order to tease apart subitizing/clumping *versus* counting. TRICK and PYLYSHYN (1989, 1994) designed two such tasks in which subjects had to enumerate a particular set of items embedded within two different types of distractors: (*a*) white *or* vertical lines among green horizontals; (*b*) white vertical lines among green vertical *and* white horizontals. They found that humans subitized for 1–3 in only the first condition, but had to count, even for such small quantities, in the second. Subitizing thus seems to fail when subjects must distinguish among various items defined by a collection of competing features (e. g., a conjunction of colour *and* shape; see PEPPERBERG 1999). The task could be adapted for Alex because he already was being tested on conjunction (e. g., being asked to identify the colour of an item that was both square and paper in a collection of differently shaped objects of various materials; PEPPERBERG 1992). He could thus be asked to label the quantity of a similarly defined subset – for example, the number of blue blocks in a set of red and blue balls and blocks. Would his numerical capacities match those of humans?

Notably, Alex's accuracy, 83.3 % (on 54 trials, PEPPERBERG 1994), matched that of humans (TRICK and PYLYSHYN 1989). His scores could also be analyzed for evidence of subitizing: Such a mechanism would be implied by data that (*a*) demonstrate a decrease in accuracy around 4 (the human subitizing limit) and (*b*) for larger numerosities, conform at least qualitatively to Weber's law – roughly stated, the greater the numerosity to label, the more imprecisely will a subject distinguish between it and nearby numerosities. That is, a subject with high accuracy on small numbers but lower accuracy for larger ones is likely subitizing the smaller ones and using some other noncounting procedure for the larger ones. So, if Alex used perceptual strategies similar to those of humans (e. g., subitizing and clumping), rather than counting, he would make no errors for 1 and 2, few for 3, and more for larger numbers. Sequential canonical analysis (GORSUCH and FIGUEREDO 1991), however, showed that errors were random with respect to number of items to be identified (PEPPERBERG 1994). In fact, most of Alex's errors seemed unrelated to numerical competence, but rather were in misinterpreting the defining labels, then correctly quantifying the incorrectly targeted subset: Eight of his nine errors were the correct number for an alternative subset (e. g., the number of blue rather than red keys; in those cases, the quantity of the designated set usually differed from that of the labelled set by two or more items, demonstrating that Alex's response was not simply a close approximation to the correct number label; Pepperberg 1994). Nevertheless, Alex's perceptual capacities might be more sophisticated than those of humans; the data, although impressive with respect to exact number, still did not justify claiming that he was definitively counting.

5. Alex's More Advanced Numerical Abilities

En route to determining the mechanism – or mechanisms – Alex used to quantify sets, I examined various other numerical capacities. In several studies, Alex was tested on comprehension of numerical labels, on his ability to sum small quantities, and on whether he understood the ordinality of his numbers. The latter task was of particular interest, because, unlike children, he had not been trained in an ordinal manner: He had first learned to label sets of three and four, then five and two, then six and one.

5.1 Number Comprehension

Although Alex could label numerical sets, he had never been tested on number label comprehension. The issue is important, because even a young child who successfully labels the number of items in a small set ("There are X marbles") might fail when shown a very large quantity and asked "Can you give me X marbles?" That is, the child might not really understand the relationship between the number label and the quantity (Wynn 1990). If labelling indeed separates animal and human numerical abilities (see above; Watanabe and Huber 2006), such comprehension-production equivalence is crucial for demonstrating nonhuman numerical competence (Fuson 1988).

To determine Alex's comprehension abilities, he was given a variation of the previous task involving simultaneous presentation of several quantities, of 1 through 6, of different items – for example, X red cork, Y yellow cork, Z green cork, or X red paper, Y red wood, and Z red cork, and queried, respectively, "What colour Z?" or "What matter X?" (Pepperberg and Gordon 2005). He received no training prior to testing. The procedure required him to comprehend the auditorially presented numeral label (e.g., X = "six") and use its meaning to direct a search for the cardinal amount specified by that label (e.g., six things), that is, know exactly what a set of "X" items is, even when intermixed with other items representing different numerical sets. Controls again involved differently sized objects so he could not respond based on contour, mass, etc.; that is, he could not perform the task without comprehending the number label. Each query also retested his ability to identify the item or colour of the set specified by the numerical label. To respond correctly, he had to process all types of information errorlessly. Some or all this behavior likely occurred as separate steps, each adding to task complexity (Premack 1983).

Alex's overall score was 58/66, or 87.9 % (first trials, binomial test, $p < 0.001$, chance 1/3). His results were compelling, particularly as no errors were made on the first 10 trials (Pepperberg and Gordon 2005); rather, errors increased with time, suggesting lack of focus or inattention as testing proceeded. Unlike young children (up to ~3 years old) described above, he understood the meaning of his number labels. How he compared to somewhat older children (≥3.5 years), who have generally begun to count in the traditional sense (Fuson 1988, Wynn 1990), was as yet unclear. He had little difficulty with numbers differing by small amounts; his errors on such trials apparently being a consequence of colour perception or phonological confusion, not numerical misunderstanding: He sometimes erred in distinguishing orange from red or yellow, a consequence of differences in parrot and human colour vision (Bowmaker et al. 1994, 1996); he also sometimes confused "wool" and "wood", or "truck" and "chalk", the latter being pronounced a bit like "chuck" (Pepperberg and Gordon 2005).

5.2 Use of "None"

The comprehension study was notable for another reason: Alex's spontaneous transfer of use of "none" – learned as a response to the queries "What's same/different?" with respect to two objects when no category (colour, shape, or material) was same or different (Pepperberg 1988) – to the absence of a set of a particular quantity. This behavior occurred on the 10th trial within the first dozen. Alex was asked "What colour three?" to a set of two, three, and six objects. He replied "five"; the questioner asked twice more, each time he replied "five". Finally, the questioner said "OK, Alex, tell me, what colour 5?", to which he immediately responded "none". Although he had spontaneously transferred this response from the same-different study to "What colour bigger?" for two equally-sized items in the study on relative size (Pepperberg and Brezinsky 1991), he had never been taught the concept of absence of quantity nor to respond to absence of an exemplar. "None", or a zero-like concept, is advanced, abstract, and relies on the violation of an expectation of presence (Bloom 1970, Hearst 1984, Pepperberg 1988). Note, too, that Alex not only had provided a correct, novel response, but had also manipulated the trainer into asking the question he apparently wished to answer (Pepperberg and Gordon 2005). Alex also correctly answered additional queries about absent sets, showing that his behavior was intentional and meaningful. Although his use of "none" was spontaneous, unlike that of the chimpanzee, Ai, who had to be trained to use the label "zero" (Biro and Matsuzawa 2001), did he really understand the *concept* of zero? Further testing was done in the next set of experiments.

5.3 Addition of Small Quantities

Interestingly, studies on addition were unplanned (Pepperberg 2006a). Students and I had begun a sequential auditory number session (training to respond to, e.g., three computer-generated clicks with the vocal label "three") with another Grey, Griffin, saying "Listen", clicking (this time, twice), and asking "How many?" He refused to answer; we replicated the trial. Alex, who might interrupt Griffin's sessions with phrases like "Talk clearly" or with the answer even though he was not being taught the procedure, said "four". Alex was told to be quiet, as the answer for the specific trial was "two". The trial was replicated yet again with Griffin, who remained silent; Alex now said "six", suggesting he had summed all the clicks. I thus decided to replicate, as closely as possible, the addition study of Boysen and Berntson (1989) on apes, and to use the experiment to study further Alex's understanding of zero (Pepperberg 2006a).

Notably, addition requires a subject to observe two (or more) separate quantities and provide the *exact* label for their total (Dehaene 1997). Only the aforementioned study, on apes, required summation *and* symbolical labelling of the sum by a nonhuman (Boysen and Berntson 1989) – that is, showed that the ape knew exactly how many items were present at the end of the procedure; however, quantity never totalled more than four. Other studies, involving additive and subtractive tasks with larger numbers (up to 10), used only one type of token and required subject to choose the larger amount, not label final quantity (review in Pepperberg 2006a). Such procedural differences are important. Use of only one token type (e. g., marshmallows) allows evaluations to be based on contour and mass, not number (note Mix et al. 2002), and when the correct response involves choice of relative amount, no information is obtained on whether the subject has "[...] a digital or discrete representation of numbers" (Dehaene 1997, p. 27).

Alex's task avoided such problems. He was presented with a tray on which two upside down cups had been placed; prior to presentation, a trainer had hidden items such as randomly shaped nuts, bits of cracker, or differently-sized jelly beans under each cup, with items in the same cup less than 1 cm from each other; we occasionally used identical candy hearts to see if accuracy was higher when mass/contour cues were available.

After bringing the tray up to Alex's face, the experimenter lifted the cup on his left, showed what was under the cup for 2–3 s in initial trials, replaced the cup over the quantity; then replicated the procedure for the cup on his right. For reasons described below, in trials comprising the last third of the experiment, Alex had ~10 s to view items under each cup before everything was covered. The experimenter then made eye contact with Alex, who was asked, vocally, and without any training, to respond to "How many total?" Each total amount was presented eight times, in random order, such that no collection was shown sequentially; collections totalled to every amount from 1 to 6. Alex was also queried eight times when nothing was under both cups. All possible addend collections were randomized (e. g., amounts adding to 6 were presented as 6+0, 5+1, 4+2, and 3+3, two times each, alternating quantities under right/left cups, and likewise for other sums). No objects were visible during questioning. To respond correctly, Alex had to remember the quantity under each cup, perform some combinatorial process, then produce a label for the total amount. He had no time limit in which to respond, given that his response time generally correlated with his current interest in the items being used in the task, rather than the task itself (Pepperberg 1988). Appropriate controls for cuing and tests for interobserver agreement were, as usual, in place. In trials for which nothing was under both cups, the goal was to determine if he would generalize use of "none" without instruction.

Alex's results were again compelling, with an overall accuracy of 41/48 or 85.4 % for first trial responses (binomial test, $p < 0.005$ chance 1/2 or 1/6); his first-trial score for each sum was 5/6 or 84.3 % (binomial test, $p < 0.02$ chance 1/3). Identical tokens did not help with accuracy. Interestingly, when given only 2–3 s, he always erred on the 5+0 sum, consistently stating "6"; when given ~10 s, however, his accuracy went to 100 %. Differences in accuracy between the shorter and longer interval trials on 5+0 trials was significant (Fisher's exact test, $p = 0.01$), but for trials on all other addends, his accuracy remained constant. If 5+0 trials under the longer time interval are used, his first trial accuracy was 43/48 or 89.6 %, $p < 0.005$. His data are comparable to those of young children (Mix et al. 2002) and more advanced than those of apes (Boysen and Hallberg 2000). His responses on 5+0 trials suggest, although again cannot prove, that he used a counting strategy for 5:

Only when beyond the subitizing range of 4 did he, like humans, need time to label the set exactly (for a detailed discussion, see Pepperberg 2006a).

Alex eventually learned to respond equally well to three sequentially presented collections and to the addition of two Arabic numerals (see below); in a few trials on the Arabic numeral addition he was also shown variously coloured Arabic numerals while the addends were hidden and asked „What colour number (is the) total?“ Although his death in 2007 precluded testing on all possible arrays, his accuracy was statistically significant and suggested addition abilities comparable to those of nonhuman primates (Pepperberg 2012).

Alex did not respond "none" when nothing was under any cup. On five trials, he looked at the tray and said nothing; on three trials, he said "one" (Pepperberg 2006a). His failures to respond suggest he recognized a difference from other trials, that is, that standard number answers would be incorrect. He understood that the query did not correspond to the number of *cups*; he never said "two". Overall, he acted somewhat like autistic children (Sherman, personal communication, January 17, 2005), who simply stare at the questioner when asked "How many X?" if nothing exists to count. His responses of "one" suggests comparison to Ai, who confused "one" with "zero". Although Alex was never trained on ordinality, unlike Ai (Biro and Matsuzawa 2001), and had learned numbers in random order (see above), he, like Ai, seemed to grasp that "none" and "one" represented the lower end of the number spectrum. Here he was asked to denote the total absence of labelled *objects*, a different task from responding to the absence of an attribute, which characterized his previous use of "none". Specifically, Alex's use of "none" was zero-like, but not isomorphic with adult human use of "zero". He did not use "none", as he did his number labels (Pepperberg 1987) to denote a specific numerosity. In that sense, he was like humans in earlier cultures, or young children, who seem to have to be ~4 years old before achieving full adult-like understanding of the label for zero (e.g., Wellman and Miller 1986, Bialystok and Codd 2000).

5.4 Ordinality and Equivalence Studies

Alex's use of "one" in place of "none" in the addition study suggested but obviously did not prove he had indeed inferred an exact number line; that is, that he understood ordinality. Ordinality is important because it is intrinsic to *verbal* counting (e.g., Gelman and Gallistel 1986, Fuson 1988). To count, an organism must produce a standard sequence of number tags and know the relationships among and between these tags; for example, that "two" (be it any vocal or physical symbol) not only comes before "four" in the verbal sequence but also represents a quantity less than "four." Children acquire ordinal-cardinal abilities in steps. They learn cardinality for very small numbers (< 4) and a general sense of "more versus less" while acquiring a meaningless, rote ordinal number series, then associate their knowledge of quantity in the small sets with this number sequence to form 1 : 1 correspondences that can be extended to larger amounts for both cardinal and ordinal accuracy (e.g., Carey 2004, see Mix et al. 2002). Children may learn associative rules that allow them to act as though they have full understanding of cardinality before they actually do (i.e., respond correctly to "How many?" but fail on "Give me X"; see above) but cannot do so with ordinality (e.g., Teubal and Guberman 2002, Bruce and Threfall 2004).

Nonhuman knowledge of symbolic ordinality is difficult to demonstrate because few animals use numeric symbols. Even for apes that referentially used Arabic symbols, ordinality did not emerge but had to be trained (e. g., Matsuzawa et al. 1991, Boysen et al. 1993, Biro and Matsuzawa 2001). Might Alex succeed without training?

I designed a task involving equivalence relations to test this possibility (Pepperberg 2006c). Specifically, would Alex, after learning English labels for Arabic numerals (production and comprehension) in the absence of the physical quantities to which they refer, use the commonality of these English labels to equate quantities (sets of physical objects) and Arabic numerals, so as to identify the *colour* of one of a pair of Arabic numbers (e. g., a blue 3, a red 4, next to each other on a tray) that is *numerically* (not physically) bigger or smaller? He already answered "What colour/matter bigger/smaller?" for object pairs and responded "none" for same-sized pairs (Pepperberg and Brezinsky 1991). To succeed on this new task, he would have to use deductions and inferences: Deduce that an Arabic symbol has the same numerical value as its *vocal label*, compare *representations* of quantity for which the labels stand, infer rank ordering based on these representations, then state the result *orally*. Specific stimuli within pairs, unlike in other nonhuman studies (e. g., Olthof et al. 1997, Olthof and Roberts 2000), would not be associated with reward of the corresponding number of items, and by requiring colour, not number, label responses and querying about both larger and smaller values, use of rote replies would be unlikely for a given pair; pairs could be presented several times with less chance of training.

Additional trials would examine more sophisticated abilities. Trials on identical numerals of different colours but of the same size (e. g., 6 : 6) tested if Alex would, as expected, reply "none" to the query as to which was bigger or smaller. Questions on numerals of the same value but different colours and different sizes (e. g., 2 : 2) would show if he would preferentially respond on the physical or numerical basis. By mixing Arabic symbols and physical items, I could tell whether he really did understand that, for example, one numeral (an Arabic 6) was bigger than five items (or an Arabic 2 as the same as two items) and cleanly separate mass and number.

Alex indeed inferred the ordinal relation among Arabic numbers without direct training of the 1 : 1 correspondence between these numerals and their corresponding object sets and without having been trained to recite the numerals in order (Pepperberg 2006c). For trials on two different Arabic numbers of the same physical size, his first trial score was 63/84, or 75 % ($p<0.01$, binomial test, chance of 1/2). If his occasional responses of the Arabic number label rather than the requested colour (technically correct, but not with respect to the actual query) were not counted as errors, his score was 74/84, or 88.1 % ($p<0.001$, binomial test, chance of 1/2). As in previous studies, errors sometimes involved yellow-orange-red confounds. When numerals were the same value-same size, his accuracy was 10/12, or 83.3 %, $p<0.01$ (binomial test, chance of 1/3; answers could be one of the two colours or "none"). For the same value–different size trials, counting as correct either "none" or the colour label of the targeted number, his accuracy was 12/12, or 100 %, $p<0.01$ (binomial test, chance of 2/3, a colour or "none"). Seven times he gave the correct colour, five times he said "none," but he gave colours most often in earlier trials and "none" most often in later trials, as though he shifted after experience with responses based on symbolic value, even though he had been rewarded for responses based on physical size. However, statistical comparisons on his first and final trials for all other number sets show no significant differences in accuracy, suggesting that no training was occurring overall.

Alex's responses to trials that mixed objects and numerals were intriguing. For arrays in which object sets were paired with a single Arabic number representing a quantity larger than or equal to the array (incongruent trials) and in which the single Arabic number represented a quantity less than the array (congruent trials), his accuracy was 16/21, or 76.2 %, $p<0.01$. However, in five trials in which a *single* object was paired with a *single* Arabic number that represented a larger quantity, Alex consistently replied "none". Only here did the physical set consistently overwhelm symbolic responses.

Overall, Alex did appear to exhibit numerical understanding far closer to that of children than other animals. Even though he had not been trained on numbers with respect to their ordinal value, he inferred this ordinality, demonstrating that he truly had a symbolic representation of number and also that he understood equivalence relations. But he, like other nonhumans and unlike humans, had demonstrated no savings in his previous learning of larger numerals. Why? Might the issue in Alex's case be the difficulty of learning to produce the English sounds? In order to produce any given English label, Alex had to learn to coordinate his syrinx, tracheal muscles, glottis, larynx, tongue height and protrusion, beak opening, and even esophagus (Patterson and Pepperberg 1998); might there be a way to dissociate vocal and conceptual learning to test this possibility?

5.5 A Symbolic Integer System

Colleagues and I came up with the idea of teaching Alex to identify vocally the Arabic numerals 7 and 8 in the absence of their respective quantities, then train him to understand that $6<7<8$. He could then be tested as to whether he understood the relationships among 7 and 8 and his other Arabic labels. If he inferred the new number line in its totality, he could be tested on whether, like children, he could *spontaneously* understand that "seven" represented one more physical object than "six", and that "eight" represented two more than "six" and one more than "seven", by labelling appropriate physical sets on first trials (Pepperberg and Carey 2012). That is, could he induce the cardinal meaning of the labels "seven" and "eight" from their ordinal positions on an implicit count list? Notably, until the ordinality training with respect to 6, he wouldn't even necessarily know that 7 and 8 were numerals, because he was also being trained to correlate phonetic sounds with alphabet letters (e. g., /sh/ with SH; Pepperberg 2007).

Even prior to all training and testing in this study, Alex seemed to have some concept of quantities greater than six. In pre-training baseline trials, when presented with sets of seven, eight, or nine items, he initially refused to answer on four of six trials; he had to be asked several times to elicit a response. Thus, when asked to label a set with quantities greater than those he already knew, he seemed to try to avoid answering (e. g., sat quietly after observing the tray, or asked to return to his cage) but, when forced to respond (being repeatedly asked until he finally produced some utterance), he used the available label ("six") that represented the largest currently trained quantity. His hesitancy to respond resembled his behavior in the earlier study on addition, in which he was asked to label a total absence of objects (Pepperberg 2006a). As before, his behavior suggested that he knew that a standard number answer would not be correct. Furthermore, when asked to provide the colour of the (absent) set of six items on trays that held various numbers of differently coloured items, including sets of seven and eight, Alex responded "none" on all four trials, but when subsequently asked on two of these trials for colours of smaller sets that were present, to ensure he was attending to the stimuli, he gave the appropriate labels. Thus he demonstrated an understanding of the exact nature of the representation of his label "six" (Pepperberg and Carey 2012); it did not immediately mean "the largest set present".

Over the course of the study, Alex did indeed learn to label the novel Arabic numerals, to place them appropriately in his inferred number line, and to label appropriately, on first trials, novel sets of seven and eight physical items. Detailed data are presented in the published paper (Pepperberg and Carey 2012); the conclusion is that Alex, like children, created a representational structure that allowed him to encode the cardinal value expressed by any numeral in his count list (Carey 2004).

6. Summary and Conclusions

Although both animals and children appear to exhibit, without overt training, sensitivities to concepts such as more *versus* less with respect to quantity (for review, see Pepperberg 2006b), acquisition of full numerical competence – both comprehending and producing exact integer number labels appropriately, actually learning to count – appears to be, at least initially, a difficult process for humans and nonhumans alike (reviewed in Carey 2009). As noted above, however, children, at around 4 years of age, integrate knowledge about small integers with their memorized count line to infer information about larger integers; without additional training, they can identify quantities like eight and twenty and then go on, albeit *via* intense instruction, to acquire advanced mathematical knowledge – beyond counting to multiplication, division, calculus, etc. Although it is quite unlikely that any nonhuman will ever progress to these latter stages, questions have always arisen as to just how far nonhumans might proceed in understanding numerical concepts. Issues as to nonhumans' lack of the kind of symbolic representation that appears critical for at least some level of number competency (e. g., Lenneberg 1971, see also Gordon 2004, Frank et al. 2008) became moot as various nonhumans acquired, if not human language, referential elements of human speech, sign, or symbol use – tools that could be used to examine whether nonhumans could acquire at least one human-like numerical ability, that of labelling *exact* sets (e. g., Matsuzawa 1985, Pepperberg 1987, 1994, Boysen 1993).

Further research through the years with nonhumans who were trained to use symbolic number representation has been fruitful, demonstrating capacities beyond those of children less than ~4 years old: capacities for labelling of larger sets, addition, understanding of ordinality and, in one case, apes' use of number symbols to solve a task – successfully choosing the smaller of two samples – that was impossible with physical stimuli because of the hedonic value of the physical array (Boysen et al. 1996). Recent studies with the Grey parrot, Alex, have now shown that a nonhuman subject – and one whose closest relative to humans lived over 280 million years ago – can demonstrate numerical competency comparable to children who understand cardinal principles, and in a manner not yet demonstrated by the phylogenetically closer ape.

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Computermodelle in der Wissenschaft – zwischen Analyse, Vorhersage und Suggestion

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Nicht nur die Technik- und Naturwissenschaften, sondern auch die Lebens-, die Sozial- und Kognitionswissenschaften, sogar Kunst und Archäologie sind immer stärker durch eine Informatisierung gekennzeichnet, die einige Disziplinen sogar revolutioniert. Standen früher Wissenschaften auf den fundamentalen Säulen Theoriebildung und Experiment, so hat sich in den letzten Jahrzehnten eine dritte gleichberechtigte Komponente herausgebildet – die der digitalen Modellierung, Simulation und Visualisierung von Strukturen und Prozessen. Der Band behandelt mathematische Grundlagen der Computertechnik, Möglichkeiten und Grenzen der Computermodellierung in den Lebenswissenschaften (Biochemie, Proteomanalyse, Systembiologie) und der Medizin (Tumorchirurgie, Hirnforschung, Rehabilitation), Computer als Dialogpartner (Spracherkennung, Schnittstelle zwischen Gehirn und Maschine), Klimamodelle, Computermodellierungen in Physik und Chemie, aber auch Probleme aus Philosophie (Simulation und Erkenntnis, Implikationen der Hirnforschung) und Ökonomie (Konsequenzen der Alterung der Gesellschaft). Die Beiträge bieten sowohl Laien als auch Experten überraschende Einblicke in eine faszinierende Forschungswelt.

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The Origins of Human and Avian Auditory-Motor Entrainment

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Abstract

Recent findings suggest that the capacity to entrain, or move in time with an auditory pulse, may have evolved as a byproduct of our capacity for vocal imitation rather than being selected for directly. However, recent work in social psychology has shown that synchronization of movement may promote prosocial behavior. This has been used to argue that entrainment, which increases the likelihood of synchrony, is adaptive and was subject to direct natural selection. In this chapter, I review the evidence that entrainment emerged as a byproduct of vocal imitation, and argue that this account is not in conflict with suggestions that synchrony may be adaptive. In particular, I propose a distinction between the capacity to entrain, an ability shared with avian species; and the innate motivation and tendency to entrain, which is present in humans but which avian species may lack. In line with this distinction, I propose that human entrainment may have evolved in at least two stages: *First*, the capacity to entrain arose as a byproduct of selection for vocal mimicry; *secondly*, the motivation to engage in entrained behavior was selected for directly, thus increasing levels of synchrony and prosocial behavior in the population.

Zusammenfassung

Neuere Erkenntnisse deuten darauf hin, dass die Fähigkeit zur Synchronisation von Verhalten mit einem externen Zeitgeber (*capacity to entrain*) in Form von rhythmischem Bewegen mit einem akustisch wahrgenommenen Takt als ein Nebenprodukt unserer Fähigkeit zur vokalen Nachahmung evolviert sein könnte, anstatt unter direkter Selektion. Aktuelle Arbeiten in der Sozialpsychologie haben jedoch gezeigt, dass Synchronisation von Bewegungen prosoziales Verhalten begünstigen könnte. Damit wurde argumentiert, dass das „Mitgehen“ mit einem äußeren Rhythmus (*entrainment*), welches die Wahrscheinlichkeit von Synchronie erhöht, adaptiv sei und direkter natürlicher Selektion unterliegt. In diesem Beitrag prüfe ich die Belege für die Entstehung des motorischen „Mitgehens“ als Nebenprodukt vokaler Nachahmung und zeige, dass dies nicht im Widerspruch zur Annahme steht, dass Synchronie adaptiv sein könnte. Im Besonderen schlage ich eine Unterscheidung zwischen der Fähigkeit zur Synchronisation – eine Leistung, die wir mit Vögeln teilen – und der immanenten Motivation und Tendenz zur Synchronisation, vor, welche beim Menschen vorhanden ist, jedoch bei Vögeln fehlen dürfte. Im Einklang mit dieser Unterscheidung stelle ich die Hypothese auf, dass menschliches Synchronverhalten in wenigstens zwei Stufen evolviert ist: Zuerst entstand die Fähigkeit zur auditorischen Bewegungssynchronisation als Nebenprodukt der Selektion auf vokale Mimikry; im zweiten Schritt wurde direkt für die Motivation sich an synchronisiertem Verhalten zu beteiligen selektiert, wodurch der Grad von Synchronie und prosozialem Verhalten in der Population erhöht wurde.

1. Introduction

Dance is a universal human behavior, appearing in cultures around the world (Nettl 1983). Dance is also ancient: Depictions of dance in cave art date back at least 9,000 years (Chakravarty and Bednarik 1997), and musical instruments such as bone flutes can be dated back to at least 40,000 years (Conard et al. 2009). Altogether, the data strongly suggest that dance is not merely a recent cultural invention, but an innate and fundamental part of the human behavioral repertoire.

If our capacity for dance is innate, this raises the question of how the human capacity for dance evolved. This question is complex, since dance is not a monolithic capacity: it involves a large set of highly distributed cognitive mechanisms, each of which may have independent evolutionary origins (Brown et al. 2006). As such, it is necessary to investigate the origins of each component of dance separately.

In our work, we have focused on one core component of dance: the capacity for auditory-motor entrainment (henceforth entrainment). Humans around the world can entrain, or align their motor actions with an external auditory pulse (colloquially, 'move to a beat') (Clayton et al. 2005). We not only have this capacity, but widely express it: humans often choose to or spontaneously begin to entrain to rhythmic and periodic sounds. When more than one person hears the same stimuli, this tendency to entrain often leads to synchrony, in which more than one person moves in the same way at the same time.

In the current chapter, we address two key questions: *Firstly*, why *can* we entrain? How did our capacity for keeping a beat emerge? We will discuss recent data suggesting that this capacity may have emerged as a byproduct of selection for another capacity, namely vocal imitation. *Secondly*, why do we *tend* to entrain? I will propose that after the necessarily mechanisms for entrainment were in place, subsequent selection may have favored those individuals with a tendency and motivation to entrain, due to the adaptive consequences of synchronization.

2. The Evolution of the Capacity for Entrainment

How did the human capacity for entrainment evolve? In recent work, my colleagues and I turned to cross-species comparative methods to address this question (Schachner et al. 2009). Our initial question was: Does any other species of animal engage in human-like auditory-motor entrainment?

Many species engage in synchronized behaviour, or other behaviour with interdependent timing, such as synchronous chorusing (e. g. Klump and Gerhardt 1992) the claw-waving display of crabs (Backwell et al. 1998), synchronized flashing displays in fireflies (Buck 1988), and trained synchronization to specific stimuli in rhesus macaques (Zarco et al. 2009). However, all of the aforementioned behaviours differ from human auditory-motor entrainment behaviour in critical ways (detailed below). These different behavioural signatures suggest that these behaviours do not depend on analogous neural mechanisms to those used in human entrainment. Because we were interested in the evolution of the particular type of neural mechanism used for human auditory-motor entrainment, these more distantly related behaviours were not of immediate interest in the current work.

In contrast, if we find behaviour in other species that features the specific behavioural signatures of human entrainment, this would suggest that both species' entrainment behaviours rely on a similar type of cognitive mechanism. Evidence of analogous mechanisms in species closely related to humans would suggest that this capacity was inherited from a common ancestor. Conversely, evidence of analogous mechanisms in phylogenetically distant species would suggest a process of convergent evolution, in which similar evolutionary pressures led similar mechanisms to evolve independently in two lineages.

3. Characteristics of Human Entrainment

Many of the features of entrainment serve to distinguish the human capacity for entrainment from the synchronized displays of other animals. These features serve as the defining characteristics of human auditory-motor entrainment.

Firstly, entrainment requires temporal prediction, not simple reaction to auditory stimuli. For example, when tapping in time with a metronome, human subjects tap slightly *before* the onset of each auditory stimulus (Aschersleben 2002). Thus, during entrainment we form a cognitive representation of the time intervals between beats, and use this representation to predict the onset time of each subsequent beat (Repp 2005).

Secondly, entrainment involves real-time monitoring of auditory input, and constant error correction of movements to match. Even if an individual begins moving to a beat accurately, without constant error correction the accumulation of motor and cognitive error would quickly lead movements to drift away from the beat (Repp 2005). This constant monitoring also enables rapid adjustment to new tempos as auditory stimuli increase or decrease in speed.

Third, human entrainment easily generalizes to new auditory stimuli. We may entrain not only to stimuli that we have heard before, but to any stimulus in which we perceive a clear periodicity within the appropriate range of speeds.

Human auditory-motor entrainment is a truly cross-modal capacity, requiring the translation of auditory input to motor output, and monitoring that output for error by constantly comparing it to the auditory input. It is not accomplished by relying on auditory output, since we are able to entrain entirely silent motor actions (Repp 2005).

Furthermore, human auditory-motor entrainment is highly flexible and robust. Both males and females display accurate entrainment, and we can entrain many body parts across a wide range of tempos. However, accuracy steeply drops off at slow tempos below ~33 beats per minute. When tapping along to a metronome at this speed, subjects' taps no longer slightly precede beats but occur after the auditory stimulus, suggesting an inability to perform accurate temporal prediction at slow tempos (Engström et al. 1996, Mates et al. 1994, Miyake et al. 2004). In addition, entrainment is more accurate for auditory stimuli than for visual stimuli (e. g. Patel et al. 2005), suggesting the involvement of a modality-specific mechanism.

4. The Vocal Mimicry Hypothesis

Crucially, the capacity to entrain to auditory stimuli is not seen in other primate species, even in great apes (Wallin et al. 2000). This suggests that our capacity for entrainment is a recent evolutionary development, emerging after our ancestry diverged from that of chimpanzees approximately 6 million years ago (Kumar et al. 2005). If this capacity does not exist in other primates, how did it evolve in our species?

Recently, Patel has proposed that entrainment may have evolved as the byproduct of selection for another capacity, namely vocal mimicry or vocal imitation (Patel 2006, 2008). According to this hypothesis, selection for vocal mimicry led to a strong coupling between auditory and motor representations. This auditory-motor linkage was also necessary for entrainment, and was later co-opted to allow for entrainment as well.

If selection for vocal mimicry results in the necessarily neural machinery for entrainment, then in the case that vocal mimicry never evolved in a particular species, that species should not have the mechanisms needed to entrain. Thus, Patel's hypothesis makes a strong prediction: The capacity for entrainment should only exist in vocal mimicking species, and never in vocal non-mimicking species.

In recent work, we aimed to answer two questions: *firstly*, is the capacity for entrainment uniquely human? Previously, entrainment was widely believed to be uniquely human (e. g. Zatorre et al. 2007, Wallin et al. 2000, Brown et al. 2006, Clayton et al. 2005, Thaut 2003, Bispham 2006, McNeill 2005). However, work had not yet focused on vocal mimicking animals, which were predicted to entrain by Patel's vocal mimicry hypothesis. *Secondly*, we aimed to test this vocal mimicry hypothesis, asking: do we only find evidence of entrainment in vocal mimicking animals, and never in species that cannot imitate sound?

We defined vocal mimicry broadly, as any species that learns vocalizations from an external auditory model.[1] By this definition, vocal mimics are still a small group, including humans, three clades of bird (hummingbird, parrot and songbird; Doupe and Kuhl 1999), two lineages of marine mammal (cetaceans and pinnipeds; Janik and Slater 1997, Rawls et al. 1985), elephants (Poole et al. 2005), and some bats (Boughman 1998).

5. Spontaneous Entrainment in Non-human Species

To test for entrainment, we first performed two case studies on an African Grey parrot (Alex) as well as a Sulphur-Crested Eleanora cockatoo (Snowball). In these studies, we simply recorded and analysed the birds' spontaneous behaviour in response to recorded music. However, we also took two steps necessary to make these sessions well-controlled experiments: *Firstly*, we eliminated visual cues, such as human movement, to ensure that the birds were responding to the auditory stimuli, not simply using visual input. *Secondly*, we included novel auditory stimuli. Using novel stimuli (created by the author using music sequencing software) meant that the birds would have to generalize any entrainment behaviour to novel sounds. This ensured that any response was not due to simple behavioural shaping, or training to respond to particular sounds with particular movements. By generalizing their entrainment to new stimuli, the birds would have to perform a behaviour analogous to human entrainment.

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[1] This ability is also termed 'vocal learning' in other literature; however the term 'vocal learning' is also used to refer to a larger category of abilities unrelated to imitation, such as the ability to learn produce innate vocalizations in novel contexts (e. g. Janik and Slater 2000), and as such was avoided here.

When we played the birds these stimuli, we saw a surprising response: At the very first hearing, Alex bobbed his head seemingly in time to the beat. This same phenomenon was seen in Snowball, who not only bobbed his head but also lifted his feet, again seemingly in time with the musical beat.

Were the birds actually entrained to the musical beat, more so than we would expect by chance? Or were our minds simply finding patterns in what is truly randomness? To analyse the data, we first performed a frame-by-frame manual coding of the birds' head location. This gave us accurate, continuous data on the birds' movements over the course of the video. Where discrete data was needed, the points at which the birds stopped moving (due to changing direction at the top and bottom of their movement cycle) were used as the beat locations. Then, we collected tapping data from humans: Subjects entrained to the same stimuli as the birds, and the timing of their taps was recorded. This data gave us an idea of the beat locations, as well as the amount of error acceptably present in human entrainment. We then examined the extent to which the birds' and humans' beats aligned in frequency and phase. Using multiple convergent analyses allowed us to characterize the data in a detailed manner, and allowed for convergent evidence of entrainment from multiple aspects of the movement signal.

In our frequency analysis, we first asked: Does the bird maintain a consistent frequency over time, or seem to be moving at a range of frequencies, as we might expect by chance? To address this, we first took a Fourier transform of the movement signal, giving us the magnitude or amount of each frequency present in the signal. If the bird is moving at one frequency more than the others, we should see a peak in the Fourier transform at that frequency. Then the question becomes: is the bird consistent enough that it is highly unlikely to have happened by chance? To address this question, we performed a Monte Carlo simulation, simulating what the data would look like if the bird were simply moving at a range of random frequencies. We simulated 5,000 null-hypothesis datasets of this type, and then asked: How likely is it that a peak as high as the peak we see in the real data would occur under the null hypothesis? This allowed us to determine a threshold for significance, such that when the peak height was higher than that threshold the bird was so consistent that it was very highly unlikely to be due to chance ($p < 0.05$).

Moving at a consistent frequency only matters if the bird is also moving at the *correct* frequency. To determine whether the birds' frequency matched that of the musical beat, we compared the peak location (which is the birds' modal frequency) to the distribution of human modal tapping frequencies, and counted anything < 2 SD from the human mean as a match.

Next we performed phase analyses. In the case of a person tapping to a beat, *phase* refers to the temporal distance between a tap and the nearest musical beat. The word phase is used because beat-based data are inherently circular. Imagine a few beats visually, with time going from left to right. If one is trying to tap to the beat, there are multiple temporal locations that are equally accurate: tapping in time with the first beat, and tapping in time with the second beat, for instance. The time in between these beats is less accurate, as a function of the temporal distance from whichever beat is closest. Thus, the most inaccurate time to tap is right in between two beats, which is maximally far from both the first and the second correct time point. Thus, as a person's taps move away from the first beat, the taps becomes more and more inaccurate only until they pass the mid-point between the beats.

At this point, the tap locations once again become more accurate as they begin approaching the second beat. This data is thus well represented as mapped onto a circle, where zero degrees is the beat location and 180 degrees is the midpoint in between two beats. The timing of each tap relative to the beat can be mapped onto a point on this circle. Because of the circular structure of the data, circular statistics serve as the appropriate methods to analyse alignment of phase, and determine whether this alignment was accurate enough to have been unlikely to occur by chance.

Our first phase analysis asked whether the bird maintained a consistent phase relationship with the musical beat, or if the bird slowly slipped out-of-time with the beat over the course of a series of movements. We would expect such slipping in the case that the bird was moving at approximately the right frequency, but was not really entrained. We commonly experience this phenomenon while driving: when we turn on music, we at times have the perception that the windshield wipers are moving in time with the musical beat. However, since the wipers are not at precisely the correct frequency, and are not correcting their speed to match subtle tempo changes in the song, the wipers slowly slip farther and farther away from the beat until we no longer perceive them as aligned. If the birds gradually slip out of phase in this way, this would suggest that they are not actually entrained, but that the matching frequency of movement happened by chance.

Conversely, if the birds retain a consistent phase-relationship with the beat over a long period of time, this would serve as very strong evidence of entrainment. Consistent phase is highly unlikely to be maintained without intentional entrainment and error-correction, because of the cognitive and motor error intrinsic to the process (Repp 2005). Without error correction we would quickly slip out of time as this error accumulated. Thus, maintaining consistent phase over time strongly supports the case for entrainment.

To determine consistency of phase, we performed a Rayleigh test for consistency of phase angle (Fisher 1983). This analysis takes into account the amount of data and length of videos in calculating how likely the data would be to occur by chance. Thus if a bird was highly aligned, but our dataset contained only 10 seconds of periodic movement in that trial, the Rayleigh test was even more stringent in its determination of significance, taking the limitation of dataset length into account (Fisher 1983).

The second analysis went further, asking if the birds were not only maintaining a consistent phase but were actually phase-matched, or synchronized with the beat. For this we performed a second type of Rayleigh test, using a specified mean direction of zero (Fisher 1983). This test detects the presence of consistency and synchrony together, and thus identified trials where the birds' movements aligned with the beats themselves, instead of consistently occurring just after or just before each beat.

Across all four of these analyses, we found robust evidence of entrainment in both of our case study subjects. Subject 1 showed evidence of phase-matched entrainment across all four analyses in two out of six trials, and non-phase-matched entrainment in another two of the six. Subject 2 showed robust evidence of phase-matched entrainment across all four analyses in three out of four trials. Notably, this subject demonstrated entrainment across a wide range of tempos, changing speed in order to match the music at tempos ranging from 108 to 132 beats per minute. In addition to performing a head-bobbing movement, Subject 2 also seemed to lift his feet in time with the music – complete analysis of this movement showed that the foot movement was also entrained (Schachner et al. 2009).

The case studies thus showed strong evidence of entrainment in non-human animals. In addition, convergent data from Patel and colleagues documented that when a song was manipulated to change its tempo, Snowball changed speeds to maintain alignment (Patel et al. 2009), further strengthening the case for entrainment.

Multiple aspects of the birds' entrainment behaviour paralleled human auditory-motor entrainment. For instance, avian entrainment does not seem to occur reflexively; the birds do not obligatorily move every time a song plays, or continue to entrain for the entire duration of the song. Thus, the behaviour does not seem to be a low-level obligatory response but instead appears volitionally controlled. In addition, the birds are able to entrain across a range of tempos, generalize the response to novel stimuli, and entrain the movement of multiple body parts. All of these qualities suggest that avian entrainment may rely on similar cognitive mechanisms to human entrainment.

6. Testing the Vocal Mimicry Hypothesis

Both of the case study subjects were proficient vocal mimics. Thus, the finding that these birds are able to entrain is consistent with the vocal mimicry hypothesis. However, in order to truly test this idea, we must show not only that entrainment appears in vocal mimicking species, but also that the capacity never appears in non-mimicking species. To support this negative claim, we need a vast comparative dataset, containing data from non-mimics as well as vocal mimics. These data should be varied enough to find any evidence of entrainment, should it exist; thus it must include examples of non-mimics from many species. In addition, we must have data from multiple animals within each species, so as to account for a large range of experiences.

To find such a dataset, we turned to YouTube.com, a vast public video database consisting of millions of user-contributed videos. We asked: do we find evidence of entrainment in vocal mimicking species, but never in vocal non-mimics? To answer this question, we conducted a series of systematic searches of the database using animal terms selected to represent species across the taxonomic tree, and added the word "dancing" to each animal search term.

While this dataset does contain some biases, such as users posting only the best videos, there is no possibility of systematic bias with regard to our question of interest, the difference between vocal mimicking and non-mimicking species, as the people posting videos were unaware of the hypotheses driving this work. In addition, vocal non-mimicking animals are better represented in the database than vocal mimics by approximately 2 : 1 (Schachner et al. 2009), increasing our relative chances of finding entrainment in this group should it exist. For these reasons, the YouTube database provides a useful and appropriate test case for the vocal mimicry hypothesis.

We performed a total of 161 searches, finding 3879 unique videos, 1019 of which contained a non-human animal. We analysed these videos for evidence of entrainment using the same motion-tracking and statistical methods used for the case studies and detailed above. In the final dataset, vocal mimics and vocal non-mimics were approximately equally represented; however, evidence of entrainment was found only for vocal mimicking species. In particular, evidence of entrainment was found in 33 vocal mimicking animals and zero vocal non-mimics, a result highly unlikely to happen by chance (Schachner et al. 2009). Overall, we found evidence of entrainment in 14 species of parrot, as well as in Asian elephants.[2]

To our knowledge, none of the species found to entrain are known to naturally entrain to sound in the wild. Auditory-motor entrainment does not seem to be part of the natural behavioural repertoire of parrot species. This detail can inform our understanding of the evolution of avian entrainment: If the capacity is truly not expressed in natural behaviour, there is no potential for this behaviour itself to increase or decrease fitness. Effectively, the behaviour does not exist, and as such cannot be selected for (or against) by natural selection. Thus it must have arisen as a byproduct of selection for another cognitive capacity. Coupled with evidence that only vocal mimicking species entrain, this lends support to the idea that avian entrainment emerged as a byproduct of selection for vocal mimicry.

Humans are only distantly related to parrots, and many more closely related species do not entrain. As such it is extremely unlikely that humans and parrots inherited the capacity for entrainment from their last common ancestor. A pattern of convergent evolution is more likely, in which similar evolutionary pressures led to the development of similar genetic and neural mechanisms in the two lineages. While it is thus possible that human and avian entrainment emerged in different ways, the close parallels between the features of the behaviour suggest similar evolutionary origins. Hence, these data make it plausible that human entrainment as well as avian entrainment may have emerged as a byproduct of selection for vocal mimicry.

To return to the first of the two questions originally posed in this chapter: Why can we entrain? These data give us a potential answer: Natural selection for vocal imitation may have given us the cognitive machinery needed for entrainment.

7. Why Do We Tend to Dance?

How did human entrainment emerge? While selection for vocal mimicry may have given us the prerequisite machinery, we still must account for another phenomenon: The universal human motivation to engage in entrained behaviour. We not only *can* move to a beat, but we actually *do* move to a beat. Entrained movement is omnipresent in human culture; in contrast, entrainment seems not to be a part of avian species' natural behavioural repertoire. How do we account for this difference?

One potential explanation rests on the idea that the tendency to entrain may have been directly selected for in subsequent evolution, for the following reason: If people tend to entrain to sounds they hear, and people tend to hear the same thing when they are in nearby locations, this will lead to synchronized movement. If synchrony is adaptive in some way, then the tendency or motivation to entrain should be directly selected for. Thus, if we start out with a population in which people differ in their capacity to entrain or in their tendency to express the behaviour, selection will favour those who are motivated and tend to entrain, as those people will experience the most synchrony.

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[2] Data from Asian elephants did show evidence of entrainment in terms of the extent of the elephants' alignment with the beat; however, this data in particular calls for further replication due to the circumstances under which it was recorded. While parrot owners reported spontaneous entrainment by the birds, the elephants' movements appear to be staged performances by professional trainers. Thus, further work should test elephant entrainment in a controlled environment.

Why might synchrony be adaptive? There are theoretical reasons to suspect that synchrony may increase social bonding and cooperative behaviour, and recent experimental work has supported this idea. For instance, synchronized marching is widely used to train the armed forces. In today's military, marching exercises are valued not for their direct use in combat, but for their ability to promote camaraderie and cooperation among the troops (McNeill 1995).

In addition, work on imitation has shown that subtly mimicking a person's posture, movements or mannerisms (a widespread phenomenon termed behavioral mimicry or behavioural matching) leads to increased liking, empathy and cooperation (e. g. Chartrand and Bargh 1999, Ashton-James et al. 2007). Since synchrony can be construed as mimicry without a delay, it seems plausible that synchrony might promote cooperation through the same mechanism as behavioural mimicry (Hove and Risen 2009). In particular, perceiving another's movements as parallel to your own may increase the similarity between one's representation of oneself and that of another (Iacoboni 2005). Since we cooperate most with similar others, this increase in self-other representational overlap would likely result in prosocial behavioral effects (Galinsky et al. 2005).

Recent experimental evidence has supported the idea that synchrony promotes prosocial behaviour. A recent paper purported to show that synchrony increased cooperation in economic games, such as the public goods task (Wiltermuth and Heath 2009); however, there is some question as to the replicability of this data (Schachner and Garvin 2010). Using other methods, additional authors have found convergent evidence that synchrony increases prosociality (e. g. Hove and Risen 2009). Based on this evidence, it seems likely that synchrony does lead to prosociality and increased cooperation.

How can this literature fit together with comparative evidence suggesting that the entrainment capacity emerged as a byproduct? These literatures are not necessarily in conflict. Entrainment is a complex capacity, which depends on many neural mechanisms and evolved in a complex process over a long period of time. The evolution of human entrainment may have occurred in two steps: *First*, selection for mimicry gave us the cognitive machinery needed to entrain. *Second*, once we had this prerequisite cognitive machinery, the tendency or motivation to entrain was adaptive; people who tended to express this behaviour more often experienced more synchrony and thus formed more cooperative relationships. Thus, the tendency or motivation to engage in entrainment behaviour was directly selected for during human evolution. By this hypothesis, entrainment is widely expressed in human behaviour but remains latent in avian behaviour because our species has experienced direct selection for synchrony, while avian species have not experienced this type of selection.

There are two reasons why avian species might not have experienced selection for the tendency to entrain. *Firstly*, it is possible that entrainment evolved in these species very recently in evolutionary time, and while synchrony is adaptive in these species as well, avian species have not yet had sufficient time for selection for the tendency to entrain to have an effect. *Secondly*, it is possible that synchronized movement simply does not confer an adaptive advantage in parrot species. This hypothesis seems plausible, since the cooperative effects of synchrony and mimicry are thought to rest on high-level abstract representations of self and other (Hove and Risen 2009). These abstract social representations may be fundamentally different in parrot species as compared to our own.

This second possibility makes a testable prediction: After engaging in synchronized movement with other individuals, parrots should not become more cooperative or prosocial, even if they are capable of entrainment. Conversely, non-human primates who are incapable of entrainment may nonetheless become more prosocial after engaging in synchronized movement. If this complex prediction were supported, this may suggest the existence of two stages of the evolution of the human capacity for entrainment: A first stage, in which the capacity for entrainment emerged as a byproduct; and a second stage in which the tendency to engage in entrained behaviour proved adaptive, and was selected for directly. This theoretical proposal thus would account not only for our ability to move to a beat, but for the widespread human propensity to groove, tap, bop or bounce in time with music and with other individuals.

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2012 jährt sich zum 360. Mal die Gründung der heutigen Deutschen Akademie der Naturforscher Leopoldina – Nationale Akademie der Wissenschaften im Jahr 1652 in Schweinfurt, und am 7. August 1687, vor 325 Jahren, gewährte Kaiser Leopold I. der Gelehrtengesellschaft besondere Privilegien. Diesen Anlässen widmet sich eine Ausstellung, die eine große Anzahl von authentischen und einzigartigen Quellen zur Geschichte der Akademie aus den Archiven der Stadt Schweinfurt und der Leopoldina als Kooperationsprojekt zunächst in Halle (Saale) und später in Schweinfurt zeigt. Der Schwerpunkt liegt auf der frühen Internationalisierung der Akademie. Die Publikation beschreibt die vorgestellten Objekte und enthält darüber hinaus eine Edition aller kaiserlichen Urkunden von 1677 bis 1742.

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From Ethology to Human Ethology
Cognitive Patterns in the Culture of the Eipo, Highlands of West-New Guinea

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Abstract

Classic ethology, as developed by Konrad Lorenz, Nikolaas van Tinbergen and others, is one version of modern evolutionary biology and documents, in pursuit of one important goal, animal behaviour. This is carried out (despite of occasionally raising young animals by hand) in a neutral and distanced approach. The ideal is to watch the behaviour of the animals in the normal habitat and social environment typical for the species. One of the aims of ethology is to establish a complete as possible ethogramme of the respective species. Human Ethology, a discipline which took shape in the 1970s, was founded, chiefly by Irenäus Eibl-Eibesfeldt, as an offspring of comparative, phylogeny oriented ethology. The typical tool to document the behaviour of members of different cultures became, upon suggestion of Hans Hass, the 90° mirror lens which facilitated filming persons interacting among each other without them posing towards the camera. In this way, the human ethology film archive of the Max-Planck-Society, housing approximately 250,000 m of footage of unstaged social interactions and unique in the world, was built up; included are films of the classic ethnographic type taken without mirror lens.

In order to include, in the collection of film documents and the eventual description of the particular culture, the sociocultural, mental sphere of that society, ethnographically and linguistically trained co-workers were part of the teams in five ‘model cultures’. Using this line of fieldwork stemming from the tradition of ethnology (participant observation and extended interviews with informants), a corpus of data is collected which does not only provide back ground information for the human ethological film documentation, but also forms the base for detailed analyses of cognitive concepts, the mental world, of the studied society as well. My contribution is built on this approach.

Ethnobotanic research carried out among the Eipo in the Highlands of West-New Guinea (the Indonesian ‘Propinsi Papua’) demonstrated the existence of a very sophisticated system of plant taxonomy and extraordinary general knowledge of plants, involving ecological and other parameters. The human mind, an incredibly efficient organ to make order in the chaos of the world, utilizes, when it comes to plants and animals, the same universal principles of hierarchical ordering and the same criteria (phaenotypic and developmental similarity) to build up a genealogical tree, just as does western botany with its backbone of Linnean taxonomy.

The Eipo language, a typical representative of the Papuan languages of the Trans New Guinea Phylum with its rather complex agglutinative structure, a large number of tenses and finite forms of the verb, was learned in a monolingual approach. In this process, I realised how easy to understand many semantic concepts were. Being thus educated with regard to Eipo language and culture it also became evident that there was no general insurmountable perceptual fence between my teachers/informants from a quasi-neolithic culture and myself. There is, I am deeply convinced, no Sapir-Whorfian chasm which renders understanding of concepts across cultural borders impossible or even very difficult. The universal nature of the human mind and the capacity for emphronesis (Theory of Mind) unite the members of our species in an epistemological continuum.

Particularly interesting is the fact that humans, most likely everywhere on this planet, express deep emotions, like being in romantic love or having lost a close person through death, in the special language of poetry instead of prose. This can perhaps be explained as a biopsychological mechanism of enhancing and structuring the emotional experience, thereby preparing the person for similar situations in the own life and that of others. The fre-

quent use of metaphors, especially in this kind of emotionally charged poetry, is another constituent of the human condition, telling of our nature as *Homo symbolicus*. Human ethology as the evolutionary biology of human perceptions, emotions, thoughts and behaviours offers insight not only into patterns of social interactions, but also into the intricate cognitive concepts so similar among humans in all cultures.

Zusammenfassung

Die klassische Ethologie, entwickelt von Konrad Lorenz, Nikolaas van Tinbergen und anderen, ist eine Form der modernen Evolutionsbiologie und hat als ein wichtiges Ziel die Dokumentation tierischen Verhaltens. Diese erfolgt (trotz gelegentlicher Handaufzucht) von einer neutralen-distanzierten Warte aus. Das Ideal besteht in der Beobachtung des Verhaltens der Tiere in ihrem angestammten Habitat und der für die Spezies typischen sozialen Umgebung. Angestrebt wird, ein möglichst komplettes Ethogramm der jeweiligen Art zu erstellen. Die Humanethologie, gegründet vor allem von Irenäus Eibl-Eibesfeldt in den 1970er Jahren, hat ihre Wurzeln in dieser Herangehensweise und nutzt ebenfalls eine vergleichende, die Phylogenese betonende Perspektive. Für die filmische Dokumentation des Verhaltens von Angehörigen verschiedener Kulturen wurden auf Anregung von Hans Hass Objektive mit Umlenkung um 90° Grad benutzt, da so die sozialen Interaktionen der gefilmten Personen ohne Posieren in Richtung Kamera aufgenommen werden konnten. Das humanethologische Filmarchiv der Max-Planck-Gesellschaft umfasst Filme ungestellten Verhaltens von etwa 250 000 m Länge, einschließlich klassischer ethnographischer Aufnahmen ohne Spiegelobjektiv.

Zur Ergänzung der ethologischen Dokumentation und für die spätere Beschreibung der jeweiligen Kultur wurde die soziokulturelle, mentale Sphäre der betreffenden Gesellschaft durch ethnographisch und linguistisch geschulte Mitglieder der Teams für die fünf „Modellkulturen“ erfasst. In dieser Weise der teilnehmenden Beobachtung und nach ausgedehnten Interviews mit Informanten entstand ein Corpus an Daten, das nicht nur als Hintergrundinformation für die Filmdokumentation genutzt werden konnte, sondern auch die Grundlage für eine detaillierte Analyse der kognitiven Konzepte, der geistigen Welt der untersuchten Ethnien bereitstellte. Mein Beitrag entstammt diesem Zugang.

Bei den Eipo im Hochland von West-Neuguinea (der indonesischen „Propinsi Papua“) wurde u. a. ethnobotanisch gearbeitet. Dabei zeigte sich, dass die Einheimischen ein außerordentlich entwickeltes System der botanischen Taxonomie und ausgezeichnete allgemeine Kenntnisse über die Pflanzenwelt, einschließlich ökologischer und anderer Zusammenhänge hatten. Das menschliche Gehirn ist phantastisch effizient, wenn es darum geht, Ordnung im Chaos der Welt zu schaffen. Für die Klassifizierung der Reiche der Pflanzen und Tiere nutzt es unabhängig von der Kultur dieselben universalen Prinzipien der hierarchischen Strukturierung und dieselben Kriterien, nämlich phänotypische und entwicklungsgeschichtliche Ähnlichkeiten, und stellt genealogische Stammbäume auf, genau so, wie es in der modernen auf Linné gegründeten botanischen Taxonomie der Fall ist.

Die Eipo-Sprache, eine typische Vertreterin der Papua-Sprachen des Trans-New-Guinea-Phylums mit einer sehr komplexen agglutinativen Struktur sowie einer großen Anzahl von Zeiten und finiten Formen der Verben, wurde in monolingualem Zugang gelernt. In diesem stets Kontext bezogenen Prozess wurde mir bewusst, wie einfach es war, viele der semantischen Konzepte zu verstehen. Ich erkannte, dass es keine prinzipiell unübersteigbaren Hürden zwischen den mich lehrenden Gewährsleuten aus einer quasi neolithischen Kultur und mir selbst gab. Ich bin tief davon überzeugt, dass die generelle Kluft im Sinne von Sapir und Whorf nicht existiert, die das Verstehen kognitiver Konzepte über kulturelle Grenzen hinweg unmöglich oder auch nur besonders schwer macht. Die universale Natur des menschlichen Denkens und die Fähigkeit für Emphronesis (*Theory of Mind*) einen die Mitglieder unserer Spezies in einem epistemologischen Kontinuum.

Besonders interessant ist das Faktum, dass Menschen, sehr wahrscheinlich überall auf unserem Planeten, tiefe Emotionen, wie jene des Verliebtseins oder des Verlustes einer nahestehenden Person durch Tod, in der besonderen Sprache der Lyrik anstelle der Prosa ausdrücken. Möglicherweise ist das ein biopsychischer Mechanismus, der emotionale Erfahrungen überhöht und damit strukturiert und so das Individuum besser instand setzt, mit ähnlichen Situationen im eigenen Leben und jenem von anderen besser umzugehen. Der häufige Gebrauch von Metaphern, wie er in dieser Art von emotional aufgeladener poetischer Ausdrucksweise vorkommt, ist ein weiteres Merkmal der *conditio humana*, das unsere Natur als *Homo symbolicus* spiegelt. Die Humanethologie als Evolutionsbiologie menschlicher Wahrnehmungen, Gefühle, Gedanken und Verhaltensweisen eröffnet Einblick nicht nur in die Muster sozialen Verhaltens, sondern auch in die komplexen kognitiven Konzepte, die in allen Kulturen eine große Ähnlichkeit aufweisen.

1. Human Ethology – A Brief Sketch

Konrad LORENZ developed previously existing concepts about the evolutionary base of animal perception and behaviour and thereby became one of the fathers of ethology. During his long detention as prisoner of war in Russia he wrote, on carefully cut out pieces of cement bags and without access to a scientific library, a fundamental text on ethology, the famous Russian manuscript (published 1992) in which he accentuated the principle of phylogenetic and functional adaptation.

After late release in 1948 LORENZ gathered some of his Viennese students (among them Wolfgang SCHLEIDT, Irenäus and Eleonore EIBL-EIBESFELDT) to start an ethological research unit in Buldern, Westphalia. LORENZ then joined forces with Erich VON HOLST and founded the famous Institute for Behavioural Physiology in Seewiesen, Bavaria, inaugurated in 1958. It was here, in the rich climate of a revolutionary beginning, sparked off by new ideas, that the new discipline was outlined and developed with original observations and experiments. Researchers and visitors, quite a few from the opposing camp of behaviourism, who lived and worked together at idyllic Ess-Lake near renowned Andechs Monastery south of Munich, contributed to the rapidly expanding ethological paradigm.

For his ground-breaking work on imprinting Konrad LORENZ was honoured by the Nobel Prize which he received, in 1973, together with his colleague and friend Nikolaas TINBERGEN, another founder of the discipline who formulated the four basic questions of evolutionary biology, and Max VON FRISCH, the Munich zoologist who deciphered the code encrypted in the dance of bees returning home from harvesting.

Irenäus EIBL-EIBSFELDT, who wrote the first encompassing text book of ethology (1967, several further editions and translations) and thereafter founded the new field of human ethology which he laid out in another substantial textbook (1984, repeatedly republished and translated into foreign languages as well) and thus continued the Lorenzian strand of ideas on the evolutionary biology of humans which had vividly been present already in DARWIN'S work (1871, 1872), too. Among those who saw the potential of human ethology as a Darwinian discipline, rooted in evolutionary biology and natural science on the one hand as well as in the traditions of the classic human sciences like ethnology/anthropology, sociology, history and the like, was Günter TEMBROCK who started to teach human ethology (cp. FREYE and TEMBROCK 1990, based on a meeting at Leopoldina, Halle) to the small sworn-in group of dedicated students gathered around this encyclopaedic mind and unbending man. Another initiative to establish the new cross-border paradigm (always a risky undertaking, because the disciplines so far protected by borders usually react quite strongly to such "illegitimate" transfer of new ideas from a "hostile" discipline) was that of Mario VON CRANACH, Klaus FOPPA, Wolf LEPENIES and Detlev PLOOG (1979) who organised a human ethology meeting at Reimers Foundation, Bad Homburg, in which EIBL-EIBESFELDT participated and contributed a chapter on "Ritual and ritualization from a biological perspective" (1979).

The research group headed by Renki EIBL and affiliated to the Seewiesen Institute, later located in nearby Erling-Andechs, carried out fieldwork, mainly in five traditional cultures (cp. EIBL-EIBESFELDT 1976, SCHIEFENHÖVEL et al. 1993), i. e.

- San hunter-gatherers of the Kalahari in Botswana;
- Himba cattle breeders of Namibia;

- Yanomami hunter-gatherers and horticulturists at the Upper Orinoco, Venezuela;
- Eipo horticulturists and hunter-gatherers in the Highlands of West-New Guinea, now called Province Papua, Indonesia;
- Trobriand Islanders, horticulturists and users of marine resources in the Solomon Sea, Papua New Guinea.

In these "model" cultures and a few others, a massive and worldwide unique film documentation (approximately 250,000 m footage of mostly 16 mm film and videorecordings) of unstaged social interactions as well as of ceremonies was made by Eibl-Eibesfeldt himself and, to a much lesser extent, by some members of the team. This archive describes universal and culture specific behaviours in societies, which at the time still followed traditional life styles; it thereby contains irretrievable documents of times gone by. At present an effort is made to have this human ethology film archive declared UNESCO World Heritage. The co-workers conducting fieldwork in one or more of the model cultures were linguistically and ethnologically trained to be able to provide detailed background information on the respective ethnic groups, including their cognitive and religious concepts (cp. Eibl-Eibesfeldt et al. 1989, Schiefenhövel et al. 1993, Heeschen 1990, 1998, Schiefenhövel 2009b).

In this way, the classic distanced, indirect ethological method of observing individuals in their natural setting, usually performed by Irenäus Eibl-Eibesfeldt using a camera with 90° lens to avoid direct pointing at filmed persons and thus getting their attention, was enriched by participant observation in the ethnographic tradition: „kijken, luisteren, opschrijven", as Jan van Baal, the doyen of Dutch ethnography, used to describe it (van Beek, pers. comm.). It was thus possible to also document the mental world of members in the respective cultures. The present contribution is stemming from this approach which attempts to go beyond externally observable behaviour to uncover cognitive elements of the universal *conditio humana* uniting, despite genetic and cultural differences, our large species.

2. The Eipo – Modern Models of the Past

At the beginning of our fieldwork, 1974, in the southern Eipomek Valley, approximately in the centre of what became named the Mek area of languages and cultures (Schiefenhövel 1976, 1991), approximately 800 Eipo lived in 5 villages in a mountainous region of the interior of West New Guinea, formerly West-Irian, now named Province of Papua on approximately 140° eastern longitude and 4° 27', southern latitude. These villages, surrounded by others whose inhabitants spoke related dialects of the Mek language, were situated in about 1,600 to 2,000 m above sea level. The climate is very wet (app. 8,000 mm rainfall per year), cold in the nights (down to app. 12 °C) and warm in the days (up to app. 30 °C). The valleys are flanked by rather steep mountains, the lowest pass to the southern sides of the central cordillera with peaks of app. 4,800 m is at 3,700 m. This illustrates the very alpine character of the habitat of this mountain Papua.

Since the Eipo have, around 1980, turned to Christianity, in a rather political than theological move (Schiefenhövel 2009b), their life has changed, in some respects quite drastically. Other facets of their culture (e.g. gardening, clan structure, family life) have largely stayed the same. Due to abolishing infanticide, a now shorter post-partum coitus taboo, an earlier menarche and simple but effective modern health care the population had at least doubled in 2010, possibly tripled and may number between 15–20,000.

At the time of our arrival in 1974 all tools were made of stone, bone, tooth or wood, there was no writing for the complex, agglutinating language, a member of the Trans-New Guinea Phylum, which I learned, *nolens volens*, in monolingual approach (cp. the dictionary: Heeschen and Schiefenhövel 1983, see below). Most marriages were monogamous, divorce was not infrequent, about 10% of the men lived in officially recognized polygynous partnerships. Polyandry was a possible, albeit very rare matrimonial choice as well. Residence was usually virilocal, descendence was patrilinear, i.e. according to the clan of the father. Political leadership for the communities was resting with influential men, traditionally called “big men” in the anthropological literature on Papuan cultures. The Eipo call these persons “*sisinang*”, the ones who have the say. These positions are strictly meritocratic. Should such alpha-man lose his vitality, social intelligence or rhetoric power, he would be replaced in a non-formal process. Women, often self-assured, impressive persons, also had a say in the society, especially on the family level.

The Eipo culture was characterised by a marked sociopolitical gender dichotomy, i.e. female and male worlds were, in many ways, separated. The men’s house (*yoek aik*) was the place for initiated males only, for political planning and the most sacred relics handed on since time immemorial. The women’s houses (*bary’ eik*) were, on the other hand, taboo for men and reserved for menstruation, birth, puerperium and times of severe disease or conflict of a woman with her husband.

The Eipo society was, as it was typical for the Papuans in general, very martial. Fights (*abala*) within the political unit of one or a few villages were classed differently than warfare (*ise mal*) against the hereditary enemies in the adjacent valley in the west. Both were carried out with remarkable aggressivity: 25% of the men died a violent death (Schiefenhövel 2001). Like other traditional societies around the globe they lacked the institution of the Third Party, which could have been called in as ombudsman or could have acted as institution with judiciary power to solve the conflict. Disagreements and bad feelings mostly sparked off by extramarital sexual affairs but also by other infringements, thus escalated from verbal quarrel to shooting arrows. Men took sides according to which of the two parties they were more related to, and often these armed conflicts would turn into a spiral of avenging violence, ending only when so many lives had been lost that the two parties decided to make peace.

3. Cognitive Concepts

3.1 Plant Taxonomy and Ethnobotany

New Guinea Highlanders are extraordinarily capable gardeners and botanists. This was becoming evident when juveniles accompanied the two botany professors of our team on their collection trips. They found it interesting that flowers, fruits and leaves were taken and prepared for conservation in newspaper, alcohol and the like. They asked, on many occasions, the two German botanists whether they knew that a particular plant A was related (“the brother”, “uncle” and similar terms) of plant B. Often, the specialists had to admit that they did not know that and sometimes they replied, that a relationship between two seemingly very different plants was not very likely. The local informants insisted, however, on this. It took the typical careful examination of the collected herbarium specimen and comparison with ones from the classic herbaria in London Kew Garden, Leiden and Bogor, Indonesia, to find out that the Eipo had been right in all cases! (HIEPKO and SCHIEFENHÖVEL 1987). An extraordinary feat of human cognitive performance. Here were people, living in neolithic conditions, without any formal education, without books, who had very clear ideas about the taxonomy of plants. And, this taxonomy is almost identical with our modern, scientific Linnaean system!

How can this happen? It sounds a bit like hocus-pocus, told by an ethnographer who is just fascinated by "his" people. In this case, Paul HIEPKO, one of the two botanists, was co-author of the monograph (op. cit.) in which these findings were published and related to comparably precise folk taxonomies (cp. BERLIN et al. 1973). It is not at all uncommon for members of traditional societies to have such very distinct, clear-cut classificatory system. The human brain is a wonderfully effective machine to create order in the chaos of the world. And it is, once one starts to think about this, no wonder that the taxonomic systems in so many parts of the world follow the same principle: similarities in morphology as criterion and a hierarchical system as structure. After all, Carolus LINNAEUS did not invent the taxonomy named after him, but "only" systematised the already existing European folk taxonomy. The hierarchical principle on which the Linnaean classificatory system is based, is found in Eipo ethnobotany as well: plants, including mosses, lichens, ferns, and mushrooms, are distinguished from animals. The criteria encompassing animal and human being and setting them aside from plants are as scientific as descriptive: *balamle, dilamle, foklamle* = it walks, it eats, and it copulates. In the world of plants the Eipo distinguish between trees and other ligneous plants, small flowering plants, weeds, grasses, sedges etc. As in the Linnaean system, it is the well-defined genetic relationship, postulated on the grounds of phenotypic similarity, which regulates the position in the classificatory system. Humans, I have no doubt, are *natural* natural scientists.

A second enigma connected to these ethnobotanic findings is, how children can learn these very precise and often complicated facts of natural science. Our teachers do everything they can, in the classroom, to make our children understand the differences between the several species of pine trees in the German forest, spending a full school hour on this topic showing pictures, schematic illustrations etc. When these kids actually go to the forest, most of them don't know anything at all. The carefully planned transfer of knowledge from the teacher's brains to that of her students failed. How come that the stone-age method of teaching and learning is so much more effective? The answer, I am convinced, lies in the completely different way of learning: classroom *versus* contextual, boring *versus* emotionally positive situation. A New Guinean child who is taught the secrets of a little plant and its "brother" or "uncle" and about their complex ecology just needs one exposure to suck up this knowledge passed on to her or him by someone of the family or a peer. Children are beautifully curious and want to know… only that we, in our school system, make such bad use of this propensity.

Another proof for New Guinea Highlanders being gifted gardeners and botanists is the fact that some plants of high economic value in the world of today were domesticated in this part of our planet. Usually, one thinks of sugar cane (*Saccharum officinarum*) to be a Cuban or Caribbean plant. But this is far from the truth. It is a gift of the early Papuans to humankind. Only in Highland New Guinea three closely related species are found: the wild non-edible *Saccharum spontaneum* (called *kwasa* in the Eipo language); a domesticated species with many cultivars, *Saccharum edule* (called *bace* in the Eipo language, *pitpit* in Neomelanesian Pidgin or Tok Pisin and *sayur lilin*, "candle vegetable" in Bahasa Indonesia, a typical New Guinean garden product of which the unfolded inflorescence is eaten, a truly delicious Papuan delight); the third species is the classic sugar cane, *Saccharum officinarum* (called *kuye* in the Eipo language), of which there are many cultivars as well.

Also taro (*Colocasia esculenta*, called *am* in the Eipo language) is the product of Papuan ingeniousness and gardening success. Approximately 8,000 years before present, it was planted for the first time in the highlands. Now many cultivars of this food plant are propagated in the vegetative method typical for virtually all Melanesian horticulture. Taro represents a type of food essential in ceremonial perspective, reflecting its ancient origin. The everyday source of carbohydrate and easily available energy today is sweet potato, *Ipopoea batatas* (called *kwaning* in the Eipo language) an import from Mesoamerica, possibly after the *conquista*, but possibly through Transpacific Polynesian contacts before the arrival of Europeans. There are more food plants domesticated by the Papuan inhabitants of Highland New Guinea, among them vegetables vitally important as sources of plant protein: *Abelmoschus manihot* (called *touwa* in the Eipo language), *Runggia klossii* (*mula*). Other traditional food plants of the Eipo, also domesticated in this part of the world, include yams (*Dioscorea alata, wanye*), *Seataria palmifolia* (*teyang*) and *Setaria plicata* (*lana*), banana (*Musa paradisiaca, kwalye;* probably domesticated in the lowlands) as well as various products of arboriculture which makes it possible to harvest the seeds of several *Pandanus* trees, e. g. *P. brosimos* and *P. conoideus*, which contain fat and (the latter) valuable substances like carotene. Fat was almost absent in the diet of the Eipo in which the average animal meat/fat consumption per person and day was below 1 g, except in women and infants were the intake was a bit higher due to insects, their larvae and other protein food directed, by taboo for males, towards those who need it most (Schiefenhövel and Blum 2007). It is quite amazing that with this basically vegetarian diet (out of necessity, not of want!) men were able to build up impressive musculature, and women were able to perform extraordinary feats of stamina when they carried (and still carry) loads of more than their own body weight for hours… with a smile on their faces.

Summing up this aspect of cognitive concepts in botany, gardening, nutrition and beneficial rules for the distribution of scarce valuable resources one can only have the greatest respect for this neolithic people whose ancestors were so creative with regard to horticulture and arboriculture and who continue to utilise their environment in intelligent ways until today.

3.2 Language

The unfortunately still influential Sapir-Whorf hypothesis *sensu strictu* (cp. Carroll 1956) claims that cultures create cognitive borders which are, if at all, hard to penetrate by outsiders. Some of these positions, like that put forward by Margaret Mead about an alternative way of life led by the Samoans (1928), have been found to be wishful thinking and far from truth (Freeman 1983). The German-born linguist and anthropologist Ekkehart Malotki has destroyed (1983) the long-held and cherished paradigm of Hopi "timelessness" with his very careful work as ethnographer and linguist dedicated to an emic approach. His publications are full of actually spoken sentences, whereas Benjamin Whorf was able to get away with his rather stark claims without any corpus of locally collected emic material. One is really left gasping, in both cases, *vis-à-vis* such horribly defective linguistics and ethnography.

When I learned, monolingually, as there was neither wordlist nor interpreters, the Eipo language, I did not find it terribly difficult to hear, as it were, with their ears and get into their minds to obtain a first grasp of their very complex agglutinative language with a bewildering number of finite forms stemming from verbal conjugation in many tenses and modes. When Volker Heeschen came back from Germany, I was able to hand over a list of about 2,000 words with preliminary translations; most of them turned out to be correct upon further checks in the ongoing linguistic work. I had given up, for the time being, to come to grips with verbal conjugation, but Volker managed to crack this linguistic bastion so that we were able to publish a sizeable dictionary (Heeschen and Schiefenhövel 1983) which does not only contain translations of Eipo lexemes but lists, sometimes over more than one page, actual usages of this particular word in spoken sentences, stories, songs, legends and religiously myths.

Some linguists wonder how the seemingly naive monolingual approach to a second language is possible. I would argue that learning another language, in probably more than 100,000 or even 2,000,000 years of human history has be going on in precisely this way: being exposed to speakers of another language and just picking it up, often with all its tricks and intricacies. The universal features of the human mind make this task relatively easy. Once I had discovered that three dialects were spoken in the same speech community and that I had to stick to the same informants teaching me phonemes and lexemes of one of the language variants, progress was made. Some of my informants, especially Kwengkweng (now Enus by Christian name) and Walabyan (now Pilipus) as well as some others, were able to creep into my brain. They understood what I wanted, namely to learn their language and to understand their culture – they represent the intellectuals in their society. Quite an amazing feat: To spend hours, sometimes whole nights, to make sure the white man had actually grasped the first elements on which they were gradually building up my at first pathetically miserable knowledge. Teaching and a perfect performance of Theory of Mind, of mind reading (which I like to call *emphronesis*) in a neolithic setting – quite astounding, near impossible if one adheres to the Sapir-Whorfian paradigm of extreme cultural relativism.

The Eipo have, in their language, many basic words which are very easy to understand, also in their often wide semantic usage. One of these words is rooted in a simple geometrical, physical concept: an acute angle, two lines branching off in a fork, a "V"-shape: *kwa*. The power of this concept became evident to us when we were telling them the Indonesian words for the tools we used for everyday purposes. "Spoon" is *sendok* in Bahasa Indonesia (they found that an ingenious thing) and "fork" is *garpu*. The Eipo immediately borrowed the new term *sendok*, but instead of *garpu* they called a fork *kwaleng sendok*: a spoon with acute angles in between, their concept of a "fork". Very clever and creative and easy for us to understand the rational behind this neologism, based on one imported and one local term. The Eipo found more such solutions to name hitherto unknown objects. Humans, for most parts of the day, are realistic beings, trying to solve problems with their functional brain, product of the evolutionary forces acting on it, throughout hominisation until the present day (Cochran and Harpending 2009). *kwa* is present in the Eipo language in many other semantic shades: *kwa yo* is a tree stem, used as a house post, with a fork at the end, in which one can place a horizontal beam carrying the roof; *yan kwa* is the V-shaped space between the first and second digit of the foot fanning out when walking; *kwakwa* is nicely descriptive term for "butterfly", as these insects open and close their wings to a V-shape, and they do that repeatedly, so the syllable *kwa* is repeated. The classic "V" in many cultures, if not in all, is the symbol for vulva and vagina, *kwate* in the Eipo language.

Sven Walter, junior linguist of our team, has published, after decades as taxi driver in Berlin, a remarkable dissertation (1988) in which he convincingly showed that there are particular principles in the Eipo language which are used to express specific action modes of verbs: *ib-* is the cognate expressing an action of constraining, of pressing, like in *mek ibmak*, they (the children) are stopping the water by a dam (a playful activity); in the form *ik-* the verb signifies the same kind of action, but this time in a more sudden, decisive movement pattern like in *ayukumna ikmak*, they are ramming the house posts in the ground, thereby exerting pressure to the sides of the hole. When the cognate takes the form *in-* or *ine* (the latter is the noun derived from this verb stem), it signifies a repetitive pressing movement, like in *kwatema ine donmal*, the snake makes a continuous movement to either side, or as in *ine,* a repetitive coughing or vocalising action. This list could be enriched by many more examples quoted in the thesis. Other cognates follow the same building principle. It is, as the late Sven Walter has demonstrated, quite clear that the Eipo language has an inbuilt system of submorphematic elements which predict the semantic value. This finding is so very important because it contradicts the hypothesis that language, in particular words, are arbitrary. The same position is taken by Socrates in the Plato's Cratylus dialogue, by Leibniz, Wilhelm von Humboldt and by other renowned linguists and philosophers, but the Saussurean mainstream view of words as happenstance conventions has it otherwise.

3.3 Verbal Art

Eipo forms of visual art were limited to decorating the body, arrows and occasionally other objects. Singing solo and in chorus (cp. Simon 1993) as well as verbal art were, however, very developed. Metaphors, sometimes daring erotic-sexual ones (see below), were used in love songs and others in other situation of deep emotionality, for instance loosing a close relative through death (Schiefenhövel 1985). It is stunning that the human brain, in moments of volcanic feelings, turns to poetry instead of prose, finds metaphors leading to impressive lyrics. In order to fully explore the emotional and cognitive aspects of Eipo poetry one would need to do a more complete analysis. For this contribution, it may suffice to include just a few examples.

Lengikner mourning the death of her nephew Ebna:

"… *Se naye na due na niye*
"… Ah dearest, my kindheart,
angun kwityapo-ab mabrubbulalum-tok gum ubnamalam-e
why don't you sit, why don't you sleep again (in the men's house) side-by-side with your initiation comrades!
berekin banmal baye buknin binamalam-e

From where dusk is lighting the sky (in the top of the funeral tree) you have taken your seat, out there, outside the village, eh.
beryoke fulubrobnye se nake an-yuk bukbuk binmalum se na niye
You, the one who had such long, slim legs, ah, my beloved. All alone you have gone, my kindheart,
dokomana gum olamnumwe-anyak an yuk bukmalam-e…
We did not show each other the cold shoulder, didn't we live so well together in one house? But still you sit there all alone, eh.
… aike dobrobbinalumwe-ake se na niye na niye se Ebne Ebne"
… only recently you have built our house, ake (and, still, you have left us),
oh kindheart, my kindheart, se Ebna, Ebna."

The deep emotion of sorrow, of irretrievable loss so very typical for our human species and observable in chimpanzees as well (Balter 2010) is one of the most solid biopsychic building blocks of our universal nature. No matter how the respective culture deals with this primordial emotion, which shape the various forms of funeral rites may take, its *primum movens* is the interpersonal bond so brutally and forever cut. We do not cry for the sake of the deceased, we cry out of a selfish motive, as texts of mourning poetry indicate (cp. Schiefenhövel 1985). For us, a classic *animal sociale*, the Other, whether it be mother, father, spouse, brother, sister, and, especially, child, is of utmost social and evolutionary importance. Death taking one of those persons deprives us of an immensely important ally in the often rough times of life amidst competition, envy and fight, a partner for cooperation and mutual protection, for care in old age, to whom we have built, through life spent together, a functionally precious relationship which roots in the emotionally charged mindset of understanding, trust, bond, and altruism.

Most interesting and illuminating is the fact that such emotional collapse does not lead to either silence or expressing one's grief in normal language, no, the volcanic forces of our limbic system make grief erupt in highly charged and highly shaped verbal accounts. Such loss often translates itself to sophisticated poetry built on images and metaphors which powerfully speak of the depth of one's defeat – not of the uncertain fate of the soul of the deceased. As stated before, grief is selfish. When Lengikner, the aunt of Ebna, sings of her nephew, she highlights how special he was, so tall and with such long legs (a sign of beauty also in this neolithic society), thereby aggravating the fact that such a fine man has gone forever.

In the mourning song of his elder brother Babesikna which he sang, for weeks, squatting near the corpse in the crown of the high funeral tree, he says:

"…nun-de kurunang-anye
"Our light-skinned, shining one,
mirin bol bobobbinnamume
even though you carried black skin.
dibnamum-ate
Just now you died.
neik-ap mabnanam abmanumwe…"
Didn't the two of us plan to sleep, side by side, in the men's house?…"

The mourner contrasts the "dark skin" of Ebna (a merely classificatory tag, the deceased did not belong to the darkest of the Eipo people, but was a member of the black-skin clan, *bol mirinang*) to him having a shining personality. Again a metaphor expressing that he was a special man. Very interesting that this metaphor builds on another universal perceptual bias typical for our species: white, light, shiny *vis-à-vis* dark and dull are antonyms of probably high symbolic power in the cultures of the world and perhaps rooted in the fact that we are diurnal animals, adapted, with most of our physiology, to acting and living in daylight whereas the night, darkness in general, has a scaring quality for humans. Thus, the negative semantic value of dark things.

Let us now turn from deep sadness to the joy of romantic love. OLETO, a beautiful, vital, intelligent woman in her end-twenties, created this song around the time we arrived in the Eipomek Valley. OLETO's song to her lover:

kokiye dam kokbare dam
By ferny-limb, by curly tree,
na lebnuke na nuknuke
I heard one say, I heard one say,
na ning guma na ning anya
What's thine is mine and is not thine.
na lebnuke na nuknuke
I heard her say, I heard her say.
kidiknamne banabname
Lost will I be and far away.
na dukiye na kokaye
My curly-limb, my ferny tree.
na lebnu ke na nuknuke
I heard her say, I heard her say.
se kayape nay kayape
Friends and gossips, old companions!
kidiknamne banabnamne
Lost will I be and far away.
se fotong o nay atiye
Oh curly-heart, oh housey-home.
na lebnuke na nuknuke
I heard me say, I heard me say.
table ya metebum
With thine axe thou sheared the slim tree,
like ya kwinebum
cut and tore the rooted wild tree.
koubuknamne webukname
Tending my garden I would be.
lung aik dam fan aik dam
Wild weed by the threshold, wild growth by the door.
kidiknamne banabnamne
Lost will I be and far away.
ya metebum ya kotobum
Thy clever axe will strike and tear.
urye ya metebum wilalyam
Here, come and fell the quick elm tree.
dibrenangkin kwinibnangkin delebnangkin
I'd know thy flesh and root it up, pull thee on to me.
fin dam sekne nab dam sekne
That flesh-bracelet, pulse-fireband,
cebroblyame sekdoblyame
flame-vine, snap it from thine arm.
ape lunge ape fane
Wild heart, weed-grass, wild growth by the door,

kwinibnangkin delebnangkin
I'll twist thee free, I'll pull thee free.
kidikse se wicape nay kayape
And lost, my sisters, friends, I be.
kidiknamne banabnamne
Lost will I be and far away.
dibrenangkin mebdeibnangkin
I'll know thy flesh; thou'lt groan for me.
se wicape nay kayape
Gossips and sisters, oh my friends!
fin dam sekne nab dam sekne
The pulse-bracelet, the wrist-vine,
tobuke dablyam lekuke dablyam
Bite it and burn with alchemy.
subkor welen korbik welen
And as the fruit-vine climbs the tree,
ati teleb welebnamne yanibnamne
I'll clamber, my housey-home, and stay,
ape yane ape fane
long legs, wild growth, at home in thee.

This love poetry of an Eipo woman has been published in the context of discussing "romantic love" (SCHIEFENHÖVEL 2009a), which, in my view, is a human universal and can probably be explained as an evolutionary "honest signal" adaptation. I will, therefore, not analyse in detail the mental concepts and symbolic imagery employed in this piece of lyrics from a group of people living in neolithic conditions, but just underline the fact that this text is beautifully comparable, in many aspects, with those from other cultures (e. g. SALOMO "The Song of the Songs" in the Old Testament, 1987, and "Under der Linden" by Walther VON DER VOGELWEIDE, 1996, to name just two), not only in its quest for form (strophic structure, often end rhyme, refrain) but also in the convincing metaphors which are used. The beloved, already married man has a lot of body hair, therefore OLETO addresses him as *kokiye* and *kokbare*, tree ferns, typical for this part of New Guinea. These trees, usually about 2–3 m high and with an umbrella-like crown, have a layer of aerial roots covering the outside of their bark and thus appear somewhat similar to the torso of a very hairy man. With these two terms, the poet not only hides the identity of her lover but also places the scene into the forest, the fringe of inhabited space, where lush plants sprout. In the vicinity are the gardens, often mentioned in the poem, where people do their heavy work of cutting trees, preparing the ground for planting, and then plant, weed and harvest. The poem oscillates between village, where strict rules forbid extramarital sex, and nature where women and men meet for sexual intercourse (taboo in the village in those days also for married couples) and where the power of lush life is around them. At the end of the poem where she expresses her deep desire to live with this man in a proper home, not only to have sex with him, she uses the metaphor of a plant climbing around a strong tree to find support, a resting place. – She succeeded and became (still is today) his second wife.

The climax of the poem, indicated also by the refrain (*kidiknamne banabnamne*) switching to past tense (*kidikse* = I actually have got lost) is when she has sex with her lover, phrased in the metaphor of making fire by pulling a section of a rattan liana forcefully and rhythmically around a dry piece of wood and some tinder, held on the ground with the feet. I believe our best writers of erotic poetry, from OVID to GOETHE and beyond, would have been happy if they had thought about an equally powerful metaphor for the sexual act: rhythmic movement, getting faster and ever more energetic, resulting in a glow and then a flame: woman and man thus united in burning orgasm.

Grief turns into poetry and love becomes lyrics. This tells us that *H. sapiens* is essentially *H. symbolicus*, that we obviously need metaphors for the expression of deep emotions. – The intriguing question is: *why* all this poetry, music, art, quest for beauty and powerful expression? In contrast to Tooby and Cosmides (2008) who think it important that emotions are recalibrated down to less powerful and less disrupting experience, I believe that the opposite might be true: that humans are creating uniquely deep psychic experiences by calibrating emotions *up* – through poetry, for instance. This view is in line with that of Oatley (2003) who sees art as a way to express an emotion in a particular language (words, sculpture, paintings…) so that we come to understand the emotion better. And that would be useful for us who live such socially and emotionally rich lives, from the onset of our species on or even earlier when our genus *Homo* came into existence.

4. Conclusions

Cognitive concepts as they unfold in language, plant taxonomy, and symbolically charged poetry *can* be discovered in the course of classic, emically oriented ethnographic fieldwork. There is no necessary insurmountable Sapir-Whorfian barrier between the mind of a person in one culture and a person in another culture. Empathy and Emphronesis (Theory of Mind, mind reading…) enable us humans to understand each other across linguistic and cultural borders. It is good that icons of cultural relativism, like M. Mead and B. Whorf, have been proven wrong through careful fieldwork of later researchers. This will happen again. The members of our species are much more universal in the ways they perceive the external world and the intrapsychic world of their fellow beings, their feelings, thoughts and behaviours, than cultural relativism claims. Of course, we are formed by the social setting we grow up in, by the ontogenetic history we have, by the ecological habitat we live in, to some degree by epigenetic heritage. But inside a thus shaped member of a particular culture lives a member of our species with its particular genome setting us aside from other animals and hominid precursors. This biological endowment makes us human and behave and think in so many universal patterns.

To include, through participant observation and in-depth interviews, mental imagery and cognitive concepts (e. g. of space, Thiering and Schiefenhövel, in press) in the endeavour of human ethology is a logical step forward from documenting behaviour in the ethological tradition and will, I am convinced, uncover many more fascinating universals thereby demonstrating the power of the evolutionary paradigm.

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Durch Lebensereignisse verbunden
Festgabe für Dorothea Kuhn zum 90. Geburtstag am 11. März 2013

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Zum 90. Geburtstag von Dorothea Kuhn, der langjährigen Herausgeberin der Leopoldina-Ausgabe von Goethes Schriften zur Naturwissenschaft, legt die Leopoldina eine wissenschaftshistorische Festschrift vor. Neben dem Leben und Wirken der Jubilarin, das u. a. mit einer vollständigen Bibliographie gewürdigt wird, sind Beiträge namhafter Wissenschaftshistoriker und Germanisten aus den verschiedenen Interessengebieten der Geehrten versammelt: zu Naturwissenschaft und Medizin, Kunst und Philosophie um 1800, zu Goethes naturwissenschaftlichen Forschungen, zu Italienerlebnissen reisender Naturforscher, zur Verlagsgeschichte, vor allem des Cotta-Verlages, zur Editions- und Buchgeschichte sowie zur Akademiegeschichte.

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Neuroethology: Do Hibernating Lemurs Sleep?

Peter Klopfer, Andrew D. Krystal, Cathy V. Williams,
and Anne D. Yoder (Durham)

With 3 Figures

Abstract

We have undertaken to characterize the brain activity of a sleeping lemur, *Cheirogaleus medius*, and to contrast it with the activity when the animal is in torpor. We suggest that the electrical activity of the brain which characterizes REM and Non-REM sleep is involved in the regulation of body temperature, determining whether it remains constant or reverts to an older, “reptilian” state, where body temperature matches that of the environment.

We are seeking to discover whether the genes that confer the capacity to switch from one state to the other, as is done by *C. medius*, are present in other primates as well. If that is so, it suggests possibilities for the treatment of a host of human diseases, to say nothing of the potential for extended travel in space.

Zusammenfassung

Wir charakterisieren die Hirntätigkeit eines schlafenden Lemurs, *Cheirogaleus medius*, und vergleichen diese mit der Hirnaktivität im torpiden Zustand. Es kann gezeigt werden, dass die elektrische Hirnaktivität sowohl des REM- als auch des Nicht-REM-Schlafes in die Regulation der Körpertemperatur involviert ist und entscheidet, ob die Körpertemperatur konstant gehalten wird oder auf einen evolutionär älteren, „reptilischen“ Zustand zurückgegriffen wird, bei welchem die Körpertemperatur der Umgebungstemperatur entspricht.

Wir werden im Folgenden versuchen herauszufinden, ob die genetische Grundlage der Fähigkeit, von einem Zustand in den anderen zu wechseln, auch bei anderen Primaten vorhanden ist. Wenn ja, zeichnen sich Wege für die Behandlung einer Reihe menschlicher Krankheiten ab, um nicht vom Potential für ausgedehnte Reisen in den Weltraum zu sprechen.

1. Introduction

Years ago, a professor at UCLA, an ardent fisherman, mused on the reasons why the largest fish were seemingly caught in the winter. During the ice-fishing season intrepid fishers would venture onto the surface of frozen lakes and punch holes through the ice into which they could dangle their lures. These were often taken by large fish. Since fish, he reasoned had an indeterminate size, the longer they lived, the larger they grew. Thus, the winter catch must have been of a disproportionate number of older fish, and fish grow old only when they are clever enough to avoid lures and hooks. But, why were they then caught in the winter if they had been smart enough to evade capture in the spring, summer and fall? Could it be that cold slowed whatever mental processes were involved in avoiding capture? A study of maze learning in goldfish soon showed that as temperatures dropped, the error rate increased. The next step was to actually measure the speed of conduction of nerve impulses, and, indeed, this speed was reduced along with the temperature. Fish are dumber when the water is colder: a great example of what we might call neuroethology. We intend to focus on a more recent example of such a study, sleep and hibernation in a lemur.

Let us remind you of Tinbergen's admonition that explaining animal behavior requires addressing four distinct questions:

- What is the function of the behavior in question?
- How did it evolve?
- How does it develop?
- What mechanisms drive or control it?

Nikko himself, and his colleagues, were largely focused upon the first two of these questions; developmental issues were most often dealt with in a purely descriptive fashion, until technological advances made possible experiments such as those by Gilbert Gottlieb and his students. Until then, the underlying neural mechanisms were more often the subject of speculation, viz, Konrad Lorenz's hydraulic model, than of experimentation, though pioneers such as Erich von Holst and Horst Mittelstaedt provided examples of what might be learned even with primitive instrumentation. By the late 1950s, however, it became feasible to wed neurobiologic techniques to an understanding of the principles of ethology. Recently, one of our students wondered whether this had altered the focus of ethologists, especially as, by the 1990s, enormous advances in brain imaging made neurobiology such a thriving field. Were studies of neural mechanisms becoming more common within ethology?

Nearly two decades ago, Pat Bateson and Peter Klopfer had put the question as a whole with regard to the future of ethology to a group of our colleagues (Bateson and Klopfer 1989). Unsurprisingly, views differed considerably, ranging from an affirmation of E. O. Wilson's prediction on the demise of ethology to the optimistic pronouncements of George Barlow (*ibid.*). In 2002, they revisited the question and asked whether there were particular trends that could be identified. They surveyed the articles published in the major behaviour journals in 1950 and again fifty years later, by examining and categorizing over 200 articles. To their surprise, they did not find many differences developing over that half century. Many more articles were authored by several rather than a single person, perhaps reflecting the increased specialization of our time. However, articles devoted to mechanisms, and particularly neural mechanisms (but with an ethological slant) were no more (or less) common than they were fifty years earlier, as was true for the other categories as well (Klopfer and Polemics 2002). Ergo, there is nothing novel about neurobiological studies in the context of ethology. So, now on to our current effort to understand the neurobiology of sleep and hibernation.

This animal is a fat-tailed dwarf lemur, *Cheirogaleus medius*, from Madagascar (Fig. 1). It is a true primate, though smaller than a squirrel, weighing approximately 200 g ± 50 g. It is endemic to the dry, deciduous forests of western Madagascar. Within the last several years, Kathrin H. Dausmann and her colleagues (Dausmann et al. 2008) documented that

Fig. 1 Photo of *Cheirogaleus* on a branch (Courtesy of David HARING, with permission).

this animal, uniquely among primates, spends the winter months in deep torpor, hibernating for as many as six months at a time. DAUSMANN demonstrated that the animals maintained a core temperature that was within ½ a degree of the ambient temperature. Interestingly, at intervals, roughly 10 days or so if the ambient temperatures were below 25 °C, a period of thermogenesis would occur, but only for a few hours and not to the point allowing arousal. Oxygen uptake, measured by DAUSMANN and by S. KOBBE varied with temperature, confirming a state of deep torpor, excepting during the occasional bouts of thermogenesis.

Sleep, marked by periods of rapid-eye movement (REM) occurring with autonomic system instability, and periods where slow-wave activity dominates the cortical EEG, appears to be necessary for survival in mammals. Indeed mammals prevented from sleeping or from achieving either REM or slow-wave EEG states inevitably die within approximately a month. How, then, do hibernating mammals keep their brains alive, given that at low temperatures there is little or no electrical activity discernible in the brain? Perhaps it is the periodic brief episodes of thermogenesis that allow sleep, though only intermittently, while in hibernation.

Not only SHAKESPEARE, but philosophers and ordinary folk alike have for centuries pondered the mystery of sleep, why it occurs, and what functions it serves. On a pragmatic level, sleep disturbances pose severe clinical problems, and deliberate sleep deprivation has become a common tool of unscrupulous interrogators. But, hibernation is not equivalent to sleep, and it appears as if the hibernating mammal can escape the usual demand for sleep. Or can it? That is the central issue we address.

What follows is the report our group prepared following our first field season in Kirindy, Madagascar, 2007, at the Deutsche Primatenzentrum (DPZ), directed by Prof. Peter KAP-

PELER. We returned to Kirindy in 2008 with much improved equipment, but the dearth of animals that season – we found but a single young female – has us wanting for additional data. We are in hopes of returning to Kirindy, and this time, together with Susan KOBBE from Dr. DAUSMANN's lab, hope to simultaneously obtain oxygen uptake records along with our brain recordings. Our improved equipment consists of miniature EEG transmitters that we mount, with tissue cement, onto the animal's back. We now use four tiny needle electrodes that run from under the scalp to the transmitter, and allow the animal to move freely. Data from the transmitter is sent to a receiver placed in close proximity to the animal, and then captured on a computer for storage.

2. Field Recording of EEGs of a Hibernating Lemur, *Cheirogaleus medius*, in Madagascar

2.1 Progress Report and Summary of Work Done in July 2007

July falls within the dry season in southern Madagascar. There was very little standing water except for shallow pools in a river basin approximately 2 km from the study site. Temperatures ranged from 10–32 ºC. The DPZ staff previous to our arrival had located several hollow trees considered likely sites for hibernating *C. medius*. From these sites the first two animals, an adult female and an adult male, were obtained for the study. Subsequent exploration of trees containing hollows suitable for hibernating *Cheirogaleus* yielded three additional animals. The animals were removed from the tree holes in the forest to a temporary enclosure at the Kirindy camp for the period of EEG recording. When recording of an individual animal was completed, the animal was returned to the original tree in which it was captured and released. In the subsequent season the animal had been lured into a nest box attached to a preferred tree and our recordings were made *in situ*.

We had expected that animals in torpor would remain quiet and immobile for several days at a stretch and rouse only for brief periods when ambient temperatures exceeded 30 °C. This was not the case, however. All subjects were quiet during the day but moved about to varying degrees during the night. Thus, it appears that they were not in deep torpor at this time, and our conclusions, tentative at best, must be qualified accordingly.

2.2 Technical Details of Recordings

Animals were gently manually restrained for application of the EEG electrodes. The top of the head was clipped on the first three animals while hair was left intact on the last two. Recording quality did not differ between the shaved and unshaved animals. Alcohol gel (Nu Prep) was used to clean the head and scalp to remove oils and improve the connection prior to mounting the apparatus. Four electrodes (10 mm in diameter) were used for recordings, two for recording EEGs, one for recording EMG, and one as a reference. All electrodes were housed in a circular, rubber cap and placed approximately 10 mm apart. A conductive paste (Ten 20 Conductive EEG paste) was applied inside the electrode to fill each electrode cup. The electrodes were then placed on the scalp and secured on the head by wrapping with expandable veterinary bandaging material around the head and under the lower jaw.

In the second season, and currently, at the Duke Lemur Center, where this work continues, we employed four needle electrodes, placed about 1 cm under the scalp, and attached to a radio transmitter secured to the animals' back with surgical tissue glue.

Initially, the electrodes were plugged into an ambulatory recording device used for capturing EEG data. The data collected were transferred to a laptop computer *via* a wireless card and recorded to the local hard drive as well as to a compact flash disc. Once the tracing quality and data capture was confirmed as adequate, the lemur was placed in a rectangular clear plastic housing container measuring approximately 15 × 20 cm for continuous recording. Leaf litter was put in the bottom of the temporary housing container to allow animals to burrow if desired. As noted, we subsequently used a wireless system and allowed the animal to remain undisturbed in its original nesting site.

3. Preliminary Interpretation of Data

In the first season, continuous EEG data were recorded from five animals over periods varying from 48 to 168 hours during our work in Kirindy. Brief interruptions in recording occurred in order to replace batteries and to re-attach recording electrodes as needed. Data were obtained during periods of wakefulness as well as prolonged periods of behavioral quiescence. Wakefulness was determined both on the basis of direct visual observation of the animals, as well as on the presence or absence of movement which is easily detected in the EEG signals (see top 30 second segment of data in Fig. 2). In addition, we used the classic hallmarks of REM and non-REM sleep to identify these states electroencephalographically. While we had identified the characteristics of these states in data we recorded at the Duke Lemur Center earlier (see Fig. 3), through analysis of the data we recorded in

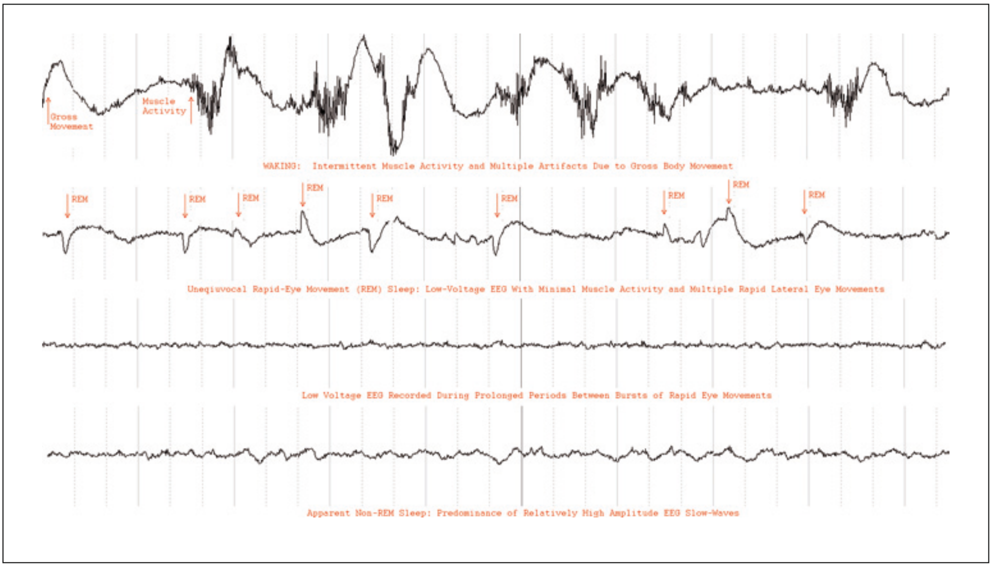

Fig. 2 Representative EEG data from 4 different states of consciousness in Kirindy (Note: Each 30-second segment of data is displayed on the identical scale and was recorded from a single lemur in Kirindy).

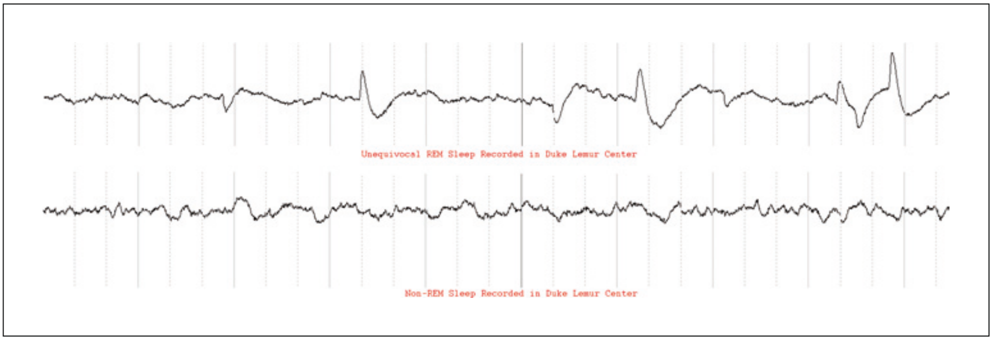

Fig. 3 EEG data recorded during REM and non-REM sleep at the Duke Lemur Center (Note: Both of the above 30-second segments of data are displayed on the identical scale and were recorded from a single lemur in the Duke Lemur Center).

Kirindy we have now established that these same characteristics can be used to identify REM and non-REM sleep in lemurs studied in the wild and that it is possible to obtain data in the field that is of comparable quality and utility to data that is obtained in the more controlled Lemur Center environment. (These characteristics are illustrated in Figures 2 and 3, which contain representative 30-second segments of data recorded in each of these states.) Rapid eye-movement sleep (REM) is characterized by absence of gross movement and by a low EEG signal voltage, relatively low amount of muscle activity and the rapid lateral eye-movements from which this state of existence derives its' name (see the second segment in Fig. 2 and the top segment in Fig. 3). Non-REM sleep, comprised of Stage 1, Stage 2, and Slow-Wave Sleep is identified by the absence of movement, the absence of REM and the presence of relatively high amplitude lower-frequency activity in the EEG (see bottom segment Figures 2 and 3).

4. Discussion

Having developed the capacity to identify the state of consciousness of *C. medius* based on the EEG and having confirmed the utility of our methods for use in the field, we applied this technology to attempt to determine whether it was possible to establish the electrophysiologic characteristics of torpor in this species from the data we collected in Kirindy. This effort was hindered by the inability to behaviourally confirm deep torpor in the animals we studied. However, there was evidence of at least partial torpor in some of the animals in the form of lowered body temperature, lowered breathing rate, and periods of relative lack of responsiveness to stimuli such as being touched, moved or handled. In this regard, preliminary analysis of the EEG data recorded in Kirindy suggests differences from the data recorded at the Duke Lemur Center which appear most likely to reflect the fact that the Kirindy animals were either in torpor or physiologically prepared for torpor neither of which was the case for the lemurs studied at Duke.

Most notably, in Kirindy we observed a substantially greater amount of REM sleep, longer periods of continuous REM, and prolonged periods of time marked by very low-voltage EEG activity, which has all of the features of REM, except for the rapid eye movements (see the 3rd segment in Fig. 2). This represents a substantial divergence from what we observed in the Duke Lemur Center data. To illustrate, the longest period of continuous REM we recorded at the Duke Lemur Center was approximately 5 minutes and the greatest percentage of REM sleep recorded was 29 % of the sleep period. In contrast, in the Kirindy data, several lemurs had unequivocal REM periods lasting over an hour and there were substantially longer periods of the low-voltage EEG activity without rapid eye-movements. In addition, among the lemurs studied in Kirindy, 60 – 90 % of the time that they were asleep or in a sleep-like state (includes torpor) they manifested REM physiology.

Fundamentally, the findings are consistent with our *a priori* hypothesis that a central function of sleep is the regulation of metabolism and temperature. However, the predominance of REM physiology was somewhat unexpected. Based on these preliminary findings we propose the novel hypothesis that hibernation in *C. medius* is accompanied by EEG activity that is of low-voltage with minimal muscle activity reminiscent of REM sleep without the usual rapid eye movements and accompanying bursts of sympathetic nervous system activity (activation of the fight-flight system). We further hypothesize that when *C. medius* is physiologically prepared for torpor or aroused from torpor, sleep is dominated by REM with the usual bursts of sympathetic activity which serves the purpose of regulating their metabolism so as to allow them to go into torpor or to meet their ongoing needs for maintaining body temperature.

If verified, these hypotheses would necessitate a significant change in how we understand the function of sleep, particularly REM sleep and its role in metabolism and temperature regulation. There are no known natural states dominated by REM sleep physiology to this degree other than sleep following REM deprivation. The possibility that REM sleep plays a central role in allowing animals to regulate their temperature to allow torpor or to maintain adequate temperature when aroused from torpor has not previously been proposed. However, this model is strikingly consistent with prior work where rats selectively deprived of REM sleep for long periods of time (weeks), become hypothermic and only raise their body temperature and survive if allowed to have REM sleep. At the same time, the observed findings appear to contradict recent studies in which a buildup of a need for non-REM but not REM sleep was observed following forced arousal of torporing ground squirrels. Further work will be needed to resolve this apparent contradiction.

In terms of our proposal regarding the EEG during hibernation itself, there is no prior literature to serve as a context. However, the model that the EEG is characterized by REM physiology without the accompanying sympathetic nervous system bursts fits nicely with two types of observations. The first is a commonality shared only by REM sleep and hibernation: they are the only known states of existence in mammals where body temperature is allowed to drift to the ambient. The other set of observations, which support our findings, are data on the relationship of sleep and metabolism obtained recently from rats by groups at Harvard (McCarley and colleagues) and Finland (Porkka-Heiskanen and co-workers). These groups have found evidence that ongoing metabolism, such as occurs over the course of the day in humans, runs down the body's energy stores and the associated by-products drive non-REM sleep. They further propose that non-REM sleep then, replenishes the depleted energy stores. This model fits with our observations due to the fact that metabolism is markedly curtailed in hibernating animals. As a result, there is nothing driving non-REM sleep physiology, such that while hibernating, there would be diminished build up of the by-products of depleted metabolism and therefore nothing to produce the slow-waves that normally appear in non-REM sleep. The expected result, then, would be prolonged EEG activity during hibernation that is without slow-waves such as we have observed.

Through carrying out further recordings at the Duke Lemur Center in conjunction with, the collection of metabolic data and by obtaining additional data from Kirindy where EEG data will also be collected coincident with metabolic data in order to confirm the depth of torpor, it will be possible to definitively test these important hypotheses. Doing so promises to fundamentally change the way we understand sleep, hibernation, metabolism, and temperature regulation.

In sum, it is our view that the electrical activity of the brain which characterizes REM and non-REM sleep is involved in the regulation of body temperature, determining whether it remains constant or reverts to an older, "reptilian" state, where body temperature matches that of the environment. We suspect that the thyroid acts as the transducer of environmental cues and serves a regulating function. We are also seeking to discover whether the genes that confer the capacity to switch from one to the other state, as is done by *C. medius*, are present in other primates as well. It has not escaped our attention that, if this is the case, it suggests an enormous range of possibilities for the treatment of a host of human ailments, to say nothing of the potential for extended travel in space.

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Song Complexity in Bengalese Finches: Sexual Selection, Domestication, and Brain Plasticity

Kazuo Okanoya (Tokyo, Japan)

With 6 Figures

Abstract

The Bengalese finch is a domesticated strain of the white-rumped munia. During 250 years of domestication, Bengalese finches have developed phonologically and syntactically complex songs. Behavioural assays showed that female Bengalese finches preferred complex songs. A cross-fostering study involving two strains revealed that certain genetic backgrounds are associated with song complexity. Observations in wild habitats suggested that song complexity might be related to pressures for species identification, which is lost in a domesticated environment. Taken together, sexual selection promoted song complexity by appealing to females and domestication exaggerated this tendency by allowing relaxation of species identification. This process is also reflected brain plasticity of the domesticated strain.

Zusammenfassung

Das Japanische Mövchen ist eine domestizierte Linie des Spitzschwanz-Bronzemännchens. Während der 250 Jahre ihrer Domestikation haben die Japanischen Mövchen phonologisch und syntaktisch komplexe Gesänge entwickelt. Verhaltenstests haben gezeigt, dass komplexe Gesänge von den Weibchen bevorzugt werden. Eine Studie mit Fremdaufzucht (*cross-fostering*) an zwei Linien hat gezeigt, dass die Gesangskomplexität mit einem spezifischen genetischen Hintergrund assoziiert ist. Beobachtungen im natürlichen Habitat weisen auf einen Zusammenhang von Gesangskomplexität und Selektionsdruck auf Arterkennung, welcher in der domestizierten Umgebung fehlt, hin. Zusammengefasst fördert die sexuelle Selektion die Komplexität des Gesanges, die attraktiv für die Weibchen ist, und die Domestikation verstärkt diese Tendenz durch einen verringerten Selektionsdruck auf Arterkennung. Dieser Prozess spiegelt sich auch in der Hirnplastizität der domestizierten Linien wieder.

1. Introduction

Birdsong is a learned behaviour that is culturally transmitted within a set of biological constraints. Birdsong can serve as an important biological model to study interactions between culture and heredity. This study examined the differences between a wild and a domesticated strain of white-rumped munia (*Lonchura striata*) in terms of their songs. The comparison between the two strains revealed evolutionary factors affecting the acoustical and syntactical morphology of species-specific songs.

Wild white-rumped munias were originally imported from the Sappo port in Sekkou-shou, China, to Nagasaki, Japan, by a federal king of the Kyu-syu prefecture in 1763 (Washio 1996). Since that time, they have frequently been imported from China to Japan, particularly during 1804–1829, when aviculture flourished in Japan. The white-rumped munia is generally brown with a white patch on the rump, as its name implies (Restall 1996). However, in 1856, birds with totally white plumage were distinguished from white-rumped munias and called Juushimatsu, society finches. Although these birds were actually imported from China, European aviculturists believed that they came from India, and domesticated white-rumped munias imported from Japan to Europe were referred to as Bengalese finches (Buchan 1976). In what follows, the Japanese strain of wild white-rumped munias will be referred to as Bengalese finches.

Bengalese finches were domesticated for their reproductive efficiency and their ability to foster other bird species, as well as their plumage (Taka-Tsukasa 1917). During the approximately 250 years of their domestication, however, song characteristics have changed substantially from those observed in the wild strain, and the purpose of this chapter is to discuss the possible behavioural and evolutionary reasons behind these differences. Figure 1 presents a photograph of a wild white-rumped munia and a domesticated Bengalese finch along with a drawing of a Bengalese finch during Edo era (ca. 1850). The drawing suggests that the Bengalese finches are domesticated strain of the white-rumed munia.

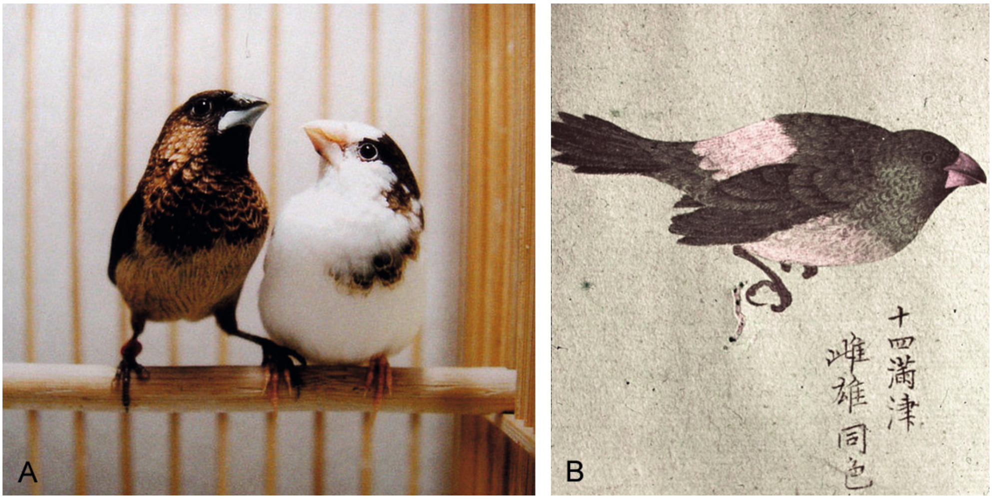

Fig. 1 (*A*): A white-rumped munia (*left*) and a Bengalese finch (*right*). Photo by Maki Ikebuchi. (*B*): A drawing of a Bengalese finch during Edo period (ca. 1850).

2. Song Differences in Two Strains

Representative sonograms from a Bengalese finch and a white-rumped munia are shown in Figure 2. Brief inspection of the sonograms suggested that these two songs are very different in acoustical morphology and the order of elements. In general, the songs of the wild strain were noise-like and the notes were ordered simply and in stereotyped fashion, whereas the songs of the domesticated strain were more narrow-banded and had complex note-to-note transition patterns. We initially confirmed these impressions with acoustical analyses of song notes and then by transition analysis of note sequences (Honda and Okanoya 1999).

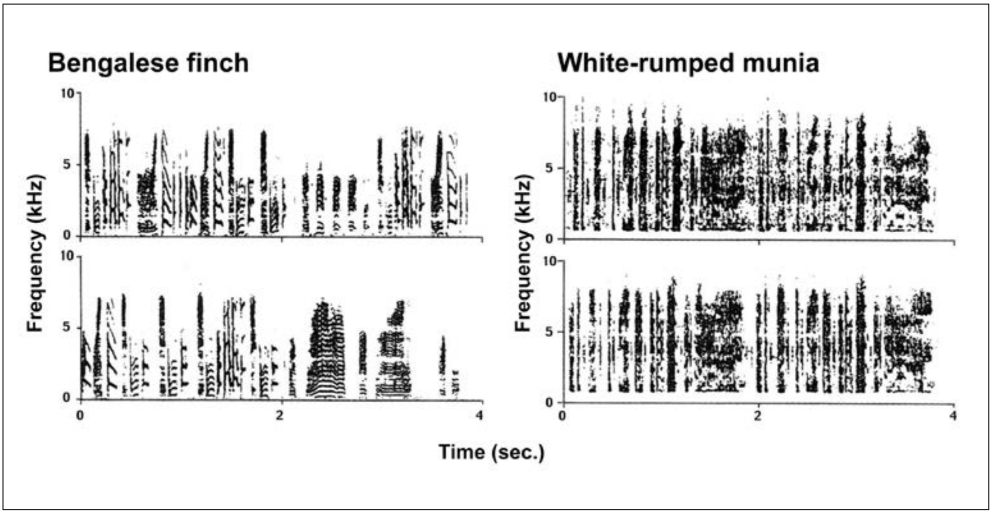

Fig. 2 Sonogram of a Bengalese finch song (*left*) and a white-rumped munia song (*right*)

Acoustical analyses revealed that the frequency of the maximum amplitude was higher in Bengalese finches than in white-rumped munias, and bandwidths 15 dB below the maximum amplitude were wider in white-rumped munias than in Bengalese finches. Furthermore, the sound density (root mean square value of 5 s of continuous singing) was, on average, 14 dB higher in Bengalese finches than in white-rumped munias when recordings were made with identical settings. However, no differences in the number of types of song elements were found between Bengalese finches (average 9.3) and white-rumped munias (average 8.4). Thus, Bengalese finch songs were higher pitched, more narrow-banded, and louder than were white-rumped munia songs, but the strains did not differ with regard to repertoire size.

The sequential complexity of the songs was evaluated with the linearity index (Scharff and Nottebohm 1991), which is the number obtained by dividing the number of unique types of song notes by the number of observed transition patterns from one note type to another. This index is 1.0 (when N is the number of note types, then this will be $N/N = 1$) when the element sequence in the song is always identical, and it will approach 0 ($N/N^2 = 1/N$) when the element sequence is completely random. Results of this analysis showed that the average linearity index was significantly lower, signifying greater complexity, in Bengalese finches (0.33) than in white-rumped munias (0.61). Representative transition diagrams from both strains are shown in Figure 3.

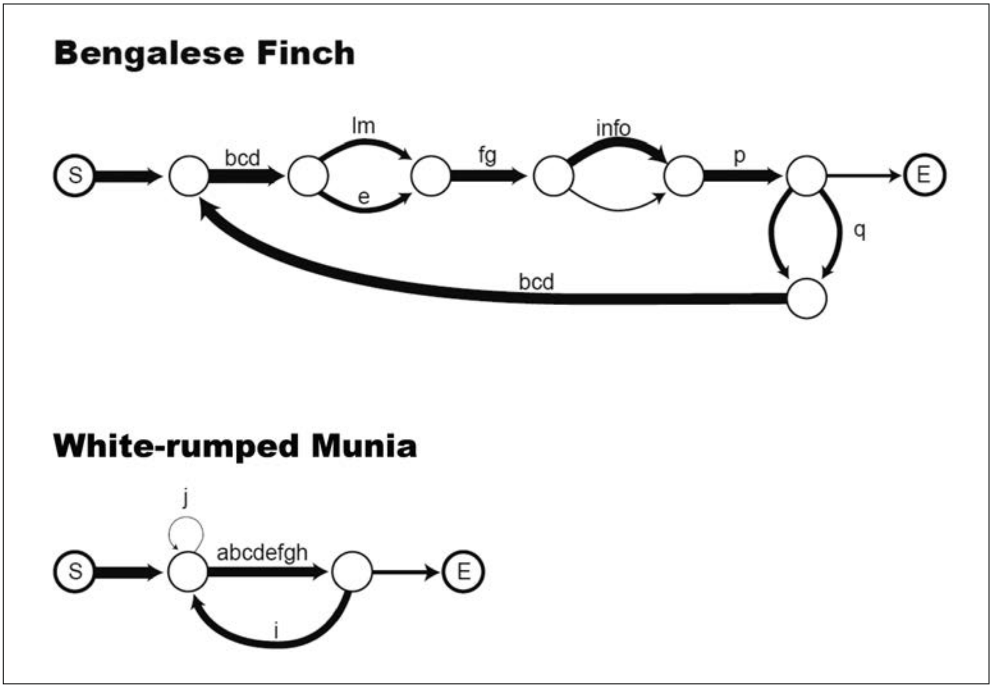

Fig. 3 Transition diagram of a Bengalese finch song (*upper*) and a white-rumped munia song (*lower*)

3. Sexual Selection

What are the functions of song complexity in the Bengalese finch? Although this species is domesticated, we hypothesized that function evolved in part as a result of sexual selection by females (Anderson 1994, Catchpole 2000, Okanoya 2002). Because the Japanese avicultural literature does not contain evidence that songs were artificially selected by breeders (Washio 1996), we assumed that breeders selected only successful pairs and that this indirectly resulted in the selection of good singers. Therefore, we further hypothesized that males and females differed with regard to song perception and that song complexity efficiently stimulated sexual behaviour in females. We evaluated the former hypothesis using heart-rate measurements and the latter using several assays that supplemented one another (Searcy 1992, Searcy and Yasukawa 1996). We first measured the reinforcing properties of a complex song using an operant task involving perch selection. Next, we measured the degree of nest building behaviour by female Bengalese finches as a function of stimulus songs. In addition, we measured the serum estradiol levels in females stimulated with complex *versus* simple songs.

3.1 Heart Rate Response to Song Novelty

Birdsong might be assessed and processed differently by each sex because its production and functional use are often sexually dimorphic. However, straightforward examination of this hypothesis has been difficult because different behavioural measures have been used to describe the process of song assessment in the two sexes. We analysed changes in heart rate as an index of song assessment in the Bengalese finch (Ikebuchi et al. 2003). In this species, only males sing, and song is used exclusively for mate attraction. Bengalese finches are not territorial, and the songs are not used in aggressive contexts. When a song stimulus was presented for the first time, the heart rate of the study participants increased. The duration of this increase in heart rate was defined as the period in which the heart rate increased by two standard deviations above that measured in the baseline interval, which was 10 s before song presentation. In both sexes, the repeated presentation of one song resulted in a reduction in the heart-rate response. The presentation of heterospecific (zebra finch) songs did not increase the heart rate of Bengalese finches. When a novel conspecific song was presented, the heart rate increased only in female and not in male birds with each presentation of the stimulus. These findings confirmed the differential responses to songs by each sex in this species: males ignored the songs of other birds, whereas females were attentive. These patterns were not due to sex differences in memory capacity; operant conditioning studies have demonstrated that males and females do not differ in their memory capacity for songs (Ikebuchi and Okanoya 2000). The results suggested that syntactically complex songs might be more potent than simple songs in maintaining arousal in females.

3.2 Reinforcing Properties of Complexity

To examine the preferences of female Bengalese finches with regard to song complexity, we employed an operant conditioning technique using the song as a reinforcer (Morisaka et al. 2008). The protocol and apparatus used by Gentner and Hulse (1998) to test song preference in female European starlings were modified for Bengalese finches. We prepared a large metal cage and placed pot-shaped nests in two upper corners. We also placed small speakers for song playback inside the nests and fastened a perch in front of each of the nest pots. A natural song sung by a male Bengalese finch was used to prepare a simple (order of song notes fixed) and a complex (order of song notes varied according to a finite-state rule) song, both of which were played back from the relevant speaker when the bird sat on the perch. A female bird was placed inside this apparatus. Four of the 8 birds tested chose the complex song, 1 chose the simple song, and the remaining 3 birds chose both songs at random. These results suggested that the song preferences of female Bengalese finches varied depending on the individual, although more tended to prefer complex to simple songs. Because only one type of song was used in the experiment, the results should be interpreted with caution. Nevertheless, such female preferences could potentially contribute to sexual selection that facilitates the evolution of complex songs in male Bengalese finches (Morisaka et al. 2008).

3.3 Nest Building Behaviour

To further demonstrate the function of song complexity, we examined the nest building behaviours of females (Eisner 1961, 1963) in response to songs with complex or simple syntax (Okanoya and Takashima 1997) using an approach first developed by Hinde and Steel (1976) and Kroodsma (1976). Hinde and Steel (1976) demonstrated that female domesticated canaries engaged in more transportation of nest material when stimulated with conspecific songs than with songs of other species. Kroodsma (1976) found that female canaries performed more nest building and laid more eggs when stimulated with large compared to small repertoire songs.

We analysed the song recordings of a male Bengalese finch and identified four distinctive song phrases (Okanoya and Takashima 1997). The four phrases in this bird's song were organized such that phrases A or B were repeated several times and phrases C or D followed this repetition, but phrases C and D were never repeated. After phrase C or D was sung once, phrase A or B was repeated. We designed a computer program to produce this sequence of song phrases (complex syntax song) or one that repeated only phrase B (simple syntax song). Phrase B contained most of the song notes that occurred in phrases A, C, and D.

We examined three groups of 4 female Bengalese finches; each finch was kept in a separate cage and they were kept together in a sound isolation box. The first group was stimulated with the song characterized by the complex syntax, the second group with the song characterized by the simple syntax, and the third group was not stimulated with any song. The number of nesting items carried each day was counted and compared among the groups (Fig. 4). Females stimulated with complex songs carried more nesting material. We further examined whether randomly generated note sequences were more effective than were syntactically synthesized ones. Females who were stimulated with random note sequences were less responsive and carried comparable numbers of nest items compared to females stimulated with the simple sequence. Although random sequences resulted in complex orderings of song notes, randomness did not generate the same female response as did complexity produced by syntax (Okanoya 2004).

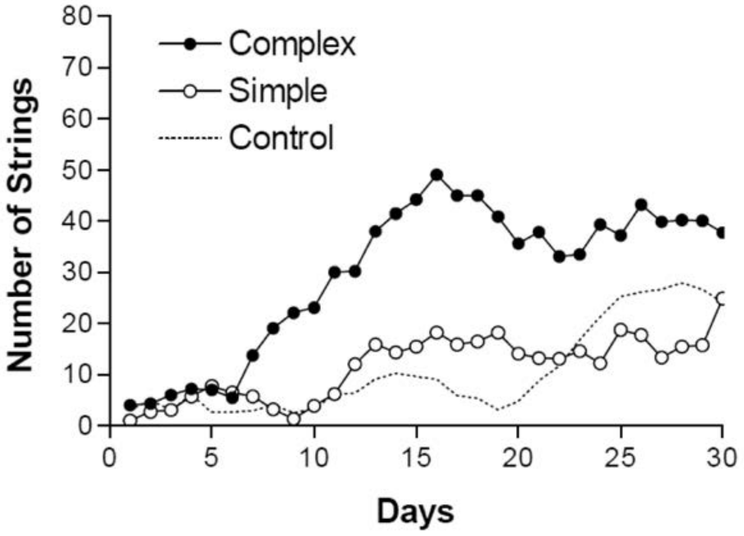

Fig. 4 Results of nest building assay in female Bengalese finches. Complex song stimulated nest carrying behaviour.

3.4 Estradiol Levels

Three groups of female Bengalese finches were used in this experiment; each group consisted of 4 separately caged females kept together in a sound isolation box (Okanoya 2004). The first group was stimulated with the song characterized by complex syntax, the second group with the song characterized by simple syntax, and the third group received no song stimulation. The levels of serum estradiol were compared among the groups before and after the experiment in order to consider baseline differences. Serum estradiol levels before and after the experiment were, on average, 0.37 and 0.76 ng mg^{-1}, respectively, in females stimulated with the complex song; 0.55 and 0.67 ng mg^{-1}, respectively, in females stimulated with the simple song, and 0.46 and 0.52 ng mg^{-1}, respectively, in females who heard a blank tape. Therefore, the complex song was more effective in stimulating female Bengalese finches into the reproductive condition.

4. Learnability: A Cross-Fostering Study

Bengalese finch songs are sequentially and phonologically complex, whereas white-rumped munia songs are simpler. To elucidate the degree to which environmental and genetic factors contributed to these differences in song structure, we cross-fostered white-rumped munia and Bengalese finch chicks (i. e., we used 7 pairs of Bengalese finches and 4 pairs of white-rumped munia and exchanged some of the eggs during incubation (Takahasi and Okanoya 2010). As a result, we obtained 14 Bengalese finch-reared male white-rumped munias and 7 white-rumped munia-reared male Bengalese finches. For comparison, we also examined 12 normally reared male Bengalese finches and 7 normally reared male white-rumped munias. When the chicks had fully matured, their songs were recorded, and phonological and syntactical comparisons were performed. Inspection of sonograms revealed that munia-fostered Bengalese finches were able to learn most of the songs sung by fostering fathers but Bengalese-fostered munias had some difficulty in learning the songs sung by fostering fathers (Fig. 5).

4.1 Constraints in Phonological Learning

The accuracy of song-note learning was measured as the percentage of song elements shared between the chick and the father. Detailed phonological analyses revealed that the accuracy of song-note learning was highest in white-rumped munia chicks reared by white-rumped munias (98 %) and lowest in white-rumped munia chicks cross-fostered by Bengalese finches (82 %). In contrast, Bengalese finch chicks exhibited an intermediate degree of learning accuracy, irrespective of whether they were reared by white-rumped munias (92 %) or conspecifics (94 %). A two-way ANOVA detected a significant interaction between genetic background and rearing environment, indicating that white-rumped munias were sensitive to their rearing environments, whereas Bengalese finches were not ($p < 0.04$). These results suggest that white-rumped munias are highly specialized for learning the phonology of their own songs but are less adaptable to learning the phonology of Bengalese finch songs. In contrast, Bengalese finches are less specialized

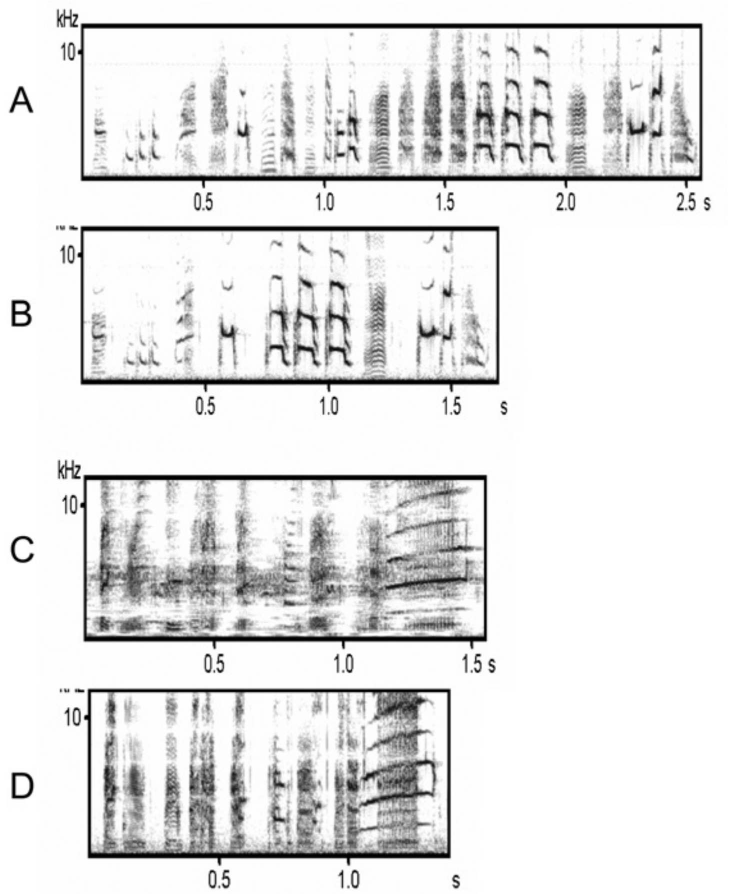

Fig. 5 Results of cross-fostering experiment. A munia chick (*B*) fostered by a Bengalese finch father (*A*) did not learn a part of the song, but a Bengalese finch chick (*D*) fostered by a munia father (*C*) had no apparent difficulty learning the song.

for learning the phonology of their own strain and more able to generalize their capacities to learn the songs sung by white-rumped munias. These findings suggested an innate bias toward species-specific phonology in white-rumped munias that might have been lost in Bengalese finches during domestication (Takahasi and Okanoya 2010).

4.2 Constraints in Syntax Learning

We used the same data set to test for a learning bias for song syntax. Similarities between the two types of song syntax were evaluated by first expressing the two songs under study as Markovian transition matrices (Takahasi and Okanoya 2010). In constructing these matrices, we considered the song notes shared by the songs of both tutor and pupil, as well as the song notes in songs sung only by tutors or only by pupils. The correlation coefficient calculated from the nonzero elements of the two matrices was used as an index for syntactical similarity. Using this method, we calculated average similarities between the songs of tutor and pupil in the four cross-fostered groups (Bengalese finches tutored by Bengalese finches, white-rumped munias tutored by white-rumped munias, Bengalese finches tutored by white-rumped munias, and white-rumped munias tutored by Bengalese finches).

Consistent with the results of the phonological learning experiment, the similarity between the songs of tutors and pupils was highest for white-rumped munias tutored by white-rumped munias (0.91) and lowest for white-rumped munias tutored by Bengalese finches (0.70). The similarities of Bengalese finches tutored by Bengalese finches (0.82) or by white-rumped munias (0.75) were intermediate in comparison with the two more extreme cases. Thus, when learning to sequence song elements, white-rumped munias were biased toward learning the linear syntax associated with their own strain and were far less adept at learning the complex syntax associated with Bengalese finches. These results supported our previous conclusion that white-rumped munias might have an innate bias for learning species-specific syntax and that this bias might have disappeared in Bengalese finches during domestication.

4.3 Learnability and Brain Plasticity

These behavioural results suggest that Bengalese finches might have a wider range of song learnability than white-rumped munias. Encouraged by this finding, we extended our research into differences in proximate mechanisms.

First, we compared between volumes of the brain nuclei that are considered to be related with song learning and control. Birds were perfused by phosphate-buffered solution containing formaldehyde through the heart after deep anaesthesia and brains were post fixed. A 50 μm thick slices were cut and these were stained by Nissle solution. Volume of song control nuclei was measured by a computer-connected microscope system. Since Bengalese and Munias has difference in body weight and overall brain volume, a brain nuclei considered to be unrelated with song control, a thalamic relay nucleus was used as reference on which volume of each of the song control nuclei was indicated (Fig. 6). Song nuclei are overall larger in Bengalese finches than in white-rumped munias (Takahasi 2006). We then examined gene-expression profiles on the brain of the two strains. We especially focused on genes that are related with synaptic plasticity including neuro-tropic factors, calcium regulations, and glutamate receptors. Although research is still in progress, we found that overall Bengalese finch brain shows higher degree of plasticity-related gene expressions (Kato and Okanoya 2010).

5. Effect of Domestication: Insight from a Field Study

We assumed that songs were kept simple in wild white-rumped munias because of specific pressures in the wild. Singing loud, complex songs in the wild is costly for at least three reasons. *First*, such songs attract predators. *Second*, they draw on cognitive resources nec-

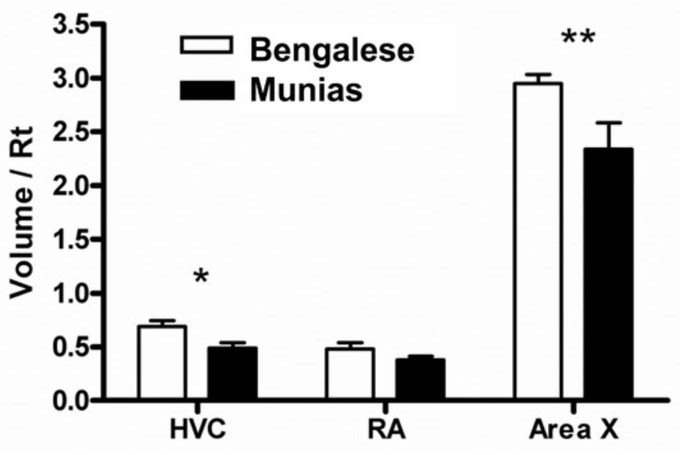

Fig. 6 Volumetric comparisons among song control nuclei in Bengalese finches and white-rumped munias. Bengalese has larger song control nuclei than munias (*P < 0.5, **P < 0.01).

essary for reacting to dangers, including predations. *Third,* the evolution and maintenance of the brain mechanisms underlying complex songs are costly. We began our fieldwork in Taiwan (Republic of China) to examine these hypotheses. However, the observation of predation in the wild is very rare, and this strategy did not allow for quantitative assessment of the hypotheses.

We examined the factors that might have accounted for the loss of the innate bias in Bengalese finches with regard to learning songs. One reason for the loss of this bias might involve an important function served by songs in the wild. Before a song can function as a mating signal to attract conspecific females, the singer must be identified as conspecific by the female. Toward this end, the song should possess species-specific characteristics. This function as an identifying mechanism might degenerate in a domestic environment because birds are paired by humans in these settings and thus do not need to seek mates on their own.

Several field studies might support this hypothesis. In the wild, white-rumped munias coexist with various sympatric species, including spotted munia. A strong innate bias toward conspecific phonology should be adaptive for species of munia in avoiding futile attempts at hybridization. In contrast, Bengalese finches are domesticated and have been subject to controlled breeding. In such an environment, a species-specific bias would be neutral and might degenerate rapidly, perhaps allowing Bengalese finches to gain a more general ability to learn a wide-ranging phonology.

We have data on the relationship between the degree of colony mixing (with spotted munia) and song linearity in wild populations of white-rumped munia (Kagawa et al. 2012). When the level of heterogeneity in the colony was higher, songs of white-rumped munia were more linear and exhibited less variable phonology. This might indicate that when more sympatric birds are present, species of munia must exaggerate their species-specific characteristics through their songs.

6. Discussion

We described acoustical and syntactical differences between wild white-rumped munias and Bengalese finches, female responses to song complexity, effects of cross-fostering, and fieldwork to identify geographic variations in songs. Integrating these findings, we can now suggest a testable scenario for song evolution in Bengalese finches.

6.1 Domestication and Sexual Selection

The cross-fostering study revealed that white-rumped munias had a narrowly tuned learning mechanism for strain-specific phonology, whereas Bengalese finches had a more broadly tuned but less accurate learning mechanism. This finding should be considered in light of the results of fieldwork that showed that higher sympatric ratios were associated with lower levels of song complexity.

Birdsong must initially operate as a species-identifier, and then it can function for sexual selection. In this regard, songs do not need to function as species markers in the absence of sympatric, closely related species. In environments characterized by the latter, however, songs should serve a sexual purpose. Domestication represents a special case in which no sympatric species exists. Because Bengalese finches no longer need to identify their species, they might have gradually lost the bias toward learning and producing species-specific characteristics in their songs. As a result of broadening the species-specific filter, Bengalese finches might have developed the ability to produce phonologically and syntactically complex songs. In this sense, song complexity might have arisen from a loss of species-specific bias rather than representing a gain in general learnability. Once constraints are weakened, female preferences might reinforce this tendency towards more complex songs. Indeed, male songs can be complex in syntactical and phonological domains to satisfy females' preference for variations.

6.2 The Evolution of Song Complexity

Based on the experimental results reviewed in this chapter, we suggest several steps that might underlie the evolution of complex song syntax in the Bengalese finch. In most estrildid finches, songs are used solely for the purpose of mating and not in male–male interactions. Thus, sexual selection is likely to have enhanced those song properties on which females base their choices, resulting in traits that are handicaps in the wild environment (Darwin 1871, Zahavi and Zahavi 1996). The following is one possible scenario that might explain the emergence of finite-state syntax in the Bengalese finch.

Complexity in song-note transitions became a sexually selected trait in white-rumped munias and was subject to individual variations due to genetic differences in neural capabilities and cultural differences in song traditions. However, the wild environment restricted the degree of possible song complexity in white-rumped munias due to the various costs associated with the maintenance of such traits, possibly including predation costs, foraging time, immunological costs associated with the production of testosterone, and a metabolic cost associated with maintaining sufficient brain capacity to underpin the song system. Furthermore, songs needed to identify species in the wild, requiring that songs avoid phonological and syntactical complexity. Thus, mutations leading to greater song complexity would not have become fixed in a population of wild white-rumped munias, especially when sympatric species were living near them.

However, domestication eliminated many of these potential costs, especially those associated with predation and foraging time. Thus, domestication relaxed the restrictions imposed on the evolution of song complexity (Okanoya 2002, Ritchie and Kirby 2007). Furthermore, it reduced the necessity for identifying members of the species *via* song. Therefore, mutations leading to song complexity through the loss of a rigid song structure were not fixed in the natural environment and were not eliminated in the domesticated environment. Changes in brain structure then allowed more elaborate songs to be learned and gave rise to the improvisation of song syntax. Genes that allowed for the learning of complex songs were selected because of the preferences of females.

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Ergebnisse des Leopoldina-Förderprogramms VII

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Die Deutsche Akademie der Naturforscher Leopoldina – Nationale Akademie der Wissenschaften bemüht sich mit ihrem Leopoldina-Förderprogramm um die Unterstützung von jungen herausragenden Wissenschaftlerinnen und Wissenschaftlern in ihrer beruflichen Weiterentwicklung durch einen Auslandsaufenthalt an einer weltweit führenden Forschungseinrichtung. Im Jahre 1996 als Projekt durch das Bundesministerium für Bildung und Forschung (BMBF) in Trägerschaft der Leopoldina eingerichtet und jährlich fortgeschrieben, wurde es 2009 Bestandteil des vom BMBF und vom Land Sachsen-Anhalt getragenen Haushalts der Akademie. Der vorliegende Band gibt einen Einblick in die Vielfalt und liefert Beispiele für die Projekte und erreichten Ergebnisse in den Jahren 2009 bis 2011. Damit werden Chancen und Ansprüche des Förderprogramms für künftige Bewerber deutlich.

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Body Size, Vocal Fold Length, and Fundamental Frequency – Implications for Mammal Vocal Communication

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With 7 Figures

Abstract

Many mammalian acoustic displays are generated by vibrations of the vocal folds. The cardinal acoustic index of periodic vocal fold vibration is the fundamental frequency (F0). Because F0 is implicated in the "advertisement" of fitness, body size and the gender of the emitter of the signal, a firm understanding of the interplay of the physiological parameters that determine fundamental frequency is critical for an accurate analysis of acoustic communication systems. Though the relationship between F0 and body size is well established in some vertebrate taxa (anura for example), it remains ambiguous in mammals. Here we review the relationship between F0 and four physiological parameters that govern it (subglottal pressure, vocal fold length, tension, and volume), and we address how variations within these parameters produce unusual results regarding the relationship between F0 and body size.

Zusammenfassung

Viele Säugetiere produzieren akustische Signale durch Stimmlippenschwingungen. Ein wichtiger akustischer Parameter, der durch die Stimmlippenschwingung bestimmt wird, ist die Grundfrequenz. Das Verständnis der Wechselwirkung verschiedener physiologischer Parameter, die die Grundfrequenz determinieren, ist wichtig für die Interpretation der Variabilität akustischer Signale. Wir untersuchen hier den Einfluss von vier physiologischen Parametern auf die Beziehung zwischen Grundfrequenz und Körpergröße. Körpergröße, eine wichtige Variable in der Verhaltensbiologie, und normalerweise eine determinierende Variable im Design von akustischen Signalen, scheint bei Säugetieren nicht mehr von gravierendem Einfluss auf die Grundfrequenz zu sein. Wir versuchen, die Frage zu beantworten, welcher von vier Parametern mit größter Wahrscheinlichkeit verantwortlich für die Entkopplung der Grundfrequenz-Körpergröße-Beziehung ist.

1. Prologue

Günter Tembrock's lectures were famous for their stirring atmosphere. He sometimes used provocative examples to make his point. I (TR) remember one example he used several times when he talked about acoustic communication. He displayed spectrograms of a Siamang (*Symphalangus syndactylus*) vocalization and a note sung by Maria Callas. He played the respective sounds (each sound was about 2 s in duration), and then asked the audience to identify the emitter of each signal. The rate of correct identification was rarely better than chance.

Selecting the “right” duration of the acoustic unit was one lesson I learned from this example. Another lesson I learned was that vocalizations can be produced with very different vocal tract and vocal fold anatomies and yet sound nearly identical. Mammalian laryngeal sound production is very complex allowing the production of sounds displaying an enormous range of variation. The key to understanding one source of this variation resides in the details of vocal fold biomechanics and physiology.

2. Introduction

Vocal communication is one of the keystones of social living (Tembrock 1996). Intraspecific variations in vocal displays allow conspecifics to acoustically identify and evaluate potential rivals, intruders, mates and allies. For example, in anurans body size can be accurately estimated by the fundamental frequency (F0) of the voice of the emitter (McClelland et al. 1996, Bee and Gerhardt 2001). This association has its physiological basis in the regimented relationship between larynx size, vocal fold length and body size (e.g. Martin 1971, Schmid 1978, McClelland et al. 1998). In mammals the results are far more complicated (e.g. Pfefferle and Fischer 2006). Fundamental frequency in many contexts is a weak predictor of the sender’s body size. While across species, larger body sizes tend to be associated with lower F0 (Tembrock 1996, Fletcher 2004), within a species, at communicatively relevant levels, the relationship between F0 and body size has become uncoupled. Of the four most relevant physiological parameters governing F0 (subglottic pressure, vocal fold length, mass and tension), vocal fold length has been singled out (repeatedly) as the responsible factor for the uncoupling of the F0-body size relationship (Fitch and Hauser 2002). The reasoning in support of the presumed uncoupling between F0 and body size is as follows: the laryngeal tissue, in particular the cartilages, is sensitive to testosterone leading to a larger overall growth in males, and this in turn leads to sexual dimorphism in larynx size in many species. Since testosterone levels vary during ontogeny between individuals and are not related to body size, larynx size and therefore vocal fold length may vary between individuals. There are at least three problems with this assumption that remain unresolved. (*a*) To what extent is larynx size connected with vocal fold length? (*b*) Does sexual dimorphism in the size of the larynx uncouple the vocal fold length-body size relationship? (*c*) Finally, is the vocal fold length parameter in mammals a good predictor of F0? Other physiological parameters important for sound production may also influence the F0/body size relationship. In this review we look at four physiological parameters and evaluate each of these for its potential to uncouple the F0-body size relationship.

3. The Larynx as Sound Source

All vertebrates risk death if foreign objects enter the trachea and eventually damage lung tissue or block the airway. The primary function of the laryngeal complex is to protect the respiratory tract during swallowing, and to provide a mechanism for organisms to seal the airway, “hold their breath”, and hence elevate intrathoracic pressure in order to stabilize the rib cage for strenuous motion of the forelimbs or abdomen (Negus 1924, Bramble and

Carrier 1983, Bartlett 1989, Miyamoto et al. 1999). The ability to vibrate tissue in the laryngeal complex for the purpose of sound production is ancillary to its fundamental function. Therefore, vocal fold evolution represents a balance between several potentially contradictory constraints. When two functions (respiration and sound production) are served by the same structure, the more vital function must by necessity exert the strongest selective force.

By the 18th century, the larynx (Fig. 1*A*) had become identified as a sound source (Dodart 1700), however, sound was assumed to be produced in a whistle-like fashion. In 1741 Ferrein proposed the idea that vocal fold vibrations were essential to the process of sound production, and Helmholtz (1863) demonstrated that air puffs produced by oscillations in the vocal folds were the primary sound source. The source-filter theory, the idea

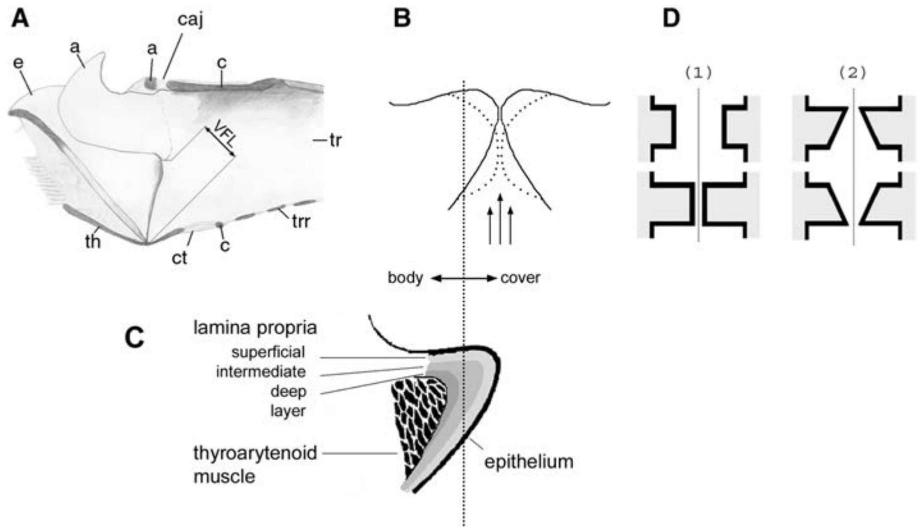

Fig. 1 (*A*) Sketch of a midsagital section of a deer larynx indicating the length of the vocal fold (changed, after Riede and Titze 2008). e, epiglottis; a, arytenoids cartilage; th, thyroid cartilage; c, cricoid cartilage; tr, trachea; trr, tracheal ring; ct, cricothyroid muscle; VFL, vocal fold length; caj, crico-arytenoid joint. (*B*) Schematic of a horizontal section of the left and right vocal fold. Glottis refers to the space between the left and the right vocal fold. The potential change in glottal shape is indicated by the difference in the position of the convergent (solid line) and divergent (dotted line) vocal folds. Arrows indicate the airflow coming from the lungs. (*C*) Schematic of a horizontal section of the left vocal fold. Vocal folds show a layered structure with three main layers: epithelium, lamina propria and the thyroarytenoid muscle. The thickness and the microstructure of the lamina propria are species-specific. In adult humans a superficial, intermediate and deep layer can be differentiated. According to the “body-cover theory”, the oscillating parts of the vocal fold are collectively called ‘cover’, while the non-oscillating base is called ‘body’. The vertical dotted line differentiating the cover and the body apply to (*B*) and (*C*). (*D*) Simulating vocal fold oscillation assumes two major movement components, 1: a latero-lateral component and 2: a cranio-caudal component. The latter leads to a repeated change between a convergent and divergent cross-sectional profile (also indicated in *B*). This out-of-phase movement of the upper and lower part of the vocal fold produces larger asymmetries in the forces acting on the folds in the opening and closing phase of the oscillation than the in- and outward movement alone, resulting in a positive pressure on the folds during the opening phase and a net energy input to the tissue maintaining a self-sustained oscillation.

that the primary sound is subsequently shaped by resonances in the vocal tract (VON MÜLLER 1840, FANT 1960) evolved from HELMHOLTZ'S initial insight. In the 20th century, VAN DEN BERG (1958) performed ingenuous light-gas experiments and thereby provided evidence for the duality between a sound source composed of vibrating tissue not affected by the gas properties, and the vocal tract, a cavity which shapes the primary sound according to its resonance characteristics. The resonances, VAN DEN BERG noted, were affected by differences in the velocity of sound propagation in different Oxygen-Nitrogen, Oxygen-Helium mixtures, and were independent of the fundamental frequency of vocal fold oscillation.

The fundamental frequency (F0) is the rate at which vocal fold vibration interrupt the flow of air as it is exhaled from the lungs and passes through the larynx. Specific mechanical and aerodynamic constraints must be met for an obstruction in a pipe or airway to be deflected or deformed and be set in oscillation by the flow of air, and the myoelastic-aerodynamic theory of sound production (VAN DEN BERG 1958, TITZE 2006) addresses these constraints.

The myoelastic-aerodynamic theory includes the fact that muscle activity positions the vocal folds and actively elongates or shortens them. Increments in the F0 of sound are closely correlated with an exponential increase in the electromyographic (EMG) activity of the cricothyroid muscle (CT) and the thyroarytenoid muscle (TA) (see for example JÜRGENS 2002 for a review of the neuromuscular control of phonation in mammals). Insufficiency of the normal activity of CT and TA (experimental neurotomy or neuropathy; e. g. JÜRGENS et al. 1978, SUTHERS and FATTU 1982) affects vocalization.

The myoelastic-aerodynamic theory also addresses the viscoelastic tissue properties of the vocal folds which determine how much the vocal folds will be deformed under a given force or pressure.

The third aspect of the myoelastic-aerodynamic theory refers to the conversion of aerodynamic energy into acoustic energy. Airflow is an essential prerequisite for phonation, and a velocity-dependent driving force is provided by airflow. The difference in the air pressure between the supra- and subglottal space (i. e. between pharyngeal/oral cavity and trachea) produces a driving pressure asymmetry on the vocal fold surface. The surface layer of the vocal folds is pliable, and the surface layer flexes as a result of the energy transfer from the glottal airflow. The flexing of the mucosal layer of the vocal folds to the passage of air is the initial step by which the larynx transforms the egressive (and sometimes ingressive) pulmonary air flow into sound (TITZE 1988). A second driving force comes from differences in the intraglottal pressure distribution created by the glottal geometry. These pressure distribution differences lead to non-uniform tissue deformation which can be characterized by a sustainable pattern of cyclic fluctuations between convergent and divergent shapes (Fig. 1*B* and *D*) (e. g. ALIPOUR et al. 2000, BERRY et al. 2001). Tissue deformations over a cycle of vocal fold vibration are accompanied by pressure changes inside the glottis (ALIPOUR and SCHERER 1997, JIANG and TITZE 1994, TITZE et al. 1993). The different pressure profiles allow the development of an oscillating force asymmetry that sustains tissue oscillation.

The mammalian vocal fold is a layered structure (Fig. 1*C*) and only the more superficial layer(s) of the vocal folds is (are) set in oscillation. Phonation in mammals is governed by species-specific differences in the composition of the vocal fold layers (Section 4), and the modulation of subglottal pressure (Section 5), vocal fold length (Section 6), and changes in the thickness or volume of the oscillating layer of the vocal folds (Section 7).

4. The Layered Structure of the Vocal Folds

Vocal fold morphology differs widely across mammalian species (e.g. Negus 1949, Schneider 1964, Harrison 1995) but one important feature is universal among mammals. The vocal fold is a multilayered structure consisting of an epithelium, a *lamina propria* and the TA muscle (Hirano 1974) (Fig. 1*C*). The morphology of the *lamina propria* is species-specific (e.g. Kurita et al. 1983, Riede 2010, Klemuk et al. 2011, Julias et al. 2013). For example in humans, it differentiates into three constituents, a superficial, an intermediate and a deep layer (Hirano et al. 1983, Ishii et al. 2000, Schweinfurth and Thibeault 2008)

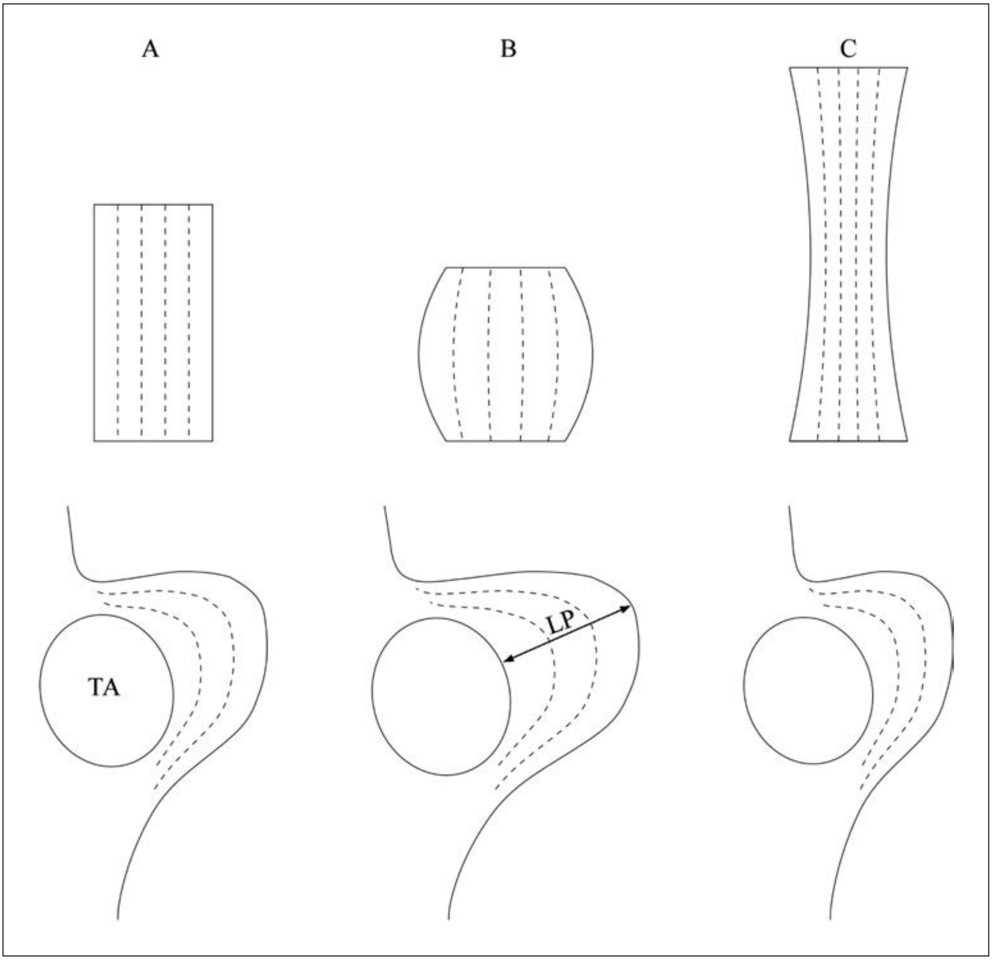

Fig. 2 Schematic indicating the behaviour of the lamina propria (LP) tissue in the mid-membraneous area of the vocal fold. The three shapes in the first row indicate the total vocal fold length. In the second row, a cross-sectional view of the vocal fold is indicated. (*A*) In a relaxed position the lamina propria has a certain thickness. (*B*) The lamina propria becomes thicker and probably more floppy once the TA muscle contracts and shortens the vocal fold. (*C*) Under strong CT muscle activity, the vocal fold becomes elongated, the lamina propria becomes stiffer, and less tissue in the intermediate layers is available for oscillation with the superficial layer of the vocal folds.

making a total of 5 layers. The three layers of the *lamina propria*, the epithelium and the TA muscle make in various combinations a "cover" layer and a "body" of the vocal fold (Hirano and Kakita 1985). Functionally, most of the vocal fold vibrations occur in the cover layer because of its high degree of compliance and proximity to the aerodynamic driving forces.

The cover consists of the epithelium and variable amounts of the *lamina propria*. The body consists of the TA muscle and the remaining parts of the *lamina propria*. Operationally, the intermediate and the deep layer of the *lamina propria* may either oscillate and contribute to the cover portion of the vocal fold, or not oscillate, and hence belong to the body portion of the fold. The more the vocal fold is stretched, the more likely the intermediate and deep layers defect the body. Thus, the vocal fold volume that is set into vibration (the thickness of the cover) can vary substantially.

The interplay of TA muscle and CT muscle contraction and relaxation are the main active components of modulating the length and thereby the tension of the vocal folds (e. g. Jürgens et al. 1978, Fattu and Suthers 1981, Kempster et al. 1988, Titze et al. 1989, Baker et al. 2001). TA and CT muscle activation alter the biomechanics of the body-cover model in the follow manner. An isometric contraction of the TA muscle provides a stiff body on which a more or less loose cover is positioned (Fig. 2*A*). A shortening of the contracting TA muscle would further loosen the cover (Fig. 2*B*) and increase its effective volume (because deeper layers of the *lamina propria* become available for being set in oscillation). This action would further lower F0, since the cover layer would at some point sit loose and floppy on top of the body. It must be noted, however, that the exact depth of vibration in the vocal folds is difficult to determine for different F0.

Contraction of the CT muscle elongates the vocal fold. This leads to a rise in tension, and reduces the effective volume of the cover in the follow manner (Fig. 2*C*). Without simultaneous TA activity, the only counteracting force would be the passive tissue properties of the vocal fold. The intermediate and deep layers of the *lamina propria* (also collectively called 'vocal ligament') are the strongest and are believed to be the main stress-carrying tissues (Perlman et al. 1984). The stiffening of the intermediate and deep *lamina propria* layer would reduce the tissue volume available for oscillation in the cover layer. Under tension only the epithelium and the superficial layer of the *lamina propria* are available for oscillation. This non-uniform stiffening of the various layers of the vocal fold make it hard to predict the effective tension and volume of the vibrating part of the vocal fold.

5. Subglottal Pressure

As lung pressure is incremented, air begins to flow through the glottis. The relevant pressure for phonation is called subglottic pressure (Ps), i. e. the pressure below the glottis inside the trachea. The minimum pressure to initiate phonation ('phonation threshold pressure', PTP) and the maximum pressure at which the vocal folds can sustain regular oscillations appear independent of body size. They depend on vocal fold tension and adduction of the left and right vocal fold (or 'glottal width') (Titze 1988). PTP in various species starts at around 0.5 kPa (Fig. 3). The upper limit for phonation is not entirely clear. Zhang et al. (2006) defined it as the *instability pressure*, i. e. the pressure at which regular vocal

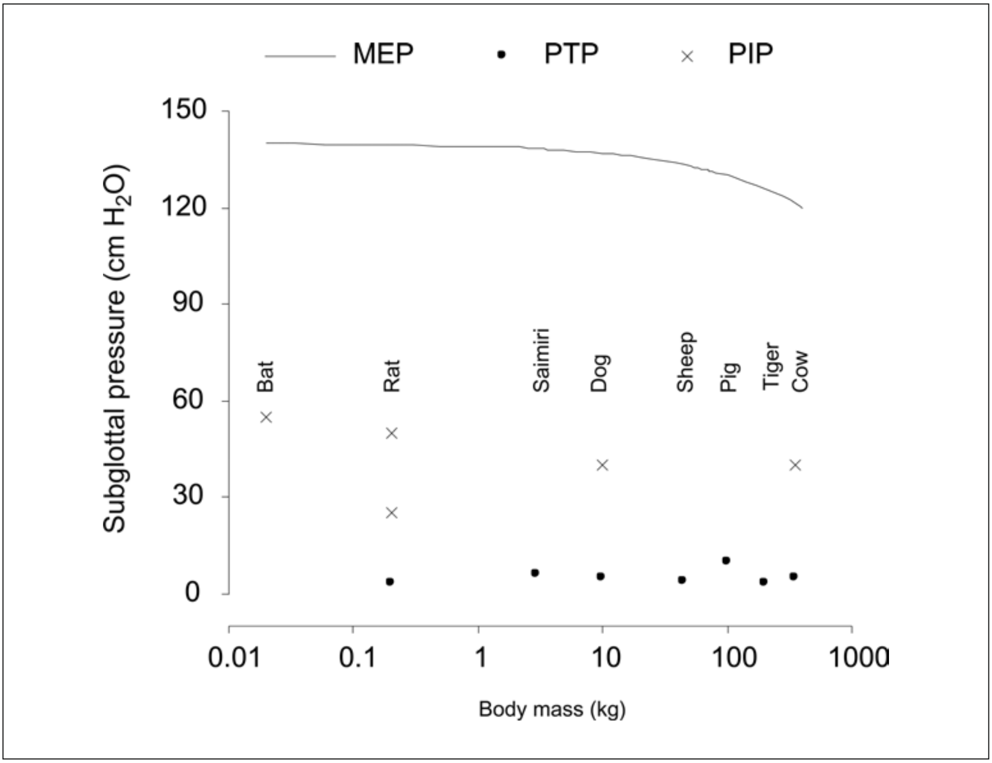

Fig. 3 Lung pressure *versus* body mass (BM). Phonation threshold pressure (PTP) (dots) (source: squirrel monkey, Brown et al. 2003; domestic dog, Alipour et al. 1997, Zhang et al. 2006; sheep, Alipou and Jaiswal 2008; human, Holmberg et al. 1988, Plant and Younger 2000, Plant et al. 2004; pig, Alipour and Jaiswal 2008; cow, Alipour and Jaiswal 2008; rat, Riede 2011; tiger, Titze et al. 2010). PTP is highly frequency dependent (Titze 1988). The measurements provided here are the lowest values reported. Highest subglottal pressure during phonation were also reported for several species (PIP) (crosses) (source: bat, Fattu and Suthers 1981; domestic dogs, Zhang et al. 2006; cow, Riede, unpublished data; human, Bouhuys et al. 1968; rat, Riede 2011). Beyond the highest subglotal pressure, phonation is either not possible or phonation attempts with such high pressures results in the production of mostly chaotic phonation. The two crosses in rats represent maximum phonation pressure during ultrasound vocalization (lower pressure) and audible vocalization (higher pressure). For maximum expiratory pressure (MEP) we have only found empirical data in humans (Neder et al. 1999).

Data for squirrel monkeys, dogs, sheep, pig, cow and tiger were collected in excised larynx experiments, i. e. during passive phonation of an isolated larynx. Data in humans, dogs and rats were collected *in vivo*. We hypothesize a decrease of the maximum expiratory pressure with body size, because the relationship between pressure inside the chest cavity and the cavity's volume follows the equation P = F/A (F – force produced by expiratory muscles, A – the average cross-sectional area of the cavity). Thus a small body produces high pressure more easily.

fold oscillation becomes unstable and eventually ceases. The highest subglottal pressure measured during phonation was around 7 kPa (Fig. 3). This value is not the highest lung pressure that most mammals can achieve. The so-called maximum expiratory pressure can significantly exceed the upper pressure limit for sustained phonation (Fig. 3).

How do variations in subglottal pressure affect F0? The relationship between Ps and F0 appears erratic. Hsiao et al. (1994) evoke vocalizations *via* brain-stimulation in seven dogs matched in size. He found that stimulation patterns that produced a 1 kPa increase in subglottal pressure produced markedly different changes in F0 for different subjects. In one dog a 1 kPa pressure increment raised F0 by only 22.4 Hz, while in another dog the same increase in pressure elevated the F0 by 118.7 Hz. This finding suggests that if dogs naturally phonate within a range of 0.1 to 4 kPa, then F0 variation strictly due to changes in subglottal pressure would range between 90 and 470 Hz for different subjects. Studies of phonation employing the excised larynx procedure in which the larynx is artificially phonated confirms this finding (Brown et al. 2003, Alipour and Jaiswal 2008). A change in Ps appears to affect F0 in an individually idiosyncratic manner.

The hypothesis that Ps is actually a minor regulator of F0 is confirmed in bats by data *in vivo* (Fattu and Suthers 1981) and in an excised larynx setup (Kobayashi et al. 2012). In the big brown bat (*Eptesicus fuscus*), Ps variation is consistently correlated with sound amplitude variation, but not with F0 variation (Fattu and Suthers 1981). In natural phonation in humans, Ps variation is used very little in order to affect F0 but is employed to regulate vocal intensity (Plant and Younger 2000, Plant et al. 2004). Ps modulation is the principal parameter humans alter to change sound amplitude (Titze 1989a).

In concert these observations suggest that while a change in Ps does have some impact on F0, this parameter is unlikely to account for much of the variation between body size and F0 in mammals.

6. Effective Vocal Fold Length

The association between vocal fold length and body size is robustly established in only a few species. For example, vocal fold length exhibits a positive correlation with body size in humans (Kahane 1978, Hirano 1983, Eckel et al. 1996, Filho et al. 2005), in European Red deer (*Cervus elaphus scoticus*) (Reby and McComb 2003), Rocky Mountain elk (*Cervus elaphus nelsoni*) (Riede and Titze 2008) and horses (*Equus caballus*) (Charuta et al. 2009). We speculate that it is likely that vocal fold length and body size are positively correlated in many more mammals. Though each individual has a given vocal fold length during quiet breathing, this length may be altered significantly during vocal behaviour to achieve a certain F0. In humans different individuals exploit vocal fold length quite differently during phonation (Hollin 1960, Nishizawa et al. 1988, Hertegard et al. 1993). For example, two subjects, similar in body size and vocal fold length during quiet breathing, may achieve the same target F0 by stretching their vocal folds by different amounts because their vocal fold tissues respond differently to the elongation. This observation complicates the relationship between F0, vocal fold length and body size both within and between species.

Humans modulate F0 by vocal fold length changes (Hollien 1960, Hollien and Moore 1960). Data by Nishizawa et al. (1988) suggest that length changes of the vocal fold that accompany the change of F0 is highly individual-specific. These authors report that in human subjects vocal fold length may vary as little as 21 % and as much as 111 % over an individual's entire F0 range (Nishizawa et al. 1988). Their data also suggest that the length change required for producing a target F0 change differs significantly between subjects (Fig. 4).

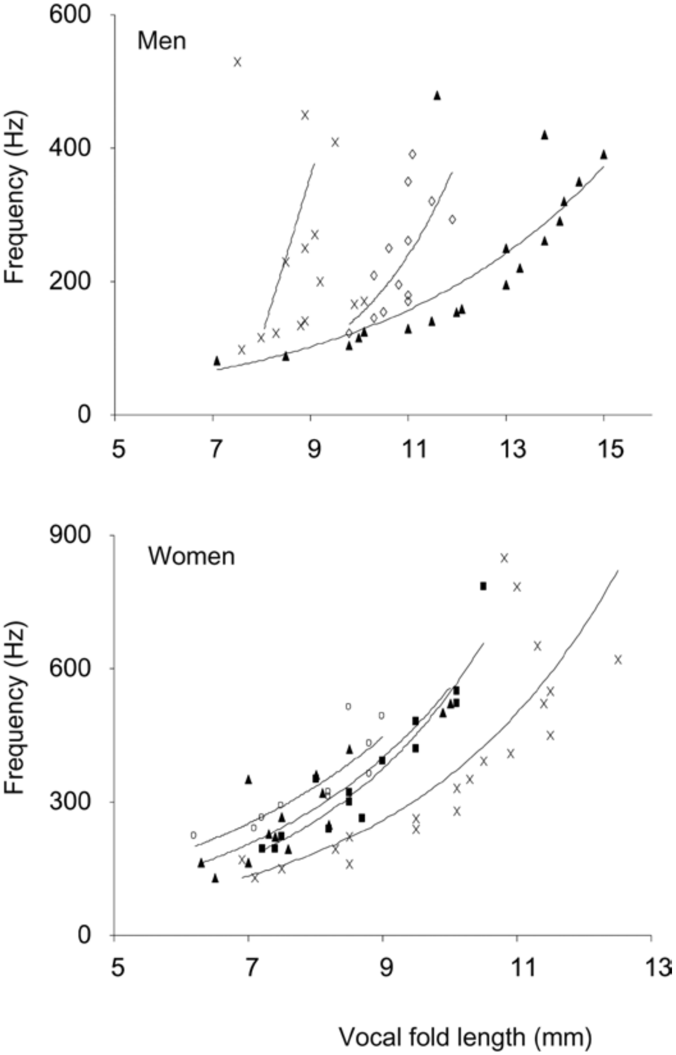

Fig. 4 Relationship between fundamental frequency and vocal fold length in three male and four female human subjects (age ranges between 23 and 33 years) after data from Nishizawa et al. (1988), at normal speaking levels. Note that the axis-scaling for men and women are different. The trend lines of the respective data sets confirm to the equation: y = a ln(x) + b.

In summary, the association between vocal fold length and body size is likely robust for measurements conducted for quiet breathing, and for measurements conducted from cadavers. However, during phonation vocal fold length is altered significantly in order to achieve specific F0 objectives. The pattern of this alteration differs between different subjects within a species (the reasons for the variable stretching of vocal folds are explained in Section 7). It should be emphasized that vocal fold length must not be confused with larynx size. Different sized larynges do not scale linearly in all of their components. In humans the larynx is sexually dimorphic. The membranous part of the male vocal fold is on average 60 % longer than in females (Hirano 1983, Titze 1989b), however, other differences in linear dimensions between the male and female larynx range from 3.8 % to 63 % (Sprinzl et al. 1999). Measurements in horse (Charuta et al. 2009) and North American elk (Frey and Riede 2013) larynges show a similar range of sexually dimorphic linear features. The external appearance of the larynx does not give a reliable impression of vocal fold length. Enlarged parts of the larynx in males need not accompany an equal increment in the length of the vocal fold (e. g. Schneider et al. 1966, Schön 1971, Frey and Riede 2003). The enlargement of the exterior dimensions of the laryngeal complex may be confined to an expansion of the intra-laryngeal cavity and this may have resonance effects (Sundberg 1974), or it may play an important role in coupling the sound source with vocal tract resonances (Titze and Story 1997, Döllinger et al. 2006, Titze 2008).

7. Effective Vocal Fold Tension and Effective Mass

The response of epithelium and *lamina propria* to force is a key factor determining at which stretching point the various layers of the *lamina propria* are part of the body or the cover portion of the vocal folds, and how the cover vibrates at various vocal fold lengths. The vocal fold is positioned between the arytenoid and the thyroid cartilage, almost like a string between its two fixation points (Fig. 5). Although the vocal fold is not a string instrument, this anatomical arrangement invites comparison of vocal fold oscillation with that

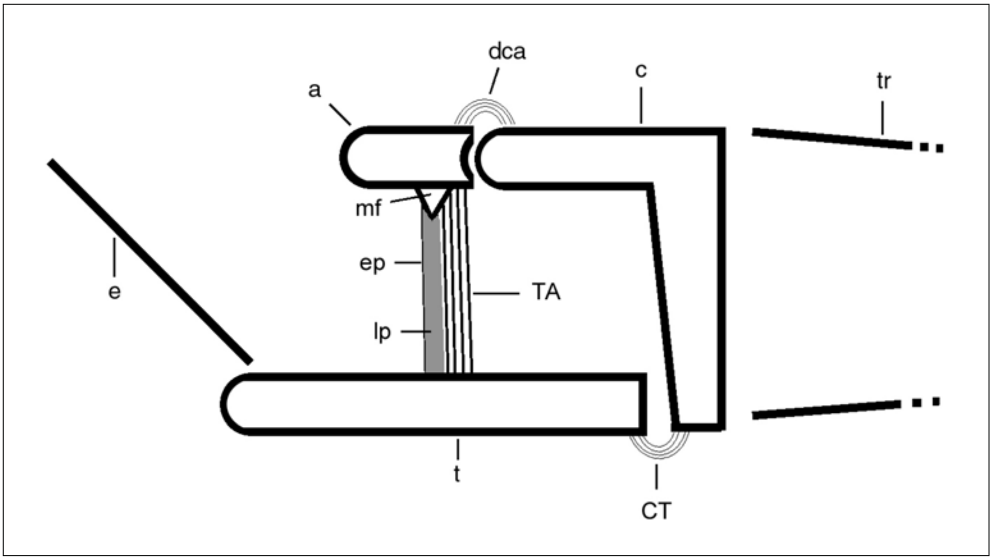

Fig. 5 Schematic of the lateral view of a larynx (comparable to Figure 1*A*). e, epiglottis; t, thyroid cartilage; a, arytenoid cartilage; c, cricoid cartilage; dca, dorsal cricoarytenoid muscle overarching the cricoarytenoid joint; mf, macula flava; ep, epithelium of the vocal fold; lp, lamina propria in the vocal fold; TA, thyroarytenoid muscle in the vocal fold; CT, cricothyroid muscle overarching the cricothyroid gap; tr, trachea.

of a string. The relationship between the two main theories discussed here (myoelastic-aerodynamic theory of sound production and the string model) is established by the relationship between the energy transfer from airflow to the tissue causing vibration and the rate at which the tissue actually oscillates, the latter determining F0. The source of energy is the airflow from the lungs which deforms the vocal folds and induces vibration.

The soft and pliable 'cover' is required since it can respond to the airstream. The mucosal wave (or surface wave) is generated because the 'cover' is easily deformed. F0 of the wave is determined by the mechanical properties of the tissue. The displacement velocity of the vocal folds is proportional to the wave speed, which in turn is proportional to elasticity and stiffness. Elasticity is the mathematical description of the tendency of an object to be temporarily deformed when a force is applied to it. Stiffness is the object's resistance to this deformation.

The string model predicts that the F0 of the vocal fold is proportional to the square root of the ratio of stress and density. It also depends inversely on string length (Equation [1]):

$$F_0 = \frac{1}{2L}\sqrt{\frac{\sigma}{\rho}}, \qquad [1]$$

where L is the vocal fold length, s is the stress developed by the vocal fold (force per unit area), and r is the tissue density (1.02 g/cm^3).

Force acts on a vocal fold in at least two directions, perpendicular (latero-lateral due to vibration) and longitudinal (dorso-ventral due to vocal fold stretching) to the axis of the fold. The perpendicular force increases as the vibration amplitude increases. The longitudinal force increases as the vocal fold becomes stretched. In reality the situation is more complex. The portion of the vocal fold close to its insertion point (*macula flava*, see Fig. 5) exhibits more pronounced bending or rotation with higher amplitudes of vibration (Hunter and Titze 2007, Zhang et al. 2009).

Longitudinal stiffness of vocal fold tissue has been measured in tensile tests in various species (Perlman and Titze 1988, Min et al. 1995, Hsiao et al. 2002, Titze and Hunter 2004, Chan et al. 2007, 2009, Riede and Titze 2008, Riede et al. 2010, 2011, Riede 2010, Klemuk et al. 2011) (Fig. 6*A*). The tensile test measures the response of a material to deformation in one direction. Strain and force are the two variables measured. Strain is the amount of deformation applied, for example the distance by which the vocal fold is elongated from its original length. The force necessary to achieve the deformation is the second variable measured. The material response can be expressed as stress (s), the quotient of force per cross-sectional area of the stretched tissue. The slope of the stress-strain curve is referred to as elastic modulus. Stiffer tissue is indexed by a larger value for its elastic modulus, and stiffer tissue is less likely to oscillate.

The following example illustrates the relationship between tissue stress, vocal fold length and F0. If F0 at 100 Hz, is produced by a 1.5 cm long vocal fold (typical parameters for an adult human male), stress in the vocal fold is approximately 9 kPa (Fig. 6*A*). Stretching that vocal fold by another 20 % (to 1.8 cm) would lower F0 to 80 Hz [if stress remained constant because of the inverse relationship between F0 and L (thin solid line in Fig. 6*B*)]. However, stress tends to increase as the vocal folds are lengthened (Fig. 6*A*). Therefore, F0 would actually increase (thick line in Fig. 6*B*). The string model allows a prediction of the relationship between stress, tissue density, vocal fold length and F0. The important point derived from this example is that tension modulation has a much more dramatic effect on F0 relative to vocal fold length modulation.

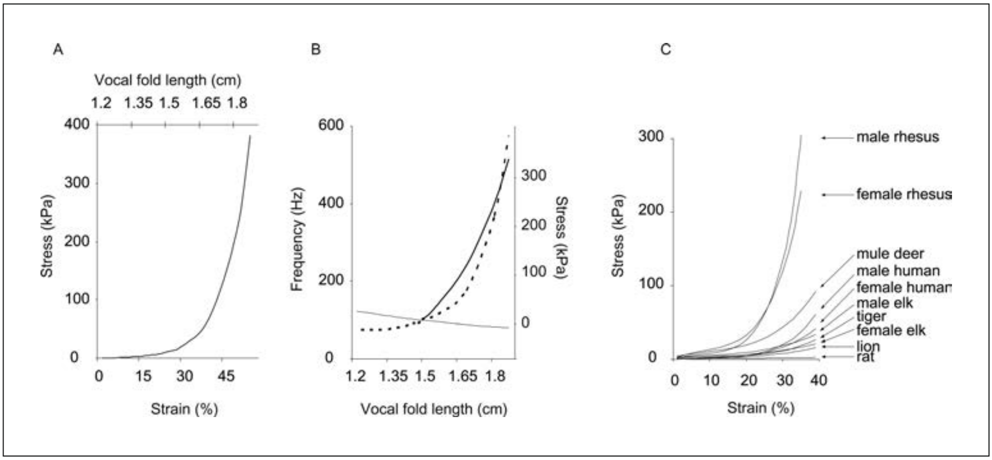

Fig. 6 (*A*) Stress-strain relationship for male human lamina propria (after data from Chan et al. 2007). The length of the relaxed vocal fold (strain 0 %) is estimated as 1.2 cm. An average length of the male vocal fold during speech at F0 of 100 Hz is estimated at 1.5 cm (strain 24 %; stress 9 kPa). In order to increase F0, the vocal fold will be lengthened, stress increases and F0 raises. (*B*) Calculation of F0 according to the string model (Equation [1]). The thin solid line depicts the relationship between F0 and vocal fold length with stress held constant at 9 kPa. The thick solid line (and its continuation as dotted line for vocal fold lengths below 1.2 cm) shows the F0 result when stress behaves more naturally (stress values were adapted from Figure 6*A*). Stress (thin dashed line) increases as vocal fold length increases. The crossing point of both curves is at vocal fold length = 1.5 cm, F0 = 100 Hz and stress = 9 kPa. Note that we have currently no knowledge about the tissue behavior for strains below 0 % (compression, see Fig. 2*B*). Therefore, the continuation of the thick solid line (F0) was drawn as dotted line for vocal fold lengths below 1.2 cm. The vocal register produced in that strain region is often referred to as 'pulsed phonation' or 'vocal fry'. (*C*) The mechanical properties of vocal fold tissue can be tested in tensile tests. Tensile tests in various species demonstrated that mechanical properties of vocal fold tissue are species-specific suggesting they are specifically designed for each species respective vocal repertoire. (sources: *Macaca mulatta*, Riede 2010; *Homo sapiens*, Chan et al. 2007; *Cervus nelsoni*, Riede and Titze 2008; *Odocoileus hemionus*, Riede et al. 2010; *Panthera leo* and *Panthera tigris*, Klemuk et al. 2011; *Rattus norvegicus*, Riede et al. 2011).

The overall stress-strain response of viscoelastic soft tissue to elongation has been differentiated into a linear low-strain and a nonlinear high-strain region. Beyond the high-strain region tissue damage occurs. Such behaviour has been demonstrated for example in blood vessels (e. g. Roach and Burton 1957, Armentano et al. 1991) but also vocal fold tissue (e. g. Hunter and Titze 2007, Chan et al. 2007, Riede et al. 2010). *In vivo* and *in vitro* testing suggests that the limit between linear and nonlinear stress response in the vocal fold lies between 20 % and 30 % elongation (Hsiao et al. 2002, Min et al. 1995, Chan et al. 2007, Riede and Titze 2008, Riede et al. 2010), damage (or 'creep') starts at around 80 % and rupture at about 200 % (Riede and Titze 2008, Riede et al. 2010). The two major fibrous protein components of the *lamina propria,* collagen and elastin, contribute differently to the mechanical properties at certain strains. In the resting position, collagen fibrils of the *lamina propria* are coiled in a helical fashion and become extended once the vocal fold elongates, therefore, they contribute little to resistance during low strain, but they contribute more to resistance at higher strain values. The elastic fibers, however, almost like a rubber band or a spring, contribute continuously to resistance as the tissue is elongated, but their relative contribution to resistance is most important in the low strain region. These effects have been studied by Roach and Burton (1957) by selective enzymatic removal of elastic or collagen fibres combined with tensile testing.

In all species tested so far, the variability of the stress-strain response between individuals is relatively large, probably greatly accounting for the enormous individual-specific patterns of vocal fold elongation to achieve various F0 phonations as explained in section 6 (Nishizawa et al. 1988).

Collagen and elastic fiber content and orientation as well as the content of other material, such as glucoseaminoglycans and fat, affect the viscoelastic properties of the vocal folds, determining oscillation characteristics during vocalization. The determination of the fiber network in vocal folds remains a challenge because micro-scale resolution is required for a relatively large structure. However, more and more data indicate that morphological differences at the molecular level contribute to vocal differences at the individual, gender and species level (Fig. 6*C*).

The relative content of elastic and collagen fibres is affected by numerous factors, for example, sex steroids. An increase in testosterone increases the collagen/elastin ratio in vocal folds just like in other soft tissues (e. g. Fischer and Swain 1980, Hammond et al. 1998, 2000). Studies in human (Chan et al. 2007), Rocky Mountain elk (Riede and Titze 2008) and rhesus monkeys (*Macaca mulatta*) (Riede 2010) vocal folds show consistent differences between males and females, the *lamina propria* of male vocal folds being somewhat stiffer compared to that for females (Fig. 6*C*). In mule deer (*Odocoileus hemionus*), a species with a limited male vocal repertoire, sexual differences in the viscoelastic properties of the vocal folds have not been identified (Riede et al. 2010). Testosterone is a dominant factor in determining voice changes throughout life (Abitol et al. 1999), but differences in vocal fold stiffness have not been rigorously linked to testosterone variations.

Other factors possibly affecting the viscoelastic properties of the extracellular matrix include repeated strain or physical exercise (e. g. Roach and Burton 1957, Woo et al. 1982, Kubo et al. 2001, Webb et al. 2006, de Boer et al. 2007, Timmermans et al. 2004), local and systemic hydration (Arnstein et al. 1989, Fisher et al. 2004, Sivasankar and Fisher 2007, Abitol et al. 1999), or vocal fold scarring following a local inflammation or a systemic infection (e. g. Berry et al. 2005).

8. Summary: Fundamental Frequency and the Acoustic 'Advertisement' of Body Size in Mammals

An animal's body size influences an organism's fitness relative to a wide array of parameters including resource defense, predator deterrence, prey capture, agility, nutritional requirements, mating success and so forth (Schmidt-Nielsen 1984). Because of the importance of body size in animal behaviour, we expect that there will be strong selection on perceivers to make use of available acoustic cues to estimate the body size of organisms in the local habitat.

A number of interconnected size-dependent factors are responsible for the observation that small animals are apt to produce (and hear) high acoustic frequencies, while large animals generally use lower frequencies. Morton (1977) was one of the first to observe this relationship between the frequency characteristics of vocal displays and body size. Terrestrial mammals exhibit an enormous range in variation in body size. The African elephant

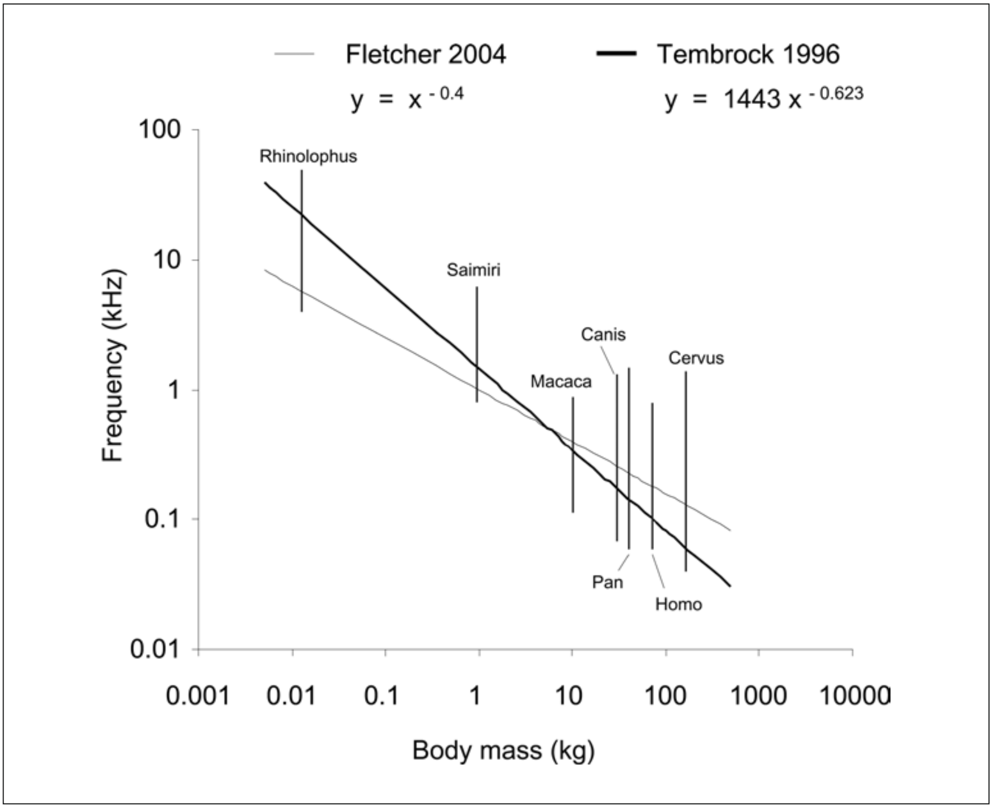

Fig. 7 Relationship between body mass (BM) and fundamental frequency (F0) for mammals. Two sources (Tembrock 1996, Fletcher 2004) investigated a larger sample of various mammals and provided linear regressions. We added F0 ranges of several species examplifying that the F0 can deviate radically from the expected F0 (sources: *Cervus elaphus*, Clutton-Brock and Albon 1979, Struhsacker 1968; *Homo sapiens,* Titze 1989b; *Pan troglodytes*, deWaal 1988, Riede et al. 2007; *Canis lupus,* Schassburger 1993, Riede et al. 2000; *Macaca fuscata*, Green 1975; *Saimiri boliviensis,* Winter et al. 1966, Brown et al. 2003; *Rhinolophus ferrumequinum*, Ma et al. 2006).

(*Loxodonta africana*) is approximately five-million times larger than the Etruscan pigmy shrew (*Suncus etruscus*). Hence, it is not surprising that across species, the F0-body size relationship holds in a general way for mammals (Fig. 7).

For many species the expected F0-body size relationship does not hold on a level that is communicatively relevant for conspecifics: for example, F0 may not predict dominance among males in a number of species (e. g. Rendall et al. 2005, Ey et al. 2007, Riede et al. 2007).

The complexity of the parameters available for modulation in the mammalian larynx has led to an uncoupling in the relationship between body size and F0. The viscoelastic properties of the *lamina propria* play probably the largest role. However, F0 regulation is multidimensional and includes the influence of subglottal pressure, as well as the length, volume, adduction and tension parameters of the vocal folds. Because subglottal pressure appears to exhibit minimal variation over a wide range of variation in the body size of various mammals, it is expected to have little impact on the relationship between body size and F0. The three laryngeal parameters: fold length, volume and tension, do have a strong impact on F0. Vocal fold length is associated with variations in body size, and this parameter is unlikely to be the key element that has resulted in the uncoupling of the relationship between F0 and body size. The data strongly suggest that the capacity to vary the tension of the vocal fold, and hence alter the relationship between the cover and body layers of the vocal fold (and the relative volume of the oscillating tissue) as well as the nonlinear stress-strain response of the *lamina propria* are the key factors that have uncoupled the association between body size and F0. In most cases these factors are poorly understood in terms of their significance for species typical F0 characteristics. So far, it is methodologically difficult to measure *in vivo* the vocal fold volume that actually oscillates under various conditions.

Critical for vocal fold design is also the extent to which nonhuman mammals engage their sound source and vocal tract filter in two fundamentally different ways. The first pattern of engagement is linear source-filter coupling, where the source frequencies are produced independently of the acoustic pressures in the airways. The second pattern of engagement is nonlinear coupling, where the airflow through the glottis is affected by acoustic pressures fluctuations in the vocal tract cavity. In the nonlinear case, the transglottal pressure includes a strong acoustic component, where the airflow through the glottis is driven by acoustic pressures of the vocal tract cavity. Nonlinear source-filter coupling has been demonstrated in computer simulations, in excised larynx experiments, in physical models, and in natural and simulated phonations (e. g. TITZE 2008, TITZE et al. 2008, RIEDE et al. 2008).

In summary the emerging literature emphasizes the fact that the vocal apparatus employed by most mammals is not simply a duplication of the human vocal folds adjusted only in scale. Rather it is the case that different mammalian taxa have introduced interesting perturbations in the "design" of the biomechanical properties, and physical dimensions of the oscillating tissues that serve as the acoustic source of their calls. Sexual selection, character displacement, and variable selection for long-distance or close-range communication may have played prominent roles in individualizing the laryngeal apparatus employed for the vocal regulation of social exchanges in mammals. Advancements in understanding the evolution and biology of vocal communication is dependent on the emergence of a rich comparative literature that systematically addresses these questions.

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On a General Theory Concerning the Special Mechanism of Signal Selection and Its Interaction with the Selection of All Other Traits

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Abstract

I present here my general theory of the selection of signals. The theory suggests that signals are selected by a selection mechanism distinct from that of all other traits, and that the Handicap Principle affects the patterns of most signals, by whatever modality e. g. voice, movement, colour patterns, chemistry, etc. A signal is defined here as a trait that benefits the signaller only as a consequence of the information it provides to a receiver.

Zusammenfassung

Ich lege hier meine allgemeine Theorie der Signalselektion dar. Diese Theorie legt nahe, dass Signale von einem Mechanismus selektiert werden, der von dem für alle anderen Merkmale abweicht, und dass das Handikap-Prinzip die Muster der meisten Signale jeglicher Modalität (z. B. Stimme, Bewegung, Farbmuster, chemisch etc.) beeinflusst. Ein Signal wird hier definiert als ein Merkmal, das den Signalgeber nur insofern begünstigt, wie es für einen Empfänger Information liefert.

1. Introduction

Signallers compete on the attention of the receivers, aiming to convince the receiver to prefer the signaller (as a mate or collaborator, etc.) or avoid it (e. g. as a rival or prey, etc.) over other signallers. The signaller invests in signalling, expecting to affect the behaviour of the receiver to fit the interests of the signaller.

It is reasonable to assume that the receiver should change its behaviour only if the information is reliable. It is thus reasonable also to assume that signals are selected by their receivers to provide reliable information. The reliability of signals is a consequence of a special investment by the signaller, an investment to which I refer as a “handicap” (Zahavi 1975, Zahavi and Zahavi 1997, 1998).

Although the Handicap Principle is now generally accepted as a common and plausible mechanism that limits the transfer of false information, most theoreticians (Grafen 1990a, b, Maynard-Smith 1991 and others) expect it to function only among individuals that conflict in their interests. However, my recent studies suggest that investment in reliability is needed even within the multicellular organism, a situation in which most cells share interests. The reason is that whoever receives information through signals (as distinct from direct observation) needs to assess the reliability of that information, since even a friend may signal false information by mistake. To conclude: I suggest that the handicap principle is involved in the evolution of all signals, whether they come from rivals, kin, friends, or among components of a multicellular organism.

2. Signal Selection as an Extended Version of Darwin's Sexual Selection

Darwin (1874) realized that evolution by natural selection could only be explained if, in addition to the selection for efficiency, there was another selection mechanism which he termed "Sexual Selection." Unfortunately, Darwin included in the umbrella term "sexual selection" both signalling for mate choice and rival deterrence (which are signals) and fighting and other traits that increase the efficiency of competition among members of the same sex, such as tending to offspring (which are not signals). This mixture of traits under the term "sexual selection" may have been responsible for the reluctance of the scientific community to accept his suggestion that two selection mechanisms function in evolution. The term "sexual selection" is used today mainly as a descriptive term for a set of traits involved in reproduction. In contrast, my definition of signal selection clearly demarcates the two mechanisms of selection within natural selection including signals related to sex as well as all other signals.

3. The Evolution of the Peacock's Tail as an Example for the Evolution of Signals

Before the tail became an elaborate trait, peacocks used their tail as a functional rudder. Peahens looking for heavy mates learned to prefer males with longer tails because heavier birds needed longer tails. At this stage, although the length of the tail provided information to the females, the tail was not a signal, since the males' investment in it did not entail an investment other than required for the efficiency of the males' movements, whether the females considered it or not.

Once females evolved a preference for longer tails, males could benefit by exaggerating the length of their tail in order to be more attractive. The extra length of the tail reduced the efficiency of the tail as a rudder, handicapping its bearer. This extra investment (in length and in reduced efficiency) is the part where the mechanism of signal selection is active. Although all males increased the length of their tail in order to be attractive, better-quality males (that were probably heavier and had longer tails to begin with) could lengthen their tails more than lower-quality males could. Once males lengthened their tails, females were able to perceive more clearly small differences in quality between males, and males displayed more clearly their advantages over competitors close to them in quality.

4. Comparing Fisher's Model of Mate Choice (an Evolutionary Stable Strategy Game) to the Handicap Principle

A different model was suggested by Fisher (1930, 1958) to explain why peahens continue to choose peacocks with elaborate trains despite the fact that these trains burden their mates as well as the female's male progeny. Fisher believed that by the end of what he called "the runaway process" all peacocks had equally long tails and hence there was no reason to prefer one male over the other. Fisher could not suggest any direct benefit to a female who chose a long-tailed mate, and based his solution on what is called at present an ESS (Evolutionary Stable Strategy) model: he suggested that when all females prefer males with a long tail, the female's sons will only be attractive if they inherit the long tail from their father. This is the "sexy son" model.

I suggest that Fisher's model is wrong in two assumptions: 1. Fisher's model assumes that all males grow their tail equally long, and 2. Fisher's model assumes that tail length is the only parameter by which females select their mate. However, peacocks, like other organisms, advertise their qualities in several ways. They grow long tails, they dance, they spread their tail and quiver it and display its colour pattern, they vocalize, and they defend their arenas. There is now also information that peacocks vary in the length of their tail in correlation to their quality (Petri et al. 1991), contrary to the assumption of Fisher's model.

5. What Would Happen if All Peacocks Grew their Tail to be of the Same Length?

The purpose of a signal is to convince the receiver to prefer the signaller over other signallers. For that end a signal has to advertise and accentuate differences between signallers. According to the handicap principle, the investment in signalling should be differential, so that low-quality signallers cannot invest in the signal as much as signallers of a higher quality.

If all peacocks were able to grow their tail equally, i. e., tail-length would no longer be correlated to the male's quality, a female that would stop considering the length of the tail when assessing a mate would improve her assessment of her mate's quality, since she would be using only other parameters that are still correlated with quality. Since at that time all males would still have long tails, even the sons of a female that does not pay attention to the length of the tail would still have long tails. But since the mother of these offspring would be choosing her mate on the basis of parameters that would still correlate to quality, her offspring would be of a higher quality than the sons of females that would still consider the length of the tail. Her daughters would inherit her success. Once many females stop preferring a mate with a long tail, a male that would grow a short and efficient tail would have an advantage over males with a long tail, the trait would spread in the population, and the tails of peacocks would be once more short and efficient for movement. To conclude, I suggest that signals that do not provide reliable information do not persist, i. e. signals do not continue to be used "because all individuals use them" as suggested by Fisher's ESS model. They evolve when they provide good differential information, and disappear when they do not provide such information.

I compare the process by which signals are selected out to the "inflation" of money. Like the inflation process of currency, when money is easy to get, money loses its value and is replaced by other currencies. A similar process affects human decorations (Zahavi and Zahavi 1997, 1998). Recently several cases have been documented in which birds changed their display under environmental conditions that reduced the investment required to produce a signal. For example, peahens in Japan, where peacocks have been bred over 200 years under low predation risks, stopped assessing peacocks by the length of their tail (Takahashi et al. 2008). Male Satin Bowerbirds stopped stealing blue decorations from the bowers of their neighbours in areas in which blue artifacts were common, and invested more in destroying their rival's bowers (Hunter and Dwyer 1997).

6. The Difference between the Selection of Signals and that of all other Traits

It is important to emphasize the difference between the selection of signals and the selection of all other traits. If the investment required in an efficient structure is reduced to the extent that all individuals can develop that trait equally – the trait persists and individuals benefit from the reduced investment. However, if all can signal alike – the signal loses its value to advertise differences between signallers, and is lost by selection. The inflation process clearly demarcates the two mechanisms involved in Natural Selection: 1. the selection for efficiency, that selects most traits, and 2., the selection of signals for the transfer of reliable information, which I term "Signal Selection". This is a fundamental difference between the selection for signals and the selection for all other traits. It is also important to emphasize that while the selection of traits that are not signals increases the efficiency of their bearers, the selection of signals decreases the efficiency of the signaller – but this decrease in efficiency is compensated for by the increase in the fitness of the signaller as a consequence of its effects on the receivers.

7. The Interaction between the Two Selection Mechanisms

It is difficult to explain how new traits, such as feathers or horns, could have evolved by the selection for increased efficiency alone. However, the selection of signals can create completely new and inefficient structures. Some of these extravagant signals, that reduced the efficiency of the signaller, could become the starting points from which selection for efficiency might develop the new efficient traits. These two ways of directional selection – one which increases efficiency and the other which reduces efficiency but increases the reliability of signals – enable natural selection to change adaptations from one peak of adaptation to another adaptive peak. Obvious examples are the evolution of feathers from the reptile scales and the evolution of horns in mammals (Zahavi and Zahavi 1997, 1998).

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Continents under Climate Change

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Der Klimawandel gehört zu den drängendsten globalen Problemen unserer Zeit. Die Menschheit steht vor besonderen Herausforderungen, um insbesondere den CO_2-Ausstoß zu senken. Führende Wissenschaftler aus der Klimaforschung betrachten die Auswirkungen des Klimawandels auf die Kontinente Europa, Asien, Afrika, Amerika und Australien sowie die Polarregionen. Dabei werden neueste Klimadaten unter globalen und regionalen Gesichtspunkten ausgewertet und Simulationsmodelle für zukünftige Entwicklungen diskutiert. Die Ausführungen bieten ein gut fundiertes Bild der Klimaänderungen, die sich weltweit bereits vollziehen bzw. in Zukunft ereignen werden, und untersuchen kritisch die Folgen für Natur, Gesellschaft und Wirtschaft. Der Kongress „Continents under Climate Change“ wurde im Rahmen der 200. Jahrfeier der Humboldt-Universität zu Berlin vom Potsdam-Institut für Klimaforschung und der Deutschen Akademie der Naturforscher Leopoldina – Nationale Akademie der Wissenschaften veranstaltet. Alle Beiträge sind in englischer Sprache verfasst.

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The Concepts of *Operant Conditioning* and *Conditioned Action* in Past and Future

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With 4 Figures

Abstract

The behaviouristic concept of operant conditioning was formulated intentionally without physiological or psychological theoretical background. It could be further developed by elaborating a signal processing network which realizes the recorded input-output-relation in the case of *rewarding*. This informational network is composed of four different signal processing elements which are connected as shown by the functional diagram.

Zusammenfassung

Der behavioristisch und damit bewusst theoriefrei konzipierte Lernprozess des ‚operant conditioning' lässt sich für den Fall der *Belohnung* und der daraufhin erfolgenden ‚bedingten Aktion' funktionell verwirklichen, indem vier unterschiedliche Elemente der Signalverarbeitung auf bestimmte Weise miteinander verschaltet werden und zusammenarbeiten – ein repräsentatives Beispiel für die vermutliche Zukunftsentwicklung in eine informationstheoretische Richtung – ein Schritt, ohne den die künftige verhaltens- und neurophysiologische Forschung kaum auskommen wird.

The ability *to learn* is one of the most extraordinary achievements of living organisms. Individual experiences such as rewards or punishments cause permanent structural changes in the system of behavioural control. If e. g. a certain behaviour is being rewarded by a pleasant experience it will subsequently be used *more frequently* by the organism. This process of learning – the scientific term is *operant conditioning* or *conditioning by reinforcement* – is described in the present treatise from four very different angles: as a result of observations and experiments, as a central term of neo-behaviourism, as a pattern of behaviour with a specific biological meaning, and as the result of the interaction of four different elementary processes in biological data processing. Thus, the transition from neo-behaviourism to an analysis based on information theory is also demonstrated.

1. Observations and Experiments, Empirical Basis

1.1 Experiment I (Skinner Box)

The *Skinner Box* is considered a classical experimental design for the detailed study of *operant conditioning* (Fig. 1). A cage contains a lever, a 'pushbutton'. If this lever is oper-

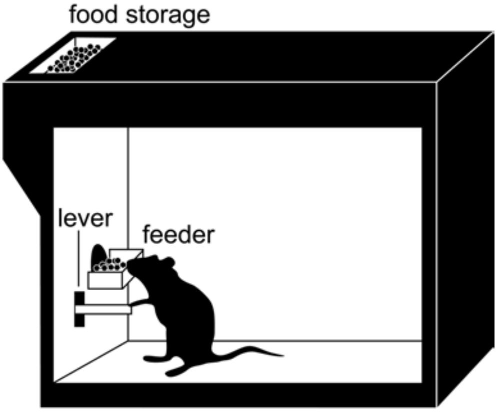

Fig. 1 Skinner Box, also known as 'problem box', in which a rat is just operating the pushbutton in order to be rewarded by food.

ated by an animal, a mechanism either rewarding (e. g. by food) or punishing it (e. g. by an electric shock) is started. In the first case, the lever will be used more frequently by the animals, in the latter less often or not at all. Here, only a scenario of *reward* will be discussed, i. e. when the behaviour is used *more frequently* based on experiences in the Skinner Box.

1.2 Experiment II

A lamb and its mother were kept jointly in an enclosure which was divided into two compartiments by a fence containing a door. The experiment was started by occasionally luring the mother into the other compartment without the lamb. Initially, the lamb did not take any notice. If it subsequently wanted to get to its mother, it could not pass the door, which was only opened – *immediately* – if the lamb *urinated*. The conditioning was thus achieved by the experimenter observing the lamb and opening the door as soon as it urinated. When the experiment was started the lamb urinated independently from external events including the separation from its mother. After a certain period of time, which differed for each lamb (1–3 days) this started to change, though: The lamb now *urinated immediately* when it wanted to get to its mother on arrival at the closed door (and was then *instantly* allowed to pass it). Thus, the lamb used urination now as a *means* to achieve drive satisfaction, after its considerably increased need to establish contact with its mother was satisfied in short temporal consequence (a learning situation). The *motivation* to establish contact with its mother was linked to the behavioural element 'urination' which was consequently employed to reach its true goal (SCHLEICHER, unpublished, HASSENSTEIN 2006, p. 237).

2. The Theoretical Concept of *Operant Conditioning*

A comparison of the two examples – the rat rewarded by food in the skinner box and the urinating lamb wanting to get to its mother – reveals a common functional context: a certain behaviour is followed by a positive experience which results in the animal memorizing

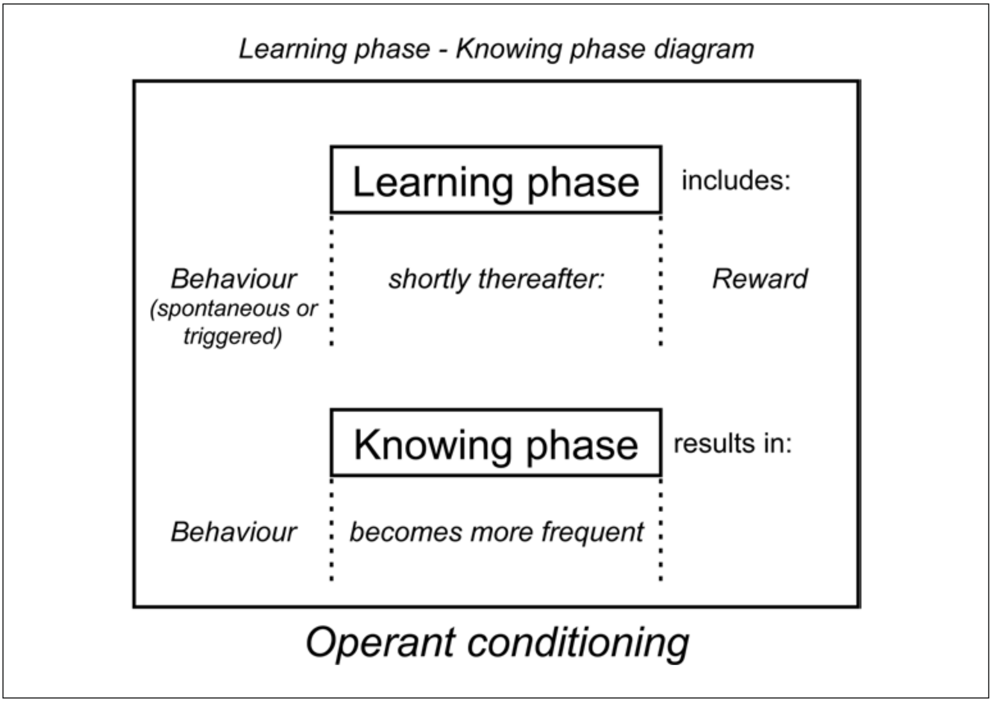

Fig. 2 Behavioural pattern of operand conditioning. See text for explanation.

the rewarded behaviour and repeating it in a respective situation in the future. This behavioural pattern is shown in Figure 2 as a 'Learning phase – knowing phase diagram' (Hassenstein 2006). The terms 'learning phase' (*Lernphase*) and 'knowing phase' (*Kannphase*) were coined by the engineer Karl Steinbuch (1961).

The 'Learning phase – knowing phase diagram' illustrates the main principle of the behaviouristic theory of learning: In the *learning phase* the desired act of behaviour is being followed by a *reward*. Consequently, in the *knowing phase* this behaviour increases in *frequency*, it becomes *'reinforced'*. By coining the term *operant conditioning*, the American psychologist B. F. Skinner (1938) established a second basic function of learning (after the *conditioned reflex*, see Pavlov 1927) in science – an important event also in the history of science.

3. Biological Meaning

From a biological perspective this functional relationship becomes immediately obvious: if learning processes are available at all then already one of them should accomplish the behaviour described above: an act of behaviour that is immediately rewarded in whatever way should be memorized and increased in frequency. When such a functional relationship has arisen it is expected to be maintained or promoted by Darwinian selection. All this seems rather obvious.

4. Focussing on Satisfaction of Drives

The ‘positive’ experiences prompting an animal to repeat such particular behaviour comprise the fulfilment of an activated motivation or need. In the examples given above these were hunger (or thirst), or the desire to establish contact with the mother, respectively. This kind of positive experience, the satiation of motivation, will now be the topic and is illustrated by a learning phase – knowing phase diagram as well (Fig. 3).

In addition to the word ‘reward’ this shows that a motivation has been fulfilled, and the label ‘becomes more frequent’ has been replaced by the explanation that this (and only this) motivation produces the behaviour in question when activated.

The diagram (Fig. 3) does not only contain the externally recognizable, directly measurable data such as the reward, e. g. the offer and consumption of food, or the frequency of the behaviour over time. Figure 3 also contains *physiological* parameters, for example ‘motivation’ and the link between motivation and behaviour. This represents a theoretical advance which has some consequences as demonstrated in the following.

By the way, the experiments forming the basis for Figure 2 depended on *hungry* animals and would not have been possible with *repleted* ones. A physiological parameter was involved there as well, even though it remained constant and thus did not become part of the definition.

Figures 2 and 3 also differ in the legend, i. e. ‘operant conditioning’ or ‘conditioned action’, respectively. The latter term establishes a parallel between this learned behaviour to ‘conditioned reflex’. At the same time, the difference is clarified: not a *reflex,* i. e. a stim-

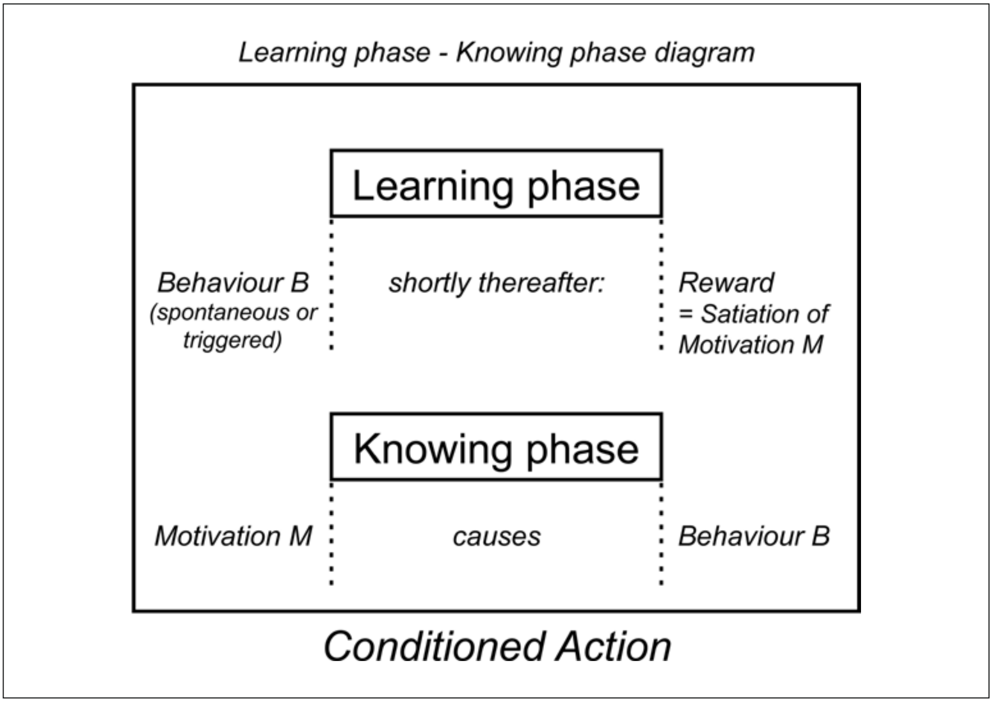

Fig. 3 Behavioural pattern of conditioned action. See text for explanation.

ulus-response-relationship is linked to a new *releasing stimulus*, but rather an *action* (e. g. motoric) will be *de novo* coupled with a *motivation* based on experience – irrespective whether this happens as a reaction to a stimulus or spontaneously.

5. Logical Analysis

The single processes involved can be extracted from the new learning phase – knowing phase diagram. Essentially, the question is how the behavioural pattern of the learning phase (and its repetition) brings about the new behavioural pattern of the knowing phase. As revealed by the following analysis, four different elementary processes are involved. One of these is obviously – this is a learning process after all – the formation of a new link, an ‘association’.

5.1 Conditional Link

Having accomplished the learning process the biological condition ‘hunger’ or generally the signal on the level of motivational activity does not only release the appetitive behaviour assigned to it, but also the newly acquired behaviour. A new signal-transmitting connection was thus formed during the learning process, namely from the information channel of motivation activation to the command line of the respective behaviour.

The final, functionally elementary process during the transition from the learning phase to the knowing phase is thus the formation of the new signal transmitting link. This new linkage does not happen spontaneously, though, but is induced by the arrival of a signal termed ‘h-signal’ which contains the information of the existence of the preconditions for the learning process in the making. A descriptive name for this functional element would thus be ‘signal-dependent linker of two signal-transmitting channels’. This linking element consequently has three inputs and one output. Hereafter, it has been termed simply after its function: ‘conditioned link’ and it has been marked in *red* in the summarizing functional diagram – see below (Fig. 4).

5.2 Coincidence Detector

The learning process depicted in the learning phase – knowing phase diagram will only occur if and when two conditions are met simultaneously: an interior signal on the accomplished behaviour and a signal on the subsequent satiation of motivation. This is evidence for the existence and performance of an interior entity especially reacting to this ‘coincidence’. This ‘coincidence-detector’ only emits its signal upon the simultaneous occurrence of both conditions stated above. This signal subsequently plays the role of the ‘h-signal’ mentioned previously containing the information ‘condition met’ and the imperative ‘form a link!’.

This second functional element derived from the learning phase-knowing phase diagram has two inputs (for the two signals which shall be linked) and one output (for the signal reporting an established ‘coincidence’). It is shown in *green* in the following functional diagram (Fig. 4).

5.3 Efferent Copy with Short Term Memory

The simultaneous input releasing the coincidence signal just mentioned really is a temporal sequence, where the *initial* behaviour (or the behavioural command) is followed with a delay by the satiation of motivation. This can also be derived from the learning phase – knowing phase diagram. Such a short temporal distance has been dubbed ‘contiguity’ by psychologists. The fact that the coincidence of an event that has *just passed* and one that *occurs presently* is functionally important here necessarily implies that the initial command signal is temporarily stored by a *short term memory* and only transmitted after a short delay – the function of the atrioventricular node of the Human heart represents an analogon. Consequently, this manoeuvre is not conducted upon the command itself (which has to be executed immediately), but using an ‘efferent copy’ branching off onto a separate track.

Thus, the third of the interacting *elementary processes* in a conditioned action is a short term memory for signals. It is shown in *black* in the following functional diagram.

5.4 Change Indicator for Motivation Activity

With regard to motivation-related processes in learning, the fulfilment of motivation is crucial (see Fig. 3). When the interior signal on the fulfilment of motivation is matched with the signal on the prior act of behaviour learning occurs. What then is the physiology behind ‘satiation of motivation’? It is the complete or partial achievement of the target of motivation resulting in a decrease or the complete removal of the arousal of motivation. Thus, concerning the coincidence detector, the relevant signal does not indicate motivation activity, but its *decrease*. From the signal on motivation activity (which starts the respec-

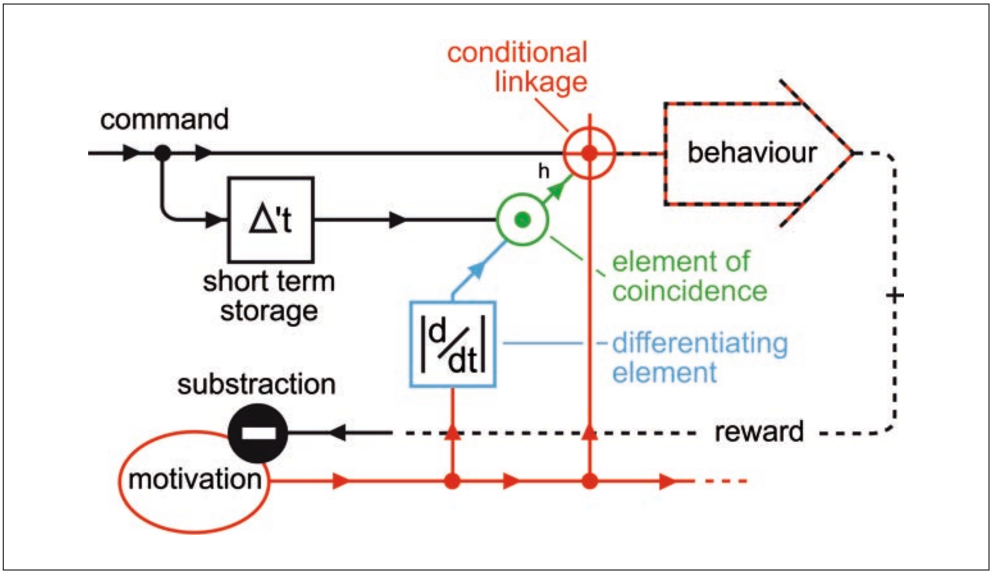

Fig. 4 Idealized and simplified functional diagram showing how operand conditioning leads to conditioned action. See text for explanation.

tive appetitive behaviour) a secondary signal is derived and fed into a c*hange indicator*, which – as indicated by its name – only produces and transmits a signal upon a *change* in signal influx (in our case: a *decrease*).

The fourth functional element necessary for the realisation of the conditioned action is thus a ‘change indicator’, in mathematical terminology a ‘differentiating element’ of the respective signal influx of the motivation activity. The change indicator possesses both a single input and output, it is shown in *blue* in the functional diagram.

6. The Resulting Functional Diagram

The functional elements described above and their links can be geometrically depicted in various ways. The previously employed colours are used in Figure 4.

The aim of this functional diagram is as follows: If the four functional elements outlined in section five are linked as shown, then the resulting functional system will ‘automatically’ realize the conditioned action. Three concluding remarks on this topic.

6.1 Behavioural Biology Can Provide Clues for Neurophysiology and Histology

If a *neurophysiologist* would find a link between short term memory, a differentiating element, a coincidence detector and a ‘conditional link’ as shown in Figure 4 without being aware of the ideas sketched above, he would hardly perceive the functional mechanism of *operant conditioning* in this. If a *neurohistologist* would indeed find the *structure* responsible for a conditioned action in one of his microscopic slides, he would only recognize and correctly interpret it as such if he would refer to the functional system derived from considerations of system theory. The insights into the functional structure of biological steering mechanisms gained by a behavioural biology based on system theory and synthesized in functional diagrams can provide clues for neurophysiologists and histologists what to look for with their methods.

6.2 Conditioned Action Inverts the Causal Relationship between Behaviour and Motivation

Upon closer inspection the behavioural pattern or functional system, respectively, depicted in the learning phase – knowing phase diagram (Fig. 3) and functional diagram (Fig. 4) achieves something surprising and remarkable: It inverts (by the process of learning) the temporal relationship ‘before and afterwards’ and thus also the causal relationship ‘cause and effect’. In the learning phase the behaviour *brings about* the satiation of motivation; in the knowing phase the activated *motivation* brings about the *behaviour* (Hassenstein 1972). Distilled into a formula this means:

$$\text{learning phase B} \rightarrow -\frac{d}{dt}\text{M leads to knowing phase} + \text{M} \rightarrow \text{B}. \qquad [1]$$

(Behaviour and motivation have been abbreviated as B and M, respectively; the arrow stands for *brings about.* The expression $\frac{d}{dt}$ means change or differential coefficient.)

6.3 Conditioned Action Can Serve as an Example to Investigate Fundamental Relationships between Psycho-chemical and Information-processing Domain

While the process suggested above is entirely causal, there is no single physio-chemical process which achieves this functional relationship between input and output signals. On a *virtual* level this is nevertheless perfectly possible, i. e. in the domain of signal transmitting channels, data processing functional elements and their complex furcations and circuits. The processes in that domain are receiving signals from the physio-chemical domain (reality) by receptors, though, and do also influence this reality by *regulating* processes. The 'conditioned action' provides a convincing example of these fundamental relationships and offers matter for various epistemological considerations.

7. Final Thoughts

The train of thoughts outlined above can be traced through the four figures and their order: *First* (Fig. 1) the situation, i. e. the experimental setting, in which the learning process of operant conditioning takes place, is illustrated. *Second* (Fig. 2) is the *behaviouristic*, i. e. theory-free, formulation of the external parameters necessary for the learning process and the newly acquired behaviour. The *behavioural-physiological* perspective (Fig. 3) requires an interior entity, a 'motivation', which plays a pivotal dual role in the learning process: It is satisfied by the reward, and *because of this* it becomes in the near future the trigger for the very behaviour which *immediately preceded* the act of rewarding. Only this functional correlation, which is rather curious in a way, enables the apparently simple and convincing imperative: "Repeat with purpose what made you successful".

A *logical analysis* has thus revealed the efficiency of *four* different signal processing entities in the learning process of 'conditioned action'. Their very different nature prevents any of them from taking over a function from another one and their concurrence is shown in a 'functional diagram' in Figures 4. The scientific content of the functional diagram is given by its *topology*, not its geometry: Which entities are connected by signal transmission? The theoretical step of determining the respective signal processing elements (Hassenstein and Reichardt 1953) cannot be skipped if the aim is to gain a comprehensive understanding of the origin of acts of behaviour such as conditioned action in the future.

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Nano im Körper

Chancen, Risiken und gesellschaftlicher Dialog zur Nanotechnologie in Medizin, Ernährung und Kosmetik

Akademiensymposium

Deutsche Akademie der Naturforscher Leopoldina – Nationale Akademie der Wissenschaften
acatech – Deutsche Akademie der Technikwissenschaften
Berlin-Brandenburgische Akademie der Wissenschaften
(für die Union der deutschen Akademien der Wissenschaften)

am 9. November 2010 in München

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Nanotechnologie rückte in den letzten Jahren immer stärker in den Fokus der Öffentlichkeit. Dies ist einerseits das Ergebnis einer vielfältigen erfolgreichen Forschungsarbeit, die zu neuen Anwendungsmöglichkeiten von synthetischen Nanopartikeln auf verschiedenen Gebieten geführt hat; andererseits werden auch Verbraucher zunehmend mit Produkten konfrontiert, die Nanopartikel enthalten. Daher stehen außer den großen Potenzialen der Nanotechnologie naturgemäß auch Unsicherheiten. Diese Publikation dokumentiert eine Veranstaltung der acatech – Deutsche Akademie der Technikwissenschaften, der Deutschen Akademie der Naturforscher Leopoldina – Nationale Akademie der Wissenschaften und der Akademienunion. Sie hinterfragt und diskutiert kritisch die verschiedenen Facetten der Nanotechnologie, insbesondere in den Bereichen Medizin, Kosmetik und Ernährung.

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The Story of Power in a Primitive Wasp Society

Anindita Bhadra (Mohanpur, India)

With 10 Figures and 1 Table

Abstract

Ropalidia marginata is a primitively eusocial wasp from peninsular India. Like other primitive wasps, this species lacks queen-worker dimorphism, but unlike other primitive wasps, the queen in *R. marginata* is a docile, rather than dominant individual, who does not use aggression to regulate worker reproduction. This is just one of the many ways in which this species is different and more advanced than other primitive societies, and this is what makes *R. marginata* the perfect model system for studying the evolution of eusociality. In this essay, I discuss two of the most intriguing questions that shape our understanding of insect societies, that of queen succession and the maintenance of reproductive monopoly by the queen – the key ingredients to the story of power.

Zusammenfassung

Ropalidia marginata ist eine primitive eusoziale Wespenart aus Indien. Wie andere primitive Wespen weist diese Art keinen Königin-Arbeiter-Dimorphismus auf. Die *R. marginata*-Königinnen sind jedoch keine dominanten Individuen, wie bei anderen primitiven Wespen, und setzen auch keine aggressiven Verhaltensweisen zur Regulation der Reproduktion der Arbeiter ein. Auch hinsichtlich weiterer Merkmale weicht *R. marginata* von anderen Arten ab und zeigt sich als weiter entwickelt, so dass sie als ideales Modellsystem für das Studium der Evolution von Eusozialität geeignet ist. Hier diskutiere ich zwei der faszinierendsten Fragen, die unser Verständnis von Insektengesellschaften bestimmen: die Königinnen-Nachfolge und die Aufrechterhaltung des reproduktiven Monopols der Königin – die wesentlichen Bestandteile einer *Story of Power*.

1. Introduction

Insect societies, like those of ants, bees, wasps and termites fascinate us by the immense diversity and complexity of their social organization. Apart from the basic scientific curiosity about the organization of their societies, we are attracted towards these insects as fellow social animals. As a child I have often played a trick on ants by putting drops of water on an ant trail, and I have watched in fascination the confusion among them, and the inevitable falling back in line. I have wondered why they form those lines, and what they keep telling each other when they meet, and how they are able to get back in to formation so easily. These are exactly the kind of questions a sociobiologist asks when he probes in to the private lives of the insects. How do the members of a colony identify each other? What are the dynamics that determine division of labour among these individuals? How do the individuals in a group communicate with each other? How does a colony decide on a new nesting site? The questions are endless, and the answers are amazing, but the biggest question of all that we want to address is why do some individuals choose to live in groups. Studies of social insects aim to provide answers to both kinds of questions, and build an understanding of the evolution of social complexity through insect societies.

Social life at any level demands the resolving of conflict and the evolution of cooperation among the individuals of the group. Studies of insect societies have therefore been aimed at understanding the mechanisms by which cooperation can be achieved and maintained in these societies. Highly evolved insect societies, like those of honeybees, hornets and most ants provide examples of complex social organization, and are good model systems for studying the intricacies of social complexity, and how cooperation can be maintained once it is achieved. However, less complex societies like those of many paper wasps and bumble bees are good model systems for studying the process of evolution of complexity through the resolving of conflict among individuals.

2. The Paper Wasp *Ropalidia marginata*

The genus *Ropalidia* exhibits diverse levels of social organization, from the nearly solitary *R. formosa*, in which nests are built in large aggregations, but each nest is occupied by a single individual (Wenzel 1987), to *R. ignobilis*, which shows the highest degree of queen-worker dimorphism recorded in an independent-founding Polistine wasp (Wenzel 1992). Yet again, there are the swarm-founding species like *R. montana*, which make large, enveloped nests, and have queens which are distinctly larger than their workers (Yamane et al. 1983). Nest architecture is also very diverse, both among the independent-founding and the swarm-founding groups of *Ropalidia* (Jeanne 1975, Kojima 1982, Yamane and Itô 1994). Due to the wide range of eusociality present in this genus, it has been considered as an important genus for the study of the evolution of eusociality in wasps (Wilson 1971). Our research group has been engaged in studying the social biology of *Ropalidia marginata*, a paper wasp from India, for about a quarter of a century.

Ropalidia marginata (Fig. 1) is an Old world species of paper wasps found in peninsular India, Sri Lanka, South-east Asia and Australia (van der Vecht 1941, 1962, Das and Gupta 1983, 1989). This species has an aseasonal, indeterminate and perennial colony cycle, which means that nest initiation occurs round the year, and nests are active throughout the year (Gadagkar et al. 1982, Shakarad and Gadagkar 1995, Chandrashekara et al. 1990, Gadagkar 1991).

They make simple uncovered nests of paper, and are therefore called paper wasps. The paper is produced by masticating cellulose that is collected usually from plant sources, and mixing it with saliva. Their open nests make *R. marginata* a convenient system for observational studies. The nests are usually found in closed spaces with small openings, inside bushes and within various man-made structures. We have sighted and collected nests from electric poles, broken pillars, crevices of buildings, electric cable boxes, switch boards, tube light holders, the bottom of park benches, and even from within dustbins and letter boxes. Nests that can be accessed only through very small openings are well protected from the hornets *Vespa tropica*, which are the prime predators of these wasps. Nest sizes

Fig. 1 A colony of *Ropalidia marginata* in the laboratory, showing marked wasps.

range from 0 to 722 cells (mean ± s.d.: 133.7 ± 119.2), with 1 to 200 females (mean ± s.d.: 21.9 ± 22.3) and 0 to 33 males (mean ± s.d.: 2.4 ± 5.4) (Gadagkar et al. 1982). Males are produced aseasonally, and are thus found throughout the year in a subset of nests in the population (Sen and Gadagkar 2010). There is only a single queen in any nest of *R. marginata*, and she is not morphologically distinguishable from the workers. The queen lays a single egg per cell, and the larvae grow inside the cells, being fed by the workers. The mature larvae spin a cap of silk on their cells and pupate inside. The adults eclose out on the nest from mature pupae.

3. The *R. marginata* Queen

The queen is the one and only egg-layer in colonies of *R. marginata*, and we have never recorded egg-laying by any other individual in the presence of the queen in our studies on this species over the last 25 years or so. Interestingly, the queen of *R. marginata* is not an aggressive individual, as is expected in primitively eusocial species. Individuals in a *R. marginata* colony can be classified into three behavioural castes: sitters, fighters and foragers, and the queen belongs to the category of the docile sitters (Gadagkar and Joshi 1983). Moreover, the queen is often not seen to participate in dominance-subordinate interactions in the colony, and she rarely occupies the highest rank in the dominance hierarchy of her colony (Chandrashekara and Gadagkar 1991). The queen in *R. marginata* is also not the central pacemaker of her colony, and workers self-regulate activities like foraging on the nest in a de-centralised fashion (Premnath et al. 1995) by means of dominance-subordinate interactions (Bruyndonckx et al. 2006, Lamba et al. 2007). This is surprising because queens of primitively eusocial species are known to control worker activities as well as to regulate worker reproduction by means of aggression.

4. The Power of the Queen

The "power" of the queen in an insect society is her ability to control reproduction in a situation of conflict. The easiest expression of power, which is also probably the easiest to understand, is sheer physical aggression. In small groups, it is convenient for an individual to achieve a status of dominance through physical aggression, as it is feasible for her to show aggression to each and every individual. This is very well documented in foundress associations in Polistine wasps, where a dominance hierarchy is established among the foundresses through dominance-subordinate interactions, and the alpha individual becomes the sole or primary egg-layer, while the rest remain on the nest as workers (Pardi 1948, West-Eberhard 1969). But in larger groups, such dominance might be difficult to attain, due to the sheer numbers who need to be dominated (Seeley 1985, Keller and Nonacs 1993). In highly eusocial species with large colonies, the queen can have power over reproduction through chemical means, by producing pheromones that can suppress worker reproduction. Such a pheromone would act through a biochemical pathway on the physiology of the workers, and prevent their ovarian development. However, as discussed by Keller and Nonacs (1993), such a system of suppression would be extremely vulnerable to cheaters, as a worker who has a genetic make-up that can help her to overcome the effect of the chemical weapon of the queen, would benefit by direct reproduction, and the "gene for selfishness" would spread in the population. Keller and Nonacs (1993) suggested an alternative mechanism of worker regulation, rather than control, where the queen's pheromone is an "honest signal" of her physiological status. Such an honest signal is perceived by the workers, and they choose to "obey" the queen's signal, as it is in their benefit to cooperate with the queen to help her raise more offspring than to produce their own sons, because the queen in the highly eusocial species is more "fit" to reproduce than the workers. The power of the queen is more easy to maintain in the highly eusocial societies, due to the combined effect of the queen-worker dimorphism and the queen pheromone. Though *R. marginata* is a primitively eusocial species, the queen does not fit into the model of aggressive control of worker reproduction, as she is a meek and docile individual, who often does not participate in dominance-subordinate interactions. How, then, does the *R. marginata* queen achieve reproductive monopoly in the colony?

5. Queen Succession

In most primitively eusocial insects, the queen is the most aggressive individual in the colony, and she is succeeded by the beta in the dominance hierarchy. This is well documented in foundress associations of Polistes (Pratte 1989) and in *R. cyathiformis* (Kardile and Gadagkar 2002, Deshpande et al. 2006). In the stenogastrine wasps, the dominance hierarchy is correlated with the age hierarchy, and also with the succession hierarchy (Cant et al. 1996, Field et al. 1999). In all these cases, the queen's successor can be identified easily in the presence of the queen, and once the queen is lost, agonistic interactions in the colony increase, and the beta establishes herself as the new alpha by stepping up her aggression (Pardi 1948, West-Eberhard 1969, Cronin and Field 2007, Röseler et al. 1986, Deshpande et al. 2006, Turillazzi 1991). In *R. marginata*, though the queen is a docile, non-interactive individual, the death or experimental removal of the queen induces a drastic transformation of the colony. One of the workers present in the colony suddenly steps up her aggression to extremely high levels, and if the queen is not replaced, this individual develops her ovaries and starts laying eggs in about a week's time, thus becoming the new queen of the colony. We designate this individual as the potential queen (Premnath et al. 1996, Deshpande et al. 2006). Interestingly, the potential queen establishes herself in the colony using extreme aggression, but over the next few days, she gradually decreases her aggression and becomes a docile queen. Though the potential queen becomes evident very soon after queen removal, we are never able to predict the identity of the potential queen when the queen is present in the colony. The potential queen seems to be an unspecialized individual in terms of her dominance rank in the queen-right colony, other behaviours, body size, ovarian development and age (Deshpande et al. 2006, Chandrashekara and Gadagkar 1991, 1992). However, it is intriguing that only one individual steps up her aggression within minutes of queen removal, suggesting that there might be a pre-designated successor to the queen in *R. marginata*.

6. Two Questions

In this essay, I will discuss two of the most intriguing questions at the time about the species that I probed into during my PhD in Prof. Raghavendra Gadagkar's lab.

6.1 Question 1: Is There a Designated Successor to the Queen in R. marginata?

Since the queen's successor is predictable in other primitively eusocial species, an obvious question that comes to mind is whether there is a designated successor to the queen in *R. marginata,* as in other primitively eusocial species. The alternative to there being a designated successor would be that there are a few individuals in the colony who are hopeful reproductives, and the successor is decided from among them somewhat randomly when the queen is removed from the colony. The swiftness with which the potential queen establishes herself in the colony, and the fact that she hardly ever faces any challenge from the rest of the workers, led us to ask the question if there is a designated individual who is obvious to all the wasps in the colony as the successor to their queen, though we cannot identify her using standard behavioural methods. This question is important and interesting because we cannot predict her using the parameters by which we can predict the potential queen in a typical primitively eusocial species like *R. cyathiformis* (Deshpande et al. 2006).

6.2 Question 2: How Does the Queen Signal her Presence and Reproductive Status to her Workers or, How Do the Workers Perceive their Queen?

We speculated that the *R. marginata* queen uses pheromones to regulate worker reproduction, since she is known to be a docile sitter. If the queen produces a pheromone, it should be an honest signal of her reproductive status, and thus the workers should perceive the presence of the queen as well as her reproductive status by such a pheromone.

While the first question addresses the mechanism of succession to power, the second studies how power is maintained in the *R. marginata* societies. In a society that seems to be arrested at a stage between typical primitively eusocial and typical highly eusocial states, these questions help us to gain interesting insights into how different factors contribute to the evolution of a high degree of co-operation and hence higher levels of eusociality.

7. The Cryptic Successor

Since we could not predict the identity of the potential queen in the presence of the queen, we considered the possibility of there being a 'cryptic successor' in *R. marginata*, who is "known" to the wasps, though she is not obvious to us. In order to test this hypothesis, we carried out the Q-PQ exchange experiment. Each experiment lasted for two days. We collected colonies and kept them in the lab. Prior to the experiment, all individuals in a colony were uniquely marked with spots of quick-drying, non-toxic enamel paints. On Day 1 of the experiment, we observed the colony for five hours. On the next day, we collected all the individuals in vials, and cut the colony into two halves, keeping about the same number of brood on both fragments. This was to ensure that the two fragments were balanced in terms of incentives for the workers to stay on the nest on re-introduction. The two fragments were indistinguishable with respect to the total number cells, largest larvae (L3), pupae and parasitized cells (paired t-test, $p > 0.05$). We then fixed these nest fragments on either side of a wire mesh partition put inside a closed wood and mesh cage (30 cm × 30 cm × 30 cm). The two halves were kept not more than 1 cm away from the mesh (Fig. 2). All the individuals were randomly assigned to one of the fragments

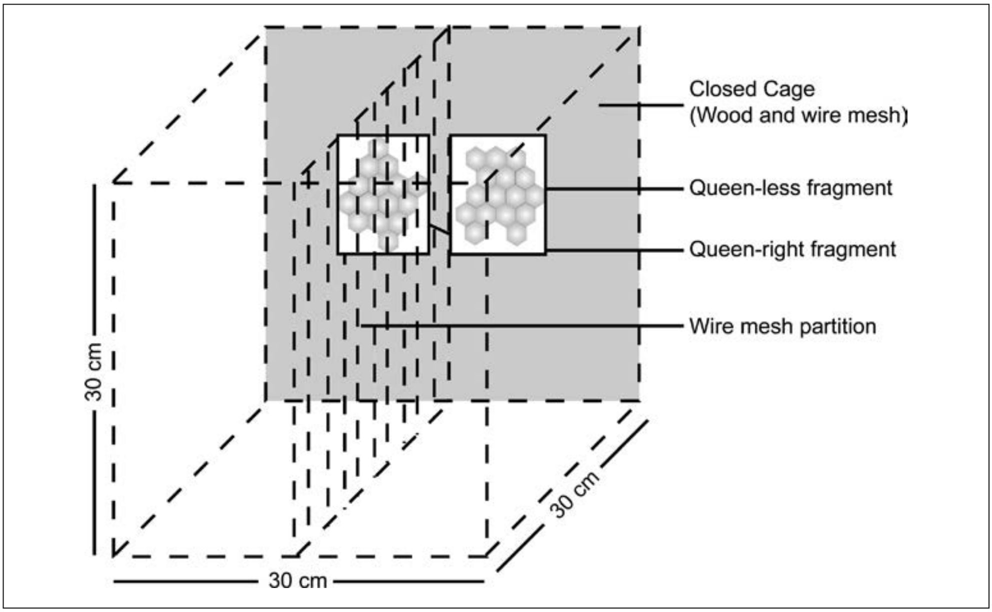


Fig. 2 The set-up of the Q-PQ exchange experiment

and were released on it, such that one side had the queen and half the set of workers (the queen-right side), while the other side had only half the set of workers (the queen-less side). The nest was observed in this set-up for two hours (Session 1). A potential queen became obvious on the queen-less side during this session by her heightened aggression, and was designated as PQ1.

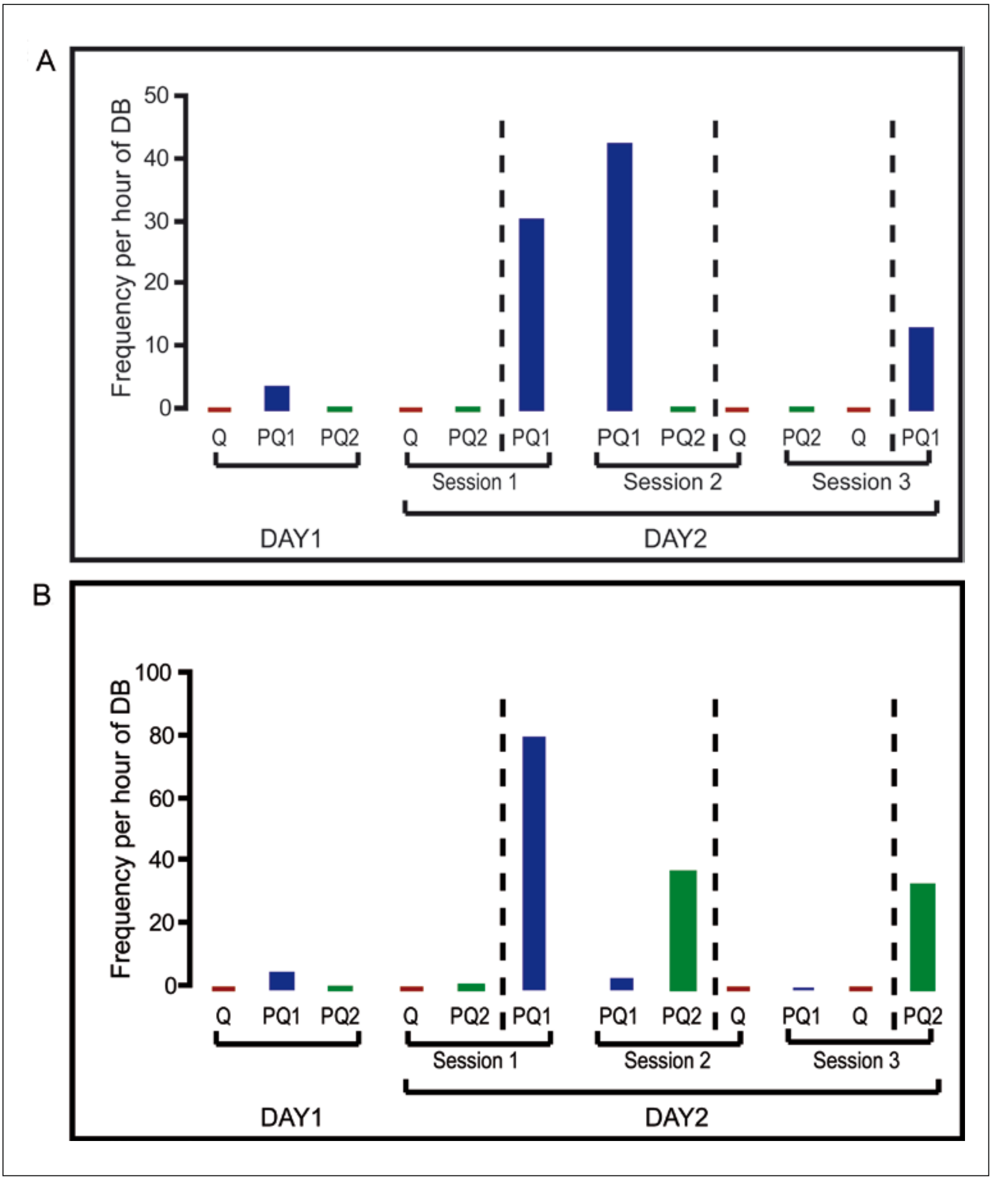


Fig. 3 Rate of aggression shown by the queen and potential queen(s) in the Q-PQ exchange experiment. The figure shows two sample nests: (*A*) a colony where PQ1 was the cryptic successor and (*B*) a colony where PQ2 was the cryptic successor.

At the end of the session, the queen and the PQ1 were collected from their respective sides and were released on the opposite sides of the mesh, such that the former queenless side now became queen-right and *vice-versa*. This was termed as a Q-PQ exchange. The logic of the experiment was that if there is a cryptic successor, there is a 50 % chance that she would be on the queen-less side in session 1, and thus would become the PQ1. Since the designated successor should be acceptable to all individuals in the colony, the PQ1 should continue to the potential queen when taken to the other side of the mesh. However, there is also a 50 % chance that the designated successor is on the queen-right side in session 1. In this case, the PQ1 should not be acceptable to the workers on the original queen-right side, and there should be a tussle between PQ1 and the cryptic successor after the first Q-PQ exchange. Hence we expected to see a PQ2 in about half the colonies in this experiment (prediction 1). Since the PQ2 should be acceptable to all the workers for us to conclude that she is the cryptic successor, we carried out a second Q-PQ exchange, with the PQ1/PQ2 as the case might be, and the queen. We expected the potential queen to be able to maintain her status in session 3, and no evidence of a PQ3 (prediction 2), if there is indeed a cryptic successor in *R. marginata*. We did eight such experiments, and in three of them, we did not have a PQ2, while in the remaining five, we had a PQ2, but in not a single of the eight experiments did we ever have a PQ3 (Fig. 3). This upheld both our predictions (FISHER's exact test: 5/8 is not different from 4/8; $p = 0.49$), and we concluded that there is indeed a cryptic successor in *R. marginata*, who alone is acceptable to all wasps as the rightful successor to the queen (BHADRA and GADAGKAR 2008).

8. We Know that the Wasps "Know"

Over and above the fact that we found evidence for a cryptic successor in *R. marginata*, one other aspect of the results was extremely fascinating and unexpected. Our expectation at the beginning of the experiment was that even if the PQ1 lost to a PQ2 in some colonies, there would be some tussle visible between the individual who had already become a potential queen and established her supremacy on one half of the colony, i. e., the PQ1, and the new individual who would suppress her and become the potential queen in the other half of the colony, i. e., the PQ2. However, contrary to our expectations, the PQ1 in the three colonies where she held her status on both sides, and the PQ2 in the remaining five colonies, did not receive a single act of aggression from any other worker when they were exchanged to the new side (Tab. 1). More interestingly, the PQ2 did not receive any aggression at all from the PQ1 in session 2, when they faced each other for the first time. In fact, in one of the five colonies, the PQ2 showed two acts of aggression to the PQ1, but she never received back any aggression. In all other cases, the PQ1 seemed to shy away from the PQ2, even before the PQ2 stepped up her aggression in the beginning of session 2. In three of the five experiments, the PQ1 received aggression in Session 2; only in one colony, two acts of aggression received were from the PQ2, while in the rest of the cases, the aggression towards the PQ1 was directed by other workers. Thus we conclude that the PQ1 "knew" the successor on exchange, and hence refrained from claiming the status of the potential queen. We therefore claim that the identity of the queen's successor is "known" to the wasps (BHADRA and GADAGKAR 2008).

Tab. 1 Subordinate behaviour shown by the potential queens in the queen-right colony, and in the three sessions on day 2. The potential queens did not receive a single act of aggression in the sessions in which they were the potential queens (marked in bold).

	DAY 1		DAY 2.1		DAY 2.2		DAY 2.3	
	PQ1	PQ2	PQ1	PQ2	PQ1	PQ2	PQ1	PQ2
V519	0.70		**0**		**0**		0	
V614	0.35		**0**		**0**		0	
V800	0		**0**		**0**		0	
V532	0	0	0	**0**	0	**0**	0	**0**
V586	0	0.70	0	**0**	1.2	**0**	0	**0**
V621	0.35	0.35	0	**0**	4.2	**0**	0	**0**
V638	0	0	0	**0**	0	**0**	0	**0**
V657	0.35	0	0	**0**	7.2	**0**	0	**0**

9. Is the Successor Really Cryptic?

We had used one-to-one interactions in the colony to build dominance hierarchies (Fig. 4) and to check if we can predict the identity of the potential queen on the basis of interactions. Since this gives a linear and hence partial view of the interaction patterns in the colony, we decided to use network analytical methods to check if the cryptic successor occupies a special position in the social network of the colony. We used data from twelve queen removal experiments to draw up 24 networks based on dominance-subordinate, one queen-right and one queen-less network for each colony (Fig. 5).

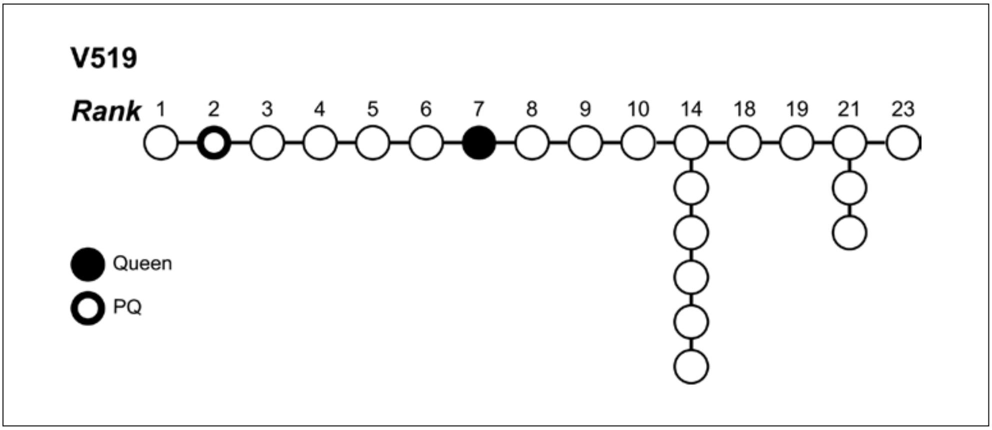


Fig. 4 The dominance hierarchy of colony V519, based on data from the queen-right colony, showing the queen as black, and the cryptic successor (PQ) as a black ring. The white circles are the remaining workers in the colony.

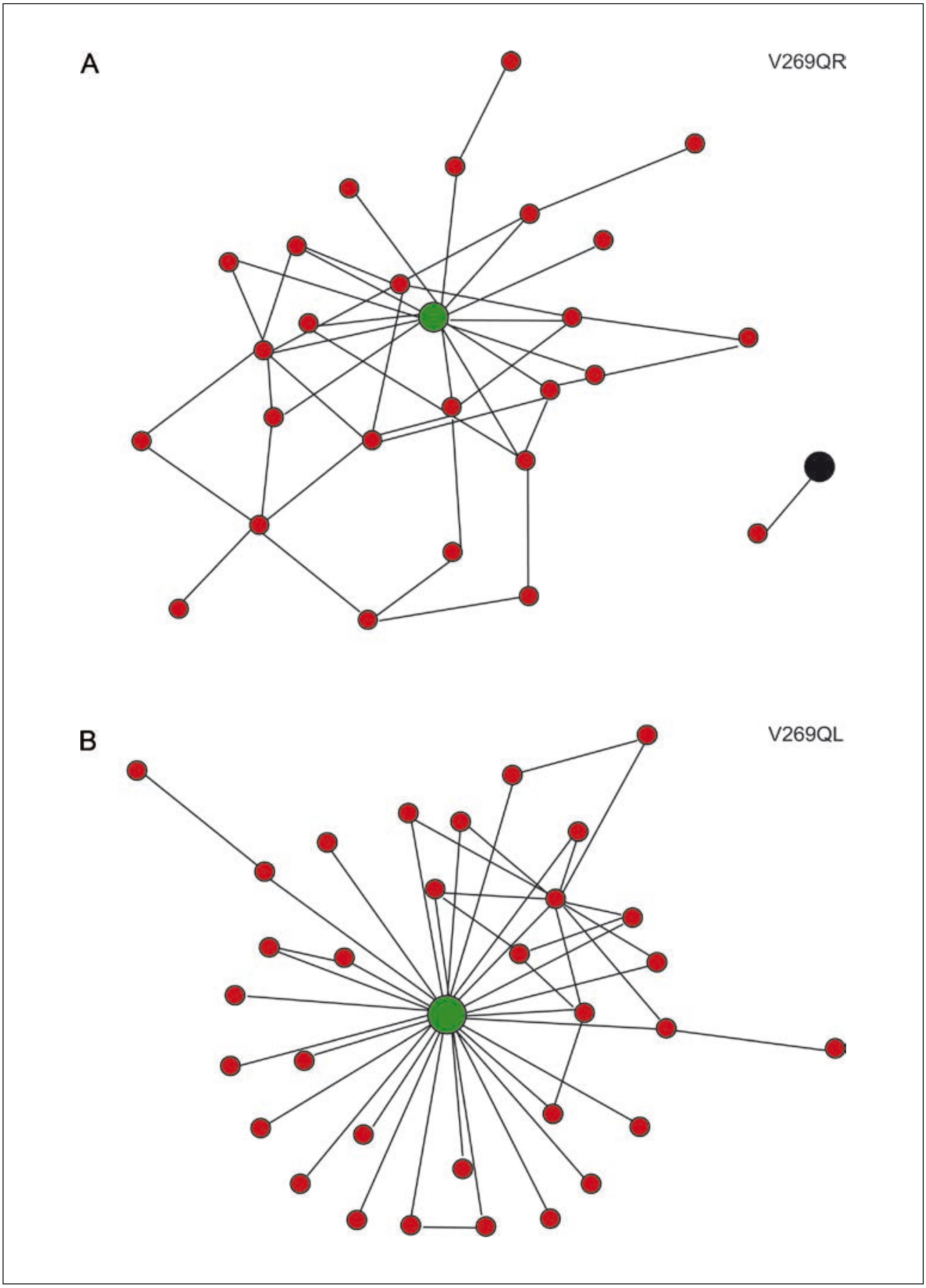


Fig. 5 Social networks of *R. marginata* based on dominance-subordinate interactions, with the queen marked in black and the PQ marked in green. The two networks shown here are (*A*) a queen-right network and (*B*) a queenless network.

We used the following local and global parameters to compare these networks:

- **Degree** (D): The D of a node is the number of direct neighbours of the node.
- **Average path length** (d): The d of a graph is defined as the mean distance between pairs of nodes. For nodes i and j, their distance is defined as the length of the shortest path between them (length meaning the number of links on the shortest path connecting the two nodes). The average characterises the whole network.
- **Clustering coefficient** (CL): The CL of a graph node quantifies how densely its direct neighbours are connected to each other. In other words, it is the number of links between its neighbours divided by the maximum number of links possible between them. It can be averaged over the whole graph if one wants to provide a global network measure. While calculating for the whole graph, it can be weighted by the size of the neighbourhood of each node; we used this as the "weighted overall" version (see UCINET, BORGATTI et al. 2002).
- **Network Centrality Index** (NCID): We calculated the degree-based network centrality index (NCID) for unweighted and undirected networks. This simply measures the number of links incident upon a node. Note that network centrality, expressed in percentages, is maximal (100 %) if a central node is directly connected to all other nodes.
- **Small World Character** (SW): The SW of a network is the ratio of the clustering coefficient (CL) and average distance (d) of the network. In regular graphs (where each node has exactly n neighbours, like on a lattice), both CL and d are high. In random networks, both measures are low. Small world networks are characterised as having mixed properties of the two, i. e. relatively high clustering but relatively low average distance. Thus, a high CL/d ratio (denoted by SW) indicates that the given network is more "small world-like" (WATTS and STROGATZ 1998).

The results were rather fascinating. The queen-right networks of *R. marginata* were significantly different from the queen-less colonies in their centrality and average path length (MANN-WHITNEY U test, P = 0.00), but were comparable in terms of their small-world char-

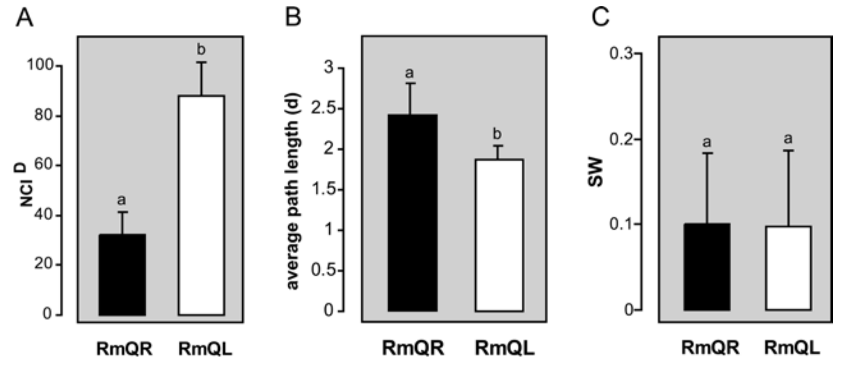


Fig. 6 The comparisons between queen-right and queen-less networks of *R. marginata* based on (*A*) NCI^D, (*B*) d and (*C*) SW.

acter (Fig. 6). The queens did not emerge as prominent nodes in the queen-right networks, and in some colonies, they were totally absent from the largest cluster of the networks, as they had not participated in any dominance-subordinate interactions.

The most fascinating result was that some of the queen-less networks were star-shaped (100 % centrality), with the potential queen being at the centre of the network. This result was so interesting because star-shaped networks are predicted in theory, and have been believed to be impossible in social groups. Hence this was the first example of a star network in a social system. It was also fascinating that this drastic change from a "democratic" queen-right network to an "autocratic" queen-less network happened due to the loss of a node (the queen) that did not feature to be important in the original network (Bhadra et al. 2009). However, though our results were quite interesting from the perspective of social network theory, we were unable to predict the identity of the cryptic successor in the queen-right network, as she did not occupy any unique position in the social network of her colony. But this study opened up a plethora of questions that could be addressed using the tool of social network analysis, some of which might even help us to identify the cryptic successor in the future.

10. Is the Queen Pheromone Volatile?

Considering that the queen uses a pheromone to suppress worker reproduction, there are several ways in which she could spread her pheromone among the workers. Two kinds of pheromones are generally known in the social insects – volatile pheromones like the queen mandibular gland pheromone, that is released in the air, and this perceived by the workers, and non-volatile pheromones that are present on the cuticle of the queen in the form of cuticular hydrocarbons, that are typically perceived by contact. In order to test if the queen pheromone is volatile or non-volatile, we carried out the mesh experiment. As in the case of the Q-PQ exchange experiment, nests were divided into two and placed on either side of a wire mesh partition. We carried out 22 such experiments, and in each of them a potential queen was obvious by her heightened aggression on the queen-less side of the mesh. The potential queens went on to develop their ovaries and lay eggs within a few days. In some of the experiments (12) the queen was taken from the queen-right side and released on the queen-less side. The potential queen soon reduced her levels of aggression to levels similar to what she showed on the normal colony, and a new potential queen established herself on the now queen-less side. This clearly showed that the potential queens failed to perceive the presence of their queens across the mesh partition, which is consistent with the idea that the queen uses a non-volatile pheromone to signal her presence to the workers (Sumana et al. 2008).

11. Is the Queen Perceived through Physical Interactions?

If the queen pheromone is non-volatile, the most likely possibility is that the queen is perceived by the workers through physical interactions with her. Here we refer to the queen pheromone as the signal. Since the queen has to reinforce the signal from time to time, it must have a finite decay time. We considered three parameters to build a model for understanding the dynamics of the communication:

- Decay time (t_d): the time needed for the queen signal to decay.
- Average signal age (t_a): the average age of the queen signal present with the PQ at any instant of time (and therefore at the time of queen removal).
- Average realisation time (t_r): the average time taken for PQ, after queen removal, to realise her absence.

The PQ should realise the loss of the queen at the instant of time when the queen signal present with her decays. Hence these three parameters are related as:

$$t_r = t_d - t_a \qquad [1]$$

Since the average age of the pheromone with the PQ at any instant of time cannot exceed the decay time of the pheromone:

$$t_a \leq t_d \qquad [2]$$

Here we estimate the realisation time both directly by observation of the behaviour of the PQ upon queen removal as well as indirectly by experimentally estimating t_d and t_a and using the above equations. If the queen transmits her pheromone by physical interactions, the realisation times estimated directly and indirectly should match.

We used data from 50 queen-removal experiments available in the lab for this analysis. First, we needed to know the value of the realisation time of the potential queen. We considered the first 30 minutes' data after queen removal from these experiments. The rate of dominance behaviour (DB) of the potential queen in this half hour was compared with the rate of DB on the entire day in the queen-right colony, and was found to be significantly higher. Hence we concluded that the potential queen realizes the absence of the queen well within 30 minutes of queen removal, and the experimental realisation time was fixed to be 30 minutes.

12. Direct Physical Interactions

In 26 out of 50 colonies the PQ did not interact with the queen of her colony even once in the 5 h of observation on day 1. This means that in these colonies the potential queens did not receive the queen pheromone for at least 5 h. Nevertheless, they did not behave as if the queen was absent. We conclude therefore that the queen pheromone cannot have a decay time of less than 300 min. Hence we set the decay time for the queen signal (t_d) to be a minimum of 300 min.

Pooling data from all the 50 colonies, we obtained the average rate of interaction of potential queens with their queens to be 0.28 ± 0.39 per h, i. e., on an average one interaction in 213 min. Hence the t_a was calculated to be 213/2 = 106.5 min. Putting these values in our model, we obtained a t_r of 300 − 106.5 = 113.5 min, which was much higher than the experimentally obtained realisation time of 30 min. Hence we concluded that direct physical interactions do not suffice for the workers, or at least the potential queen, to perceive the presence of the queen in the colony (Bhadra et al. 2007).

13. Relay Interactions

It is possible for two individuals to interact with each other through a third individual, i. e., through a relay mechanism. For example, in Figure 7, the queen interacts once in 50 min with B directly, but through C, she interacts with B once in every 30 min. Hence the shortest path between Q and B is not the direct connection, but the indirect connection through C. We considered this possibility for the communication of the queen's presence to the workers. Using the Dijkstra's algorithm, we calculated the shortest paths between all pairs of individuals, whether direct or indirect, and modelled information transfer by the shortest path in a set of simulations. In our models, the efficiency of interactions between the queen and the potential queen increased by 12.5 % on an average. We then used the data from the 50 colonies to check if relay was indeed being used by the wasps. All queens who had not interacted directly with the potential queens now interacted through relay, the highest rate being once in 340 min. Hence the signal could not decay before 340 min, and the t_d was fixed to be 340 min. Considering all 50 colonies together, the mean relay transmission time was 102.9 min. Hence the t_r was calculated to be $340 - 102.9 = 237.1$ min, which is again much higher than the experimentally obtained realisation time of 30 min. Hence we concluded that though relay can enhance the efficiency of interactions in the colony, it is not the mechanism by which the potential queen perceives the presence of the queen in *R. marginata* (Bhadra et al. 2007).

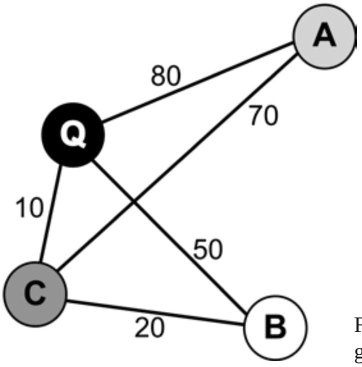


Fig. 7 An illustration to represent the interaction pattern in a group where indirect interactions can be effective.

14. Rub Abdomen Behaviour

Since it was obvious that the queen does not use physical interactions to signal her presence to the workers, we considered the possibility that the queen might be applying her pheromone on the nest surface, from where it is perceived by the workers. We considered this possibility because we had noted a specific behaviour that was shown mostly by the queen, in which she rubbed the tip of the ventral side of her abdomen on the nest surface while walking on the nest (Fig. 8). We hypothesized that she might be using this behaviour to apply her pheromone on the nest surface. We carried out focal behaviour samplings of the rub abdomen behaviour (RA) eight in nests of *R. marginata*, and calculated the fre-

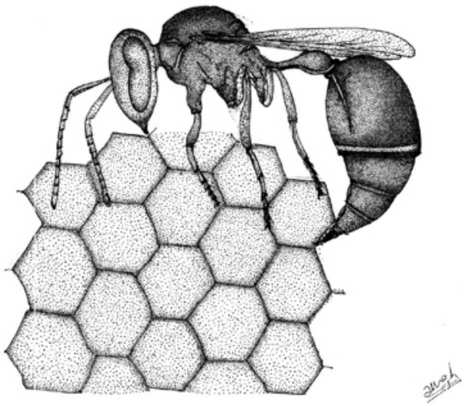


Fig. 8 An illustration to show the posture taken by a wasp for the rub abdomen behaviour. (Drawing: Dr. Thresiamma Varghese)

quency per hour of RA. The queen was found to be showing this behaviour most often, at a rate of once in 23 min. This fitted in quite well with the observed realisation time of 30 minutes, and hence we found support for our speculation that the queen applies her pheromone on the nest surface using the rub abdomen behaviour (Bhadra et al. 2007).

15. The Dufour's Gland

The most likely source of the queen pheromone could be a gland present in the abdomen of the wasp, opening near the sting. We considered the possibility of the Dufour's gland being the source of the queen pheromone, because it has been shown to be involved in nestmate recognition in Polistes (Dani et al. 1996a, b), among other functions like egg-marking pheromone, trail pheromones etc in ants. More interestingly, orphaned honeybee workers who lay eggs are seen to have Dufour's gland pheromones like their queens (Dor et al. 2005, Katzav-Gozansky et al. 1997, 2002, 2004). We carried out a bioassay using the potential queen to test the hypothesis that the Dufour's gland is the source of the queen pheromone in *R. marginata*. This experiment involved two individuals, one who was the observer, and the other who carried out the dissections. We observed a normal colony for half an hour, and then removed the queen and a random worker from the colony. A potential queen was seen to establish herself in all colonies in the second session. The experiment involved three kinds of treatments: queen's Dufour's gland extract, worker's Dufour's gland extract, and Ringer's solution. We used Ringer's to crush in the entire gland, as the use of an organic solvent would have disturbed the nest. In the third session, we applied either one of the two kinds of extracts or the Ringer's solution on the nest surface and carried out observations for half an hour. The potential queens were seen to reduce their aggression in the queen treatments, as they would have done if the queens had been returned to the colonies (Fig. 9).

However, they did not change their aggression in the other two kinds of treatments. Thus we concluded that the Dufour's gland is indeed the source of the queen pheromone in *R. marginata*. We then carried out GC-MS analyses of the queen and worker Dufour's

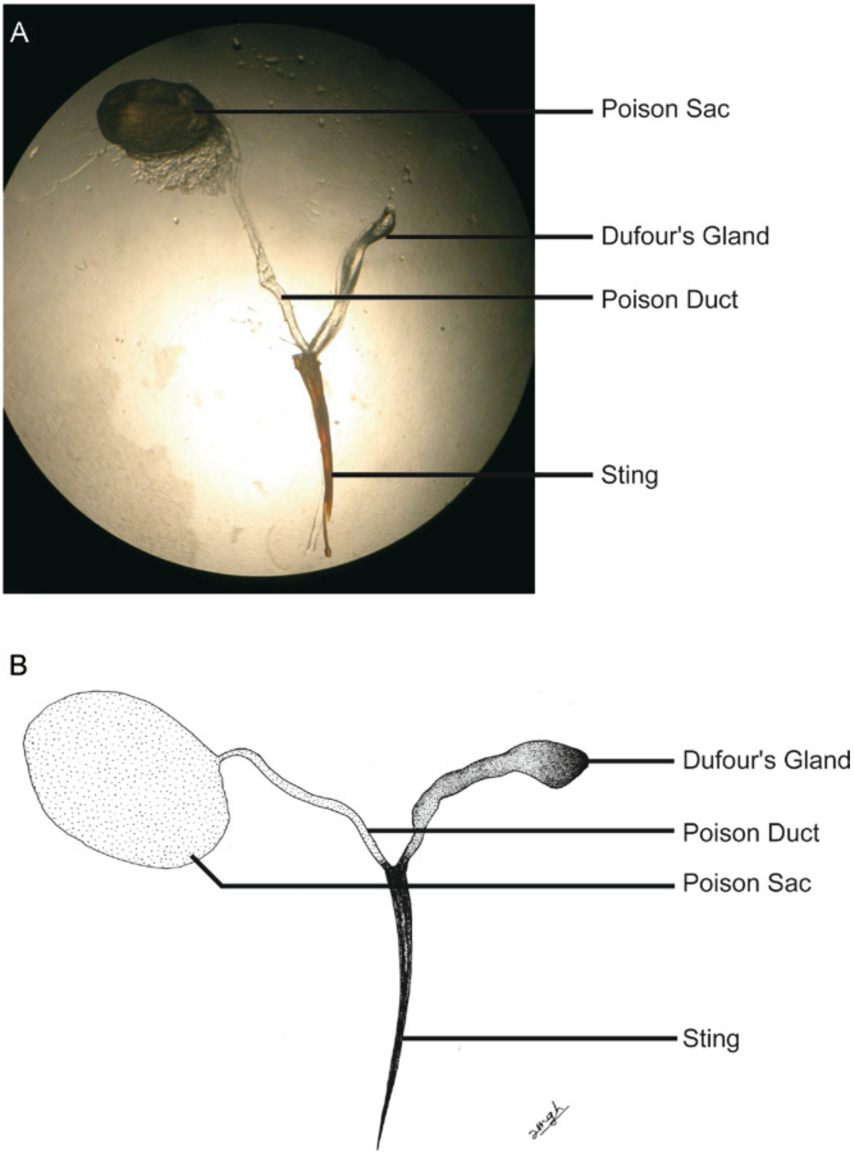
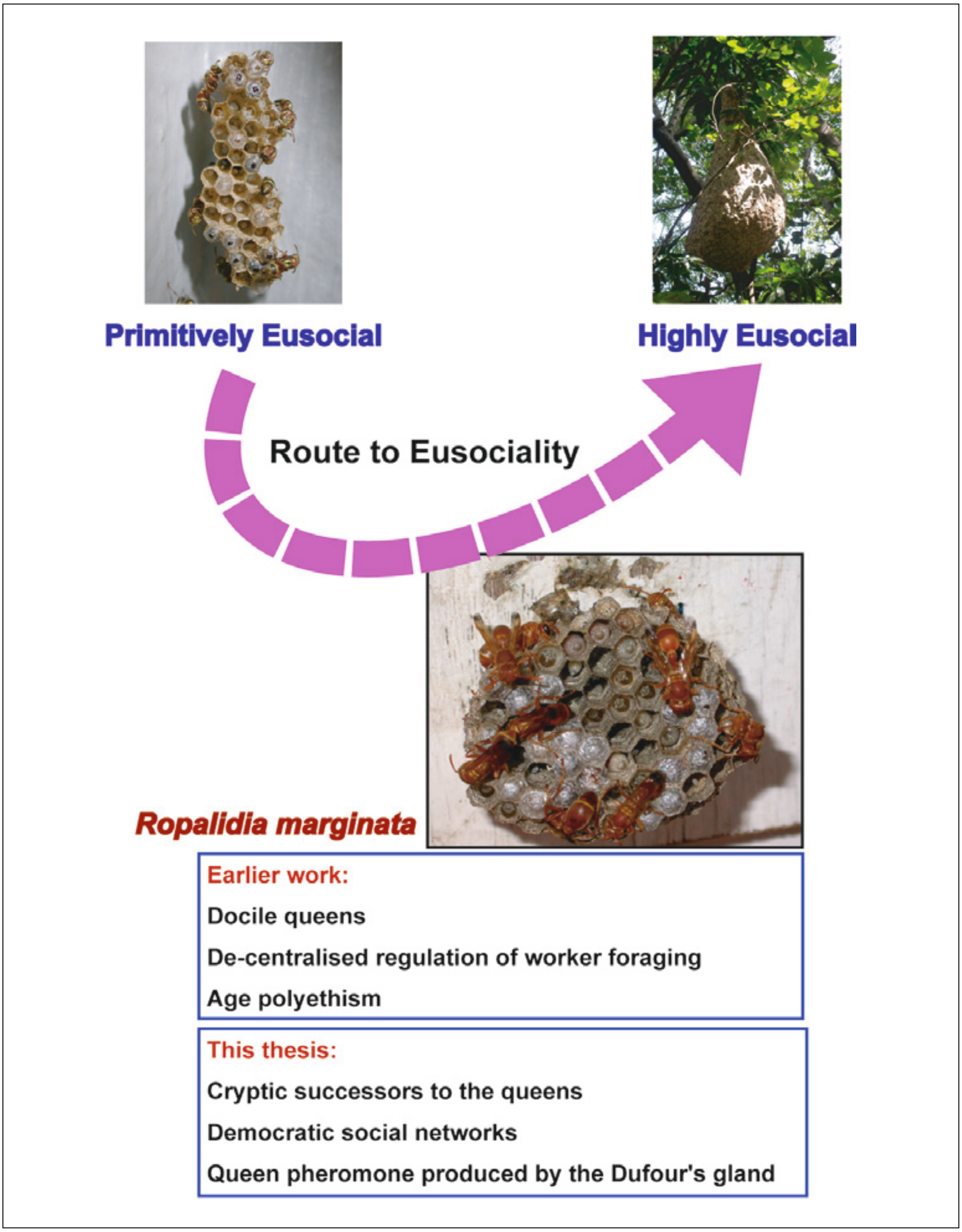


Fig. 9 A photograph of the dissected out Dufour’s gland in *R. marginata* (*A*) and a schematic drawing of the gland associated with the sting apparatus (*B*). (Photo: Aniruddha Mitra, Drawing: Dr. Thresiamma Varghese)

glands from six colonies, and the individuals in the two categories were classified separately, with 100 % correct classification by their Dufour’s gland profiles. This confirmed that the queen had a different chemical signature in her Dufour’s gland as compared to the workers, and this could thus be an honest signal of her reproductive status (Bhadra et al. 2010).

16. Towards the Evolution of Eusociality

R. marginata behaves more like a highly eusocial species than like a primitively eusocial one in various ways. The presence of a queen pheromone, which does not only serve to



Earlier work:

Docile queens

De-centralised regulation of worker foraging

Age polyethism

This thesis:

Cryptic successors to the queens

Democratic social networks

Queen pheromone produced by the Dufour's gland

Fig. 10 Towards the evolution of eusociality signal the queen's presence in the colony, but also acts as an honest signal that regulates worker reproduction (because the queen clearly uses no other means to control worker reproduction), is a major step towards a highly eusocial system.

Interestingly, the queen's pheromone in *R. marginata* seems to be produced by the Dufour's gland, which is known to be used for general functions like nestmate recognition in other wasps, but honeybee egg-laying workers of de-queened colonies mimic the queen's Dufour's gland secretion. So, the *R. marginata* queen seems to have acquired a chemical signature, which is similar to those of the egg-laying workers of highly eusocial species rather than the queens of primitively eusocial wasps (Dani et al. 1996a, b, Dor et al. 2005, Katzav-Gozansky et al. 1997, 2002, 2004). The queen's successor in *R. marginata* is a designated individual who alone is acceptable to all individuals in the colony, but unlike in other primitively eusocial species, is not obvious to observers on the basis of behaviour and anatomy. We have speculated that the wasps probably identify their queen's successor by some subtle cue like smell. This form of identification would be expected in a species with more evolved levels of sociality, because not only would the successors be required to evolve chemical cues that are signals of their potential to be future queens, but the workers would also have to evolve mechanisms of perceiving such a signal.

Moreover, the signal would have to be differentiated by the workers as distinct from the queen pheromone. A third factor by which *R. marginata* societies are different from the typical primitively eusocial *R. cyathiformis* societies is the democratic social network of its queen-right stage. Considering the various features of this highly fascinating society, we can probably characterize *R. marginata* as a "highly evolved primitively eusocial" wasp (Fig. 10).

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Structure of Navigational Memory in an Insect, the Honeybee

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With 5 Figures

> "Progress in science depends on new techniques, new discoveries, and new ideas, probably in that order."
>
> Sydney BRENNER

Abstract

Discoveries in biology require reliable data. Inappropriate methods may lead us astray. This simple insight is often overlooked as long as more appropriate methods are not at hand. Behavioural science is believed to depend on just the patience and dedication of the researcher. Careful observations and unbiased protocols are thought to provide us with all what we need to collect when studying animal behaviour. Such an opinion can in fact be rather dangerous because our senses may not capture the sensory world of the animal in question, we may not be able to keep our attention alive long enough, we may not realize the effects of selective attention and bias, and we may simple not be sensitive enough for the fine details and richness of animal behaviour. It is, therefore, indispensable to be critical about the methodological approaches and seek for objective ways to collect and record the relevant data. I want to illustrate these considerations in studies on navigation and communication in honeybees. It will be shown that wrong conclusions were derived from data collected by an inappropriate method (measuring vanishing bearing of displaced animals), and only the implementation of a rather sophisticated method, the harmonic radar, allowed us to uncover the mistakes we made before. I want also to sensitize our caution about the parsimony argument, the idea that formally simpler concepts of the processes behind animal behaviour are more likely closer to the neural mechanisms underlying a particular behaviour.

Zusammenfassung

Alle Entdeckungen beruhen auf zuverlässigen Daten. Diese einfache Einsicht wird leicht übersehen, wenn keine geeigneten Methoden zur Verfügung stehen, ein Umstand, der für die Verhaltensbiologie besonders relevant ist. Es ist ja nicht ungewöhnlich, dass wir Beobachter weder die sensorischen noch kognitiven Fähigkeiten haben, Verhaltensweisen von Tieren angemessen und quantitativ zu erfassen. Daher ist es gerade in der Verhaltensbiologie so wichtig, sich kritisch mit den verwendeten Methoden auseinanderzusetzen. Ich möchte diese Thematik am Beispiel der Forschungen zur Navigation und Kommunikation von Honigbienen darstellen. In diesem Bereich hat uns eine unangemessene Methode (die visuelle Bestimmung der Verschwindepunkte) in die Irre und zur Entwicklung von unzutreffenden Konzepten geführt. Erst der Einsatz einer geeigneten und objektivierenden Methode (das harmonische Radar) hat uns in die Lage versetzt, die notwendigen Daten zu sammeln. Über diese Daten will ich auf dem Hintergrund der früheren Beobachtungen berichten.

1. The Question, the Concepts, and the Methods

Animals as well as humans are not lost in the environment but appear to know where they are and where to go, fly or swim next. The question addressed in this chapter is to elucidate what is meant with ‘know’. Animals may be guided in their motor programs by sources of information emanating from the goal they are heading to. Odours released from food or a sexual partner is such a source. Visual gradients like the brightness and spectral composition of the ambient light may lead an animal in a particular sector of the environment. The goal may also be seen as a beacon and steered to. In fact, all senses contribute to orientation in space, and often it is the combination of several stimulus modalities that guide an animal along a gradient or toward a location. In these conditions the knowledge lies in the association between the guiding stimuli and the motor programme, a knowledge that might be innate, learned or combinations of these two basic forms of information for animal behaviour.

The guiding posts leading an animal to a particular location may also consist of spatially distributed objects. In these cases the animal has to recognize and discriminate objects, and has to learn the arrangement of these objects as seen from a fixed vantage point. Steering toward that vantage point and thus to the known place for recognizing the goal may be performed by sequential steps of reducing the deviation from the learned arrangement of the objects. It has been argued that, e. g., in the case of insects close to the entrance of the colony or a feeding place, this form of stepwise improvement of matching between the learned view of objects at the vantage point may even be retinotopically fixed, and memory may exist simply as a form of imprint of the picture into fixed retinal positions (Cartwright and Collett 1983). Such a relocation strategy at a vantage point and thus the goal is considered to be computationally rather simple, and therefore quite attractive for the modelling of animal orientation, but it is questionable whether it is indeed a strategy used by any animal under natural conditions. Particularly the notion that the memory of object arrangements is retinotopically fixed is rather unlikely even in an insect like *Drosophila* flying stationary in an arena (Heisenberg 1995). I shall refer to the above mentioned behaviours of guiding motor programmes as *orientation* and distinguish it from *navigation*.

Navigation in my understanding requires steering toward a goal without having access to signals emanating from the goal itself or its immediate surroundings. In such a situation animals refer to a memory of spatially related guiding posts that do not need to be accessible at the location where decisions are being made. The processes behind navigation can be multi-fold. One possibility is that navigation results from an extension of the local matching procedure mentioned above. Animals may learn object arrangements from sequences of several to many ‘vantage points’, and may find back to the goal by retrieving the memory of sequences of picture memories. Each of the vantage points may allow the animal some discrepancy between the learned and the actually experienced object arrangement, und thus the animal may find back to the final goal by sequentially improving the matching allowing it to be placed outside of the exact sequence of picture memories.

Since animals always start their explorations of the environment at a particular location it is this location that they may want to return to. A typical example is a mammal, a bird or an insect that begins its exploration at the nest site. Returning to the nest might be accomplished solely on the basis of internal sources of information. The animal may register and store the rotatory and translatory components of short sectors of its exploratory path and return to the starting point by integrating these components together with an addition of an angle of 180°. This strategy is called path integration or dead reckoning, and has been found in animals as divergent as spiders and humans. The rotational component is usually measured with respect to a far distant signal e. g. the sun, moon or stars which has the advantage that movement induced parallax of the signal does not needed to be taken into account. Distance travelled needs to be measured rather precisely, and walking animals like ants are known to somehow count their steps (Wittlinger et al. 2006), whereas flying insects like the bee measures distance visually by the flow field of the structure of the ground (visual odometer, Esch et al. 2001, Srinivasan et al. 1996).

Path integration is considered to be essentially an egocentric form of navigation because the information may come solely from internal sources. If the animal is passively dislocated to an unexpected site it will not be able to find its way back but rather will apply the information acquired during the last period of path integration behaviour. This property offers a very simple and reliable test for an egocentric reference based on path integration. Animals are transported to a release site, and they will head off in a direction predicted by the path integration process of the immediate past. It has been argued for insects that egocentric path integration might be the only or the primary form of navigation (Wehner and Wehner 1990). However, it needs to be kept in mind that such a simple understanding of path integration can lead astray if animals learn to relate its path integrator to landmarks (see below). The critical test will be whether a displaced animal finds back to its goal or is lost. Certainly, there is the possibility that egocentric path integration and matching of picture memories may be combined, and this seems to be the current notion behind the understanding of insect navigation.

There is an alternative to this idea. Exploring animals experience the environment as a stable and reliable distribution of spatially related objects. These objects may be locally restricted, extended or at such a far distance that their appearance does not change during exploration. The latter ones can be earth bound as for example the horizon or it can be the sun, the moon, the earth magnetic field or steady winds. If the animal compensates the movement of the sun with an internal clock, the sun will also provide a stationary reference system. Local and extended objects (we shall call them gradients) are embedded in a frame of compass directions and the information provided by path integration. Furthermore, local objects and gradients may be experienced during exploration in sequence with certain spatial relations. These spatial relations change during exploration, and it is this change that may provide information about the spatial layout of the environment. An animal trying to learn these spatial relations needs to associate a multitude of sequentially experienced parameters within the frame of compasses and additional reference systems possibly including egocentric ones. It is still unknown how animals are able to create such an allometric, geocentric internal representation of space that is often referred to as a cognitive (or mental) map (Tolman 1948).

The structure of a cognitive map would allow an animal to localize itself within the environment irrespective of how it reached the current location, and to perform novel paths to an intended goal along a short connection (novel shortcut). Such a behaviour requires the capacity of spotting the current location and to estimate the direction and distance to the intended goal. Additional properties of a cognitive map can be assumed. The animal may be able to decide between two or more goals on the basis of the expected outcome when arriving at the goal, it may qualify these goals (nest, feeding sites, higher or lower ranking feeding or nest sites), and may make its decision dependent on its own motivational state.

I shall provide evidence that honeybees appear to navigate according to a spatial memory that can be best conceptualized as a cognitive map if all evidence of navigation experiments is taken together. I will also ask which properties their navigational memory has, and how it is used both for navigation and communication.

Traditional thinking about navigation in insects was based on the notion that a tool box of rather simple sensory-motor routines is at the animal's disposal and their stepwise application may lead to the solution of isolated, rather independent navigational tasks. These robot-like concepts arose from experiments based on the analysis of route learning, sometimes even at such a small scale that target-related orientation – rather than navigation – was tested (see above). The focus on small scale orientation in flying insects like the honeybee was unavoidable in the past because no methods existed until recently to follow the flight path over distances of several hundred meters. Such a method exists now, the harmonic radar (Riley et al. 1996), and data collected with this new technique have revolutionized our thinking about honeybee navigation (Fig. 1, Menzel et al. 2005, Riley et al. 2005).

In addition to the methodological problems, a conceptual limitation hindered our understanding of navigation in honeybees. Bees were trained to fly along a route from the hive to the feeder. Under these conditions bees learn the vector components of the route by their path integration process. When they are transported to an unexpected release site they follow this vector memory during their initial flight path because it is the only active form of working memory controlling navigation at this moment. Since only the initial flight path could be observed without the harmonic radar, and only the vanishing bearings of the bees were determined it was concluded that bees navigate only with respect to their egocentric path integration process and apply learned vectors (Wehner and Menzel 1990). This conclusion was based on inappropriate data. Meanwhile we know that the conclusions were incorrect.

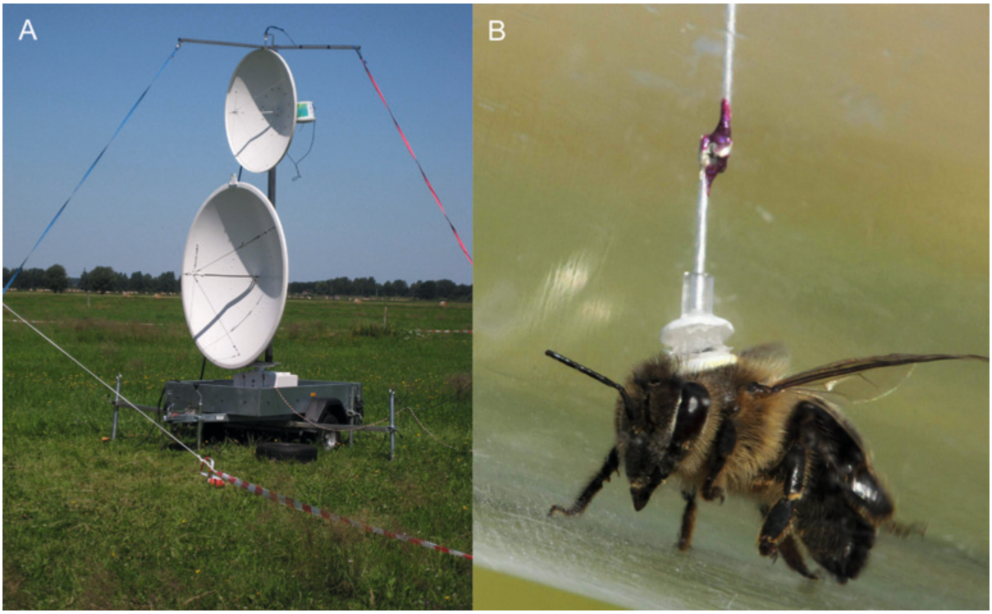

Fig. 1 (*A*) The harmonic radar system consists of a sending radar beam (large antenna) and a receiving antenna connected to an amplifier which detects the first harmonic of the radar wave. The transponder carried by the bee on the thorax (*B*) emits this harmonic when it receives the radar pulse. Bees have no problems flying with the transponder. The two radar antennae rotate once in three seconds providing a radar paint (measurement of the transponder) every 3 s. The system can detect bees over a distance of up to 1 km. (*B*) A bee carrying a transponder.

One may ask why the weakness of the data and the undue conclusions were not realized for quite some time since a prediction of this conclusion was not met by navigating bees and this was known to us already at the time the concepts were developed, namely that bees are not lost as predicted when they were transported to an unexpected release site. The reason lies in the fact that the results from vanishing bearing measurements for route trained bees fitted so well the simplistic concept developed on the assumption that bees possess only egocentric vector information and close-up picture matching.

There was an additional argument in favour of the simplistic interpretation. Bees communicate the vector, distance and direction, to a food source, a potential nest site and other locations e.g. places of water and resin using a ritualized movement, the waggle dance (von Frisch 1965). When a bee performs a waggle dance inside the dark hive on a vertical comb it translates the direction of the outbound flight relative to the sun into an angle relative to gravity during the waggle phase. Flight distance is encoded in the speed with which the waggle runs are performed. Bees attending a waggle dance (called the recruits) apply this vector information in their outbound search flights (Riley et al. 2005) indicating that they have just decoded the vector message of the dance. It was tempting to conclude that bees refer just to the experienced or the communicated vector information and nothing else. I will show below that this is not so. Dance communication in bees offers a window into their knowledge about their navigational space, and the new data on the integration of own navigation experience of recruits and the information gathered from dance communication have changed our understanding of the structure of memory bees refer to when navigating.

2. Experimental Data

2.1 Path Integration: An Egocentric Strategy?

When a bee leaves the hive the first time in its life or when the hive has been moved to a new place it performs one or several orientation flights. During these flights it does not visit flowers but appears to collect information about the environment of the nest. Using harmonic radar Capaldi and others (2000) showed on the basis of a few exploratory flights that bees keep the trip duration in consecutive orientation flights rather constant, but fly faster during the second and third flight, so that the later flights appear to cover a larger area than the earlier flights. Capaldi observed in addition that successive flights are typically restricted to a well-defined, narrow sector around the hive, an observation that could not be confirmed by new radar measurements. The new data indicate that orientation flights provide bees with the opportunities to become exposed to different landscape features (including the hive's position) from different viewpoints, supporting the view that they may store landscape information in a progressive fashion.

It has been assumed that bees control their orientation flights only by path integration but our recent experiments show that they are able to fly back to the hive if they are transported to a release site within the explored area after they have returned to the hive. Since the memory involved in path integration is most likely set to zero after return to the hive bees must have learned already features of the landscape that allow them to localize themselves relative to the hive. This interpretation is supported by the finding that bees transported into an area they had not explored do not return to the hive or only after long search flights. These data clearly indicate that path integration during exploratory flights are connected to learning about the features of the landscape possibly leading to an allocentric rather than pure egocentric reference.

2.2 Remembering Where to Go (Learning and Applying Flight Routes)

Foraging honeybees usually follow straight flight trajectories to and from specific locations (e. g. a feeding place) and the hive. If they are caught at the moment they depart from the hive, and then are released at different spots in the field, they vanish in the direction they would have taken if they had not been moved to the release site, meaning that they fly in the correct compass direction but along a false route relative to the goal they were originally travelling to. They perform in a similar manner when caught at the beginning of their homeward flight at the feeder. Once again, they fly along the pre-displacement compass direction, thus along a false route with respect to the actual location of the release site and the hive. All four motivations of flight directions were tested (arrival and departure at hive and feeder respectively), and this rule applies equally well (Menzel et al. 1996). Since the bees' compass bearings in this type of experiments resemble the global vectors observed in desert ants, it was concluded that honeybees also use vector memories from path integration mechanisms that develop through their regular flights, and these may be the only memories they refer to when released at an unexpected site. Several findings argue against this conclusion.

(*1.*) It was assumed that the vector memory is set to zero when the animal has arrived at the intended goal (hive or feeder). This is not the case in foraging bees. If an animal is displaced immediately after the arrival at the hive or the feeder it will continue to fly in the same direction as it was flying just before capture, however, the flight direction is less accurate and not all animals perform these directed flights. This observation indicates that indeed working memory of the flight vector becomes weaker after its application but is not fully erased. It was also shown that keeping the animals restrained in a dark box before release, flight vectors become less accurate, and animals collected after departure may switch to a feeder directed flight after kept caged for an hour (Dyer et al. 2002).

(*2.*) Flight vectors are not independent of prominent extended landmarks. If bees were trained for example along a row of trees and bushes and were displaced to a further distant release site they steered closer to the tree line already during the initial part of their flight. It has been observed already by von Frisch (1965) that bees perform rather stereotyped flight routes relative to extended landmarks. Bees also relate the direction relative to the sun with reference to extended landmarks when the sky is fully overcast (von Frisch 1965, Dyer and Gould 1981), a behaviour probably indicating that they have calibrated the sun compass relative to extended landmarks. These and other data clearly show that landmarks are learned during route flights, and bees are not blind to the spatial relations of landmarks. Furthermore, bees flying according to the vector information stored in their working memory when released at an unexpected site adapt their vector flight components to landmark features (Menzel et al. 2005) indicating that they register the mismatch between the actual experience after displacement and their expectations about landmarks if they were not displaced.

(*3.*) Bees do not need to be trained along a route for successful homing. Consider the following experiment (Menzel et al. 2000). One group of bees was trained to forage on a stationary feeder placed 300 m away from the hive, and another group was trained to forage on a close feeder (10 m distance) that rotated around the hive. Hence the foragers from the latter group had not learned a flight vector connecting the hive and a fixed, distant foraging location. However, in spite of lacking this experience, they returned home equally well from various possible directions, and nearly as quickly as the animals from the former group, which had experienced route training to one of the release sites. The results of this experiment could not be explained by reference to local navigation strategies, due to the lack of landmarks in the vicinity of the hive and the actual distance to the different released sites. The data also excluded the possibility that bees applied a random search strategy.

(*4.*) Local landmarks remind the bee about the appropriate home vector. Consider the following experiment (Menzel et al. 1996). We trained the same group of bees to two different locations in the morning and in the afternoon. Then we collected bees at the moment when they departed from the hive and transported them to the incorrect feeding site (in the morning they were released at the afternoon site, and *vice versa*). Here they vanished toward the hive indicating that they used the local landmarks to identify the location, switched motivation (they were collected when motivated to fly out to the feeder) and retrieved the correct vector memory for return flights to the hive. Obviously, the vector memory from route flights is rather flexible and can be replaced by context stimuli, but only if the local features of the landscape reminded them about a particular home vector. If the bees were released at a remote site (several kilometres away) they behaved as expected, they flew in the morning and the afternoon the respective vector they would have taken at the hive.

We then next asked which direction hive departing bees take when released half way between the morning and afternoon feeding sites, a site they had not been before. Half of these bees behaved according to their working memory, they flew into the direction which they would have taken from the hive if they were not displaced. The other half flew directly toward the hive. These latter bees changed their motivation (return to the hive) and applied a novel flight direction. At the time of publication of these data we hesitated to conclude that bees might have referred to map-like spatial memory structure although they behaved according to a geocentric reference system. We argued that bees may have flown a kind of a compromise vector between the two vectors from the morning and the afternoon feeding site because the release site may have resembled partially landmark properties of both sites. In retrospect this is rather unlikely because the distances between hive and feeder and between the two feeders were about 900 m, and local landmarks half way between the two feeders were very different from those of both feeding sites. Now on the basis of the overwhelming data from radar tracks (see below) we are less reluctant to look at these results as the first indication of a geocentric map-like memory structure in bees.

2.3 Communicating Where to Search

In the waggle dance a bee executes fast and short forward movements straight ahead on the vertical comb surface, returns in a semicircle in the opposite direction and starts the cycle again in regular alternation (each waggle dance involves several of these cycles, von Frisch 1965). The length of the single waggle-runs and the number of sound pulses increases with the distance flown to reach the source, and their angles relative to gravity correlate with the direction of the foraging flights relative to the sun's azimuth in the field and sun-linked patterns of polarized skylight. Thus, by encoding the visually measured distance and the direction toward the goal, the waggle dance allows colony members to share information about the distance and direction toward a desirable goal. Although Karl von Frisch used the term 'dance language', Premack and Premack (1983) correctly stated that the honeybee dances should not be called a language, based on the argument that there is no evidence that the bees can judge whether their dances conform to anything in their surroundings. This question can be addressed by asking whether a bee receiving information from the dance responds differently to the information depending on its own experience. Such experiments were performed meanwhile, and it was found that indeed the recruits behave differently according to their own experience in the environment (see below). The term 'language' is still misleading, because there is (as far as we know) no semantics or grammar in the ritualized movements of the dance, although the different context conditions in which dances are performed (foraging for nectar, pollen, water or resin and in a group of swarming bees) are interpreted by the recruits correctly. 'Indexical' or 'iconic' (Bermudez 2003) would be better descriptive terms to characterize the informational status of the dance.

Radar tracking experiments of dance recruited bees proved Karl von Frisch right (Riley et al. 2005). Recruits flew the vector communicated by the dance. In response to the Riley et al. (2005) paper it had been questioned whether recruits may have been attending dancing bees before and may have followed a foraging bee toward the feeding site before it was equipped with a radar transponders and tracked. Since we had a complete protocol of animals foraging at the feeder we could exclude the possibility that the tested animals visited the feeder before, but we could not exclude that such a bee may have returned to the hive without landing at the feeder. This is a realistic probability because very few recruited bees which were released at the hive with a radar transponder in fact landed at the feeder in our experiments. The reason for such a behaviour may lie in the fact that we did not use any odour marks. In our recent experiments we monitored recruits during dance performance, and excluded the possibility that the recruits had attended a dance before their flight was monitored with the radar (Menzel et al. 2011). We also never observed a recruited bee to exit the hive together with a bee that had performed a dance or a foraging bee at the feeding site. Thus recruited bees fly in isolation and follow the vector information transmitted in the dance.

It has been argued above that the navigational strategies applied by foraging bees cannot be fully appreciated if one assumes a hive-centred egocentric form of spatial memory. Instead, it seems that the orientation flights of young or reorienting bees lead to a map-like spatial memory that appears to be derived from repetitive exposure to the same landmarks from different viewpoints. Given this capacity and the fact that bees are recruited by a dancing bee only after they performed their orientation flights, it is tempting to assume that a bee attending a dance might recall from its memory of landmarks and homing vectors a corresponding outbound vector that is related to expected location. Under these conditions neither the dance behaviour nor the flight path of a recruited bee would be guided solely by the vector parameters but rather by an 'expectation' to arrive at a particular location. A component of this 'expectation' would be the route to be followed, as embedded in the map-like memory including sequences of landmarks. Indeed, already von Frisch (1968) stated that the effectiveness of waggle dances (in terms of successful recruitment) depends upon the foraging experience of the dance followers. When two groups of fellow bees visited two different (and currently exhausted) unscented feeding places, contact with a dancer indicating the accustomed goal is much more effective than contact with a dancer indicating the unfamiliar one.

Figure 2 (*A*, *B*) shows data that illustrate this effect. Bees that experienced a feeding site before they attended dances may fly either according to the dance information (toward FD, the feeder indicated by the dance, Fig. 2*A*) or resume their foraging behaviour at the experienced site (toward the former trained feeder, FT, Fig. 2*B*). We asked whether the decision for FD and FT depends on the number of waggle runs followed by the recruited bee and found that more information is needed by recruits to fly to FD. Bees that followed fewer waggle runs either flew to their experienced feeding site, returned to the hive after a short excursion or did not leave the hive. Following many waggle runs (in our experiment on average 25) allows for the possibility that a recruit may average over many waggle phases and level out their scatter, a property possibly of particular importance for the waggles after a left and a right return run. These waggle phases differ particularly strongly in their angle to gravity (de Marco et al. 2008). The variance of dance directions appears to be smaller than the variance of the waggle run directions (Riley et al. 2005), and thus it is quite possible that bees average across multiple waggle runs, however, this needs to be examined with specifically designed experiments combining video recording of waggle runs and radar tracking of recruits.

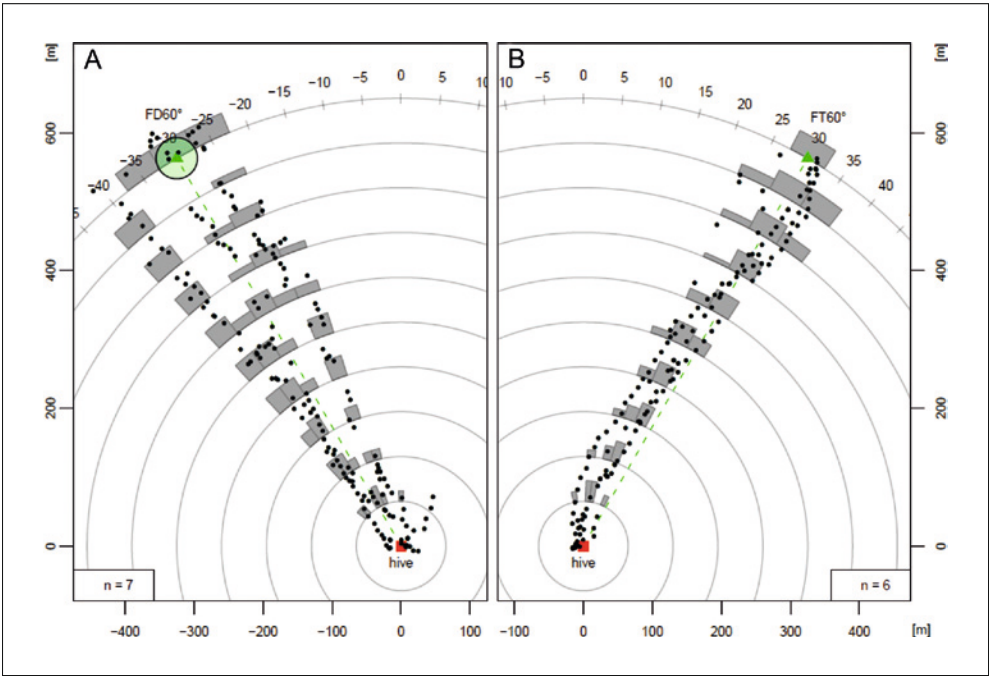

Fig. 2 Radar paints of recruited bees. The recruited bees were foraging for a few days at the feeding site FT (*B*). Then they experienced for a day that their feeding site FT did not provide any food anymore. A day later two other bees danced for feeder FD (*A*). The FT foraging bees attending the dance were equipped with a transponder when leaving the hive. Some of these bees flew toward FD (*A*), some of them to FT (*B*). The vectors toward FD and FT appeared under an angle of 60° as seen from the hive and had about the same distance (650 m).

Obviously dance communication involves a motivational and an instructive component, the former needing less information transfer, the latter more. The motivational component appears to remind a recruit about its own foraging experience. The signals included in this form of communication are certainly manifold (olfactory, gustatory, acoustic, vibratory). It is well documented that floral odours carried by the dancer stimulate recruits to leave the hive, and if the odour reminds them about their own foraging goals they return to these feeding sites (von Frisch 1965, Grüter and Farina 2009). Thus floral odours may have a particularly high potential to motivate recruits to take up their former foraging activity again, but this does not reduce the importance of the ritualized motor patterns of the waggle dance to encode the outbound vector to a new site. Since our experiments did not include any artificial odour marks the motivational component had to be triggered by the motor components of the dance and possibly pheromonal stimuli emanating from a dancing bee.

Given the rich navigational memory one may ask what is communicated by the waggle dance, just the outbound vector or the location of the goal. In the first case the amount of vector information accumulated by the recruit may have just to pass a threshold, and it will apply the respective information. In the latter case, the recruit would compare the expected properties of the indicated location with its own knowledge about this and potential other options for foraging according to its own experience, and reach a decision where to fly. Support for this latter view comes from experiments in which we recorded the flight paths of recruits that decided between their own foraging memory and the information they collected in dance communication (Menzel et al. 2011) (Fig. 3*A*, *B*). We found that recruits performed differently depending on the difference between their own foraging experience and the information transmitted during the dance. The parameter varied in these experiments was the angular difference between the vector pointing from the hive to the experienced feeding site of the recruits (FT in Fig. 2*B* and 3*B*) and the dance location (FD in Fig. 2*A* and 3*A*). If the angle was small (30°, Fig. 3*A*, *B*) fewer bees flew to FD than to FT as compared to a larger difference (Fig. 2*A*, *B*) indicating that they compare the potential outcome of their outbound flights and reach a decision already inside the hive.

Furthermore, some bees deviated from the course toward FD during their outbound flights and crossed over to FT (Fig. 3*A*; compare with Fig. 2*A*). Most importantly, after arriving at either FD or FT they may perform cross flights to the respective other location indicating that the spatial representation of the two sites are integrated in a common frame of reference. We conclude from these observations that both locations FD and FT are stored in spatial memory in such a way that bees are able to fly from one to the other location directly following a novel short cut. Bees cannot have been guided by beacons at the respective locations or by any particular structure of the environment (e. g. the profile of the horizon) because there was just nothing at FT, and FD was marked by a person sitting in front of s small feeder who could be seen by the bee at the best at a distance of < 50 m.

The terms ‘knowledge, compare, expect and decide’ used here do not refer to any high order mental processes but rather capture the neural operations in working memory that underlie decision making processes at the level of implicit forms of knowledge (a discussion of the first author’s perspective can be found in (Menzel 2007, 2009a). An essential component of such neural processes will be a common representation of experienced and

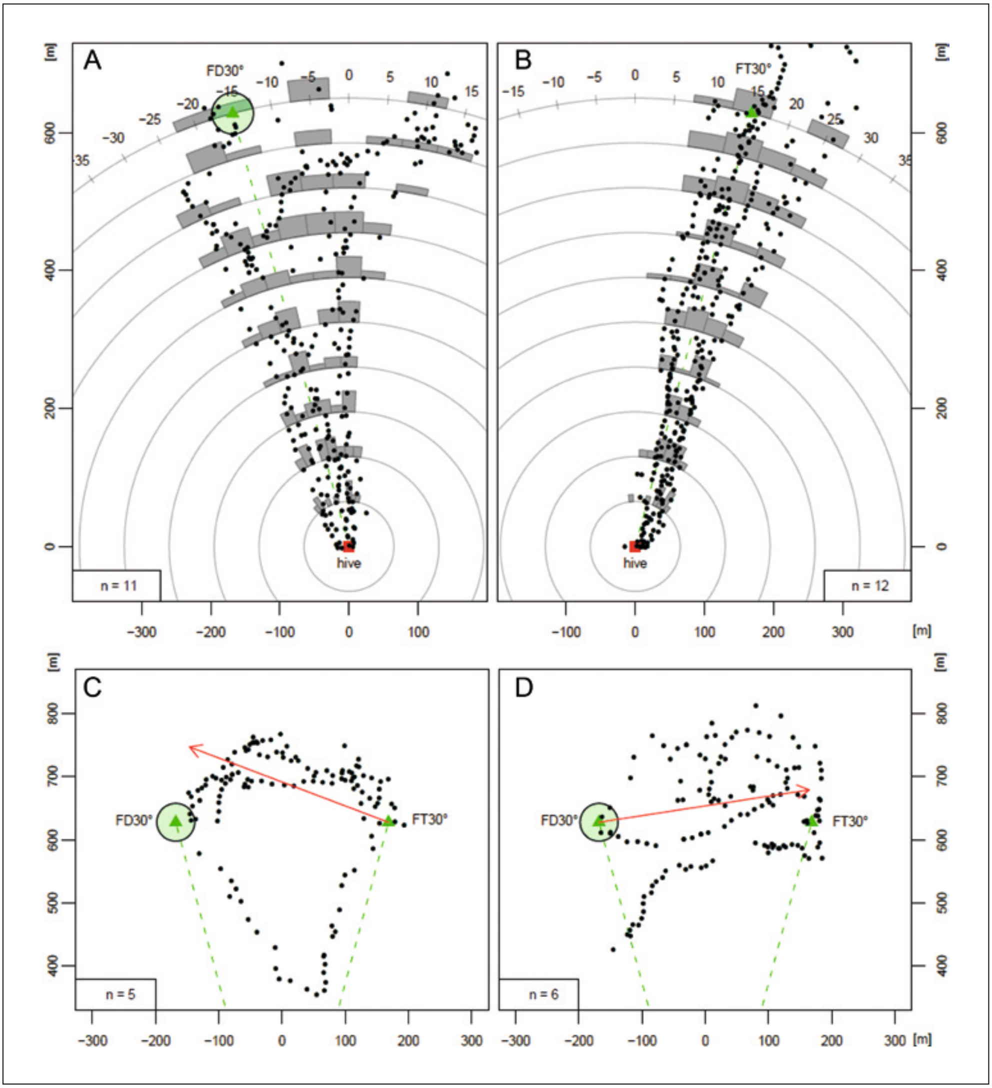

Fig. 3 Radar paints of recruited bees. The recruited bees were foraging for a few days at the feeding site FT (*B*). Then they experienced for a day that their feeding site FT did not provide any food anymore. A day later two other bees danced for feeder FD (*A*). The FT foraging bees attending the dance were equipped with a transponder when leaving the hive. Some of these bees flew toward FD (*A*), some of them to FT (*B*). The vectors toward FD and FT appeared under an angle of 30° as seen from the hive and had about the same distance (650 m). Notice that some flights toward FD were redirected toward FT half way to FD. Compare with Fig. 2*A*, *B*. (*C*), (*D*): Cross flights of recruits after they had arrived either at FT (*C*) or FD (*D*).

communicated spatial relations. Since we interpret our radar tracking data to document a rich form of a common geocentric memory as the structure of navigational working memory it is tempting to conclude that vector information from the waggle dance is incorporated into such a common memory, and thus has a geocentric structure, too.

2.4 Homing Flights and Decision Making in Flight

In displacement experiments performed long before we used radar tracking we observed that return rates dropped to 50 % for releases at ≥ 500 m distances, and 10 % for releases ≥ 1000 km (MENZEL et al. 2000). DYER and others (1993) found that the return rate depended strongly on the direction of displacement. Behind a natural barrier bees did not return for even shorter distances. In our radar experiments bees returned home along straight flights from all directions around the hive over distances of a few hundred meters (MENZEL et al. 2005). A few examples are shown in Figure 4 together with a distribution of homing points. Bees return over distances of up to several hundred meters in an open and flat pas-

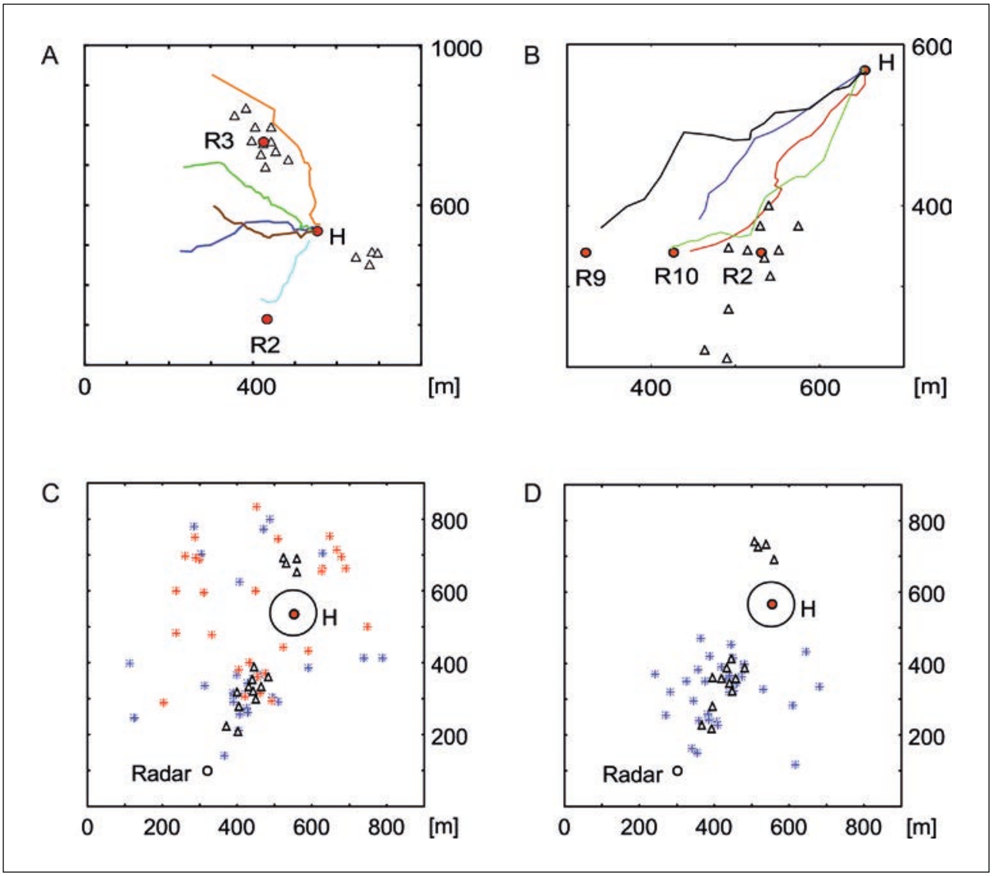

Fig. 4 Radar tracks of the homing component after displacement. (*A*): These bees were trained to a feeder 200 m east of the hive. Then they were collected at the feeder when flying back to the hive and released at R2 or R3. (*B*): These bees were recruited by dances of foraging bees indicating a feeder 200 m east of the hive. The bees were released at either R2, R9 or R10. (*C*): Locations of homing points of bees foraging at a feeder 200 m to the east of the hive (blue stars) and of bees that were trained to a feeder close to the hive (10 m distance) that rotated around the hive (red stars). These bees were released under sunny weather conditions. (*D*): Homing points of bees foraging at a feeder 200 m east of the hive. The bees were released during overcast weather conditions. Notice the different scales.

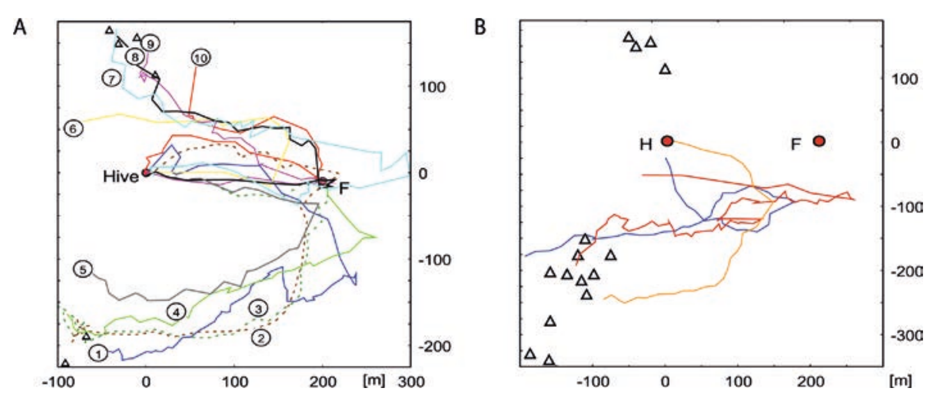

Fig. 5 Final part of 13 flight tracks of foraging bees that flew back to the hive *via* an area close to the feeder (F, radius 50 m). (*A*): shows 10 (out 29) flights tracks which we published in Menzel et al. (2005). One of these bees landed at the feeder. (*B*): shows three more tracks that did not quite reach the area of the feeder but performed somehow similar flights.

ture. As described above they could not have been guided by the panorama or a beacon at the hive. We observed an accumulation of homing points along a long ranging landmark (the border between two pastures with differently cut grass) and in the vicinity of a group of landmarks (tents) in the south of the bee hive, but homing flights were found from all other directions around the hive.

Most interestingly, bees trained to a feeder returned home not only by direct flights to the hive but also *via* the feeder. Figure 5 shows not only the 10 (out of 29) animals that were published as examples of those displaced foragers that took the way *via* the feeder (Fig. 5*A*) but three more flights which appeared to follow the same strategy but with less accuracy (Fig. 5*B*). The ability to decide between the hive and the feeder as the destination for a homing flight requires some form of relational representation of the two locations. Given the fact that neither of these two locations could be approached with the help of a beacon nor with a matching of picture memories of the panorama as seen from the location where these flights started, we are left with the interpretation that either a geocentric map or a procedure equivalent to the integration of long ranging vectors may explain the findings.

3. Conclusion: The Geocentric Format of Working Memory is Best Conceptualized as Cognitive Map

The essence of the navigational problem – whether an animal is able to infer a direction of movement along a novel path aiming toward another location that is not directly accessible – cannot be addressed by laboratory-like conditions. Questions that are not asked in an experiment cannot be answered by it, and applying inappropriate methods like determining only vanishing bearings or analysing the behaviour of only route trained animals, will not help to discover novel navigation behaviour. Working under natural conditions may limit the possibility of untangling the relevant parameters. However, tracking the flights of bees with harmonic radar allows collecting the relevant data also under natural conditions. In addition, new paradigms are required. The communication between colony members provides us with an excellent tool to unravel the knowledge base of navigation in bees.

Novel flight paths performed by displaced bees indicate a geocentric (cartographic) organisation of spatial memory. Searching bees decide between different destinations possibly creating ‘expectations’ about locations. The information transmitted in the dance appears to encode a location as defined by the navigational memory. Recruits interpret the information collected *via* the dance differently according to their own experience. They decide to follow the received information depending on their former experience in relation to the indicated location.

As I see it four arguments have been put forward against the hypothesis that bees navigate with reference to a memory structure that is best described as ‘cognitive map’ introduced by Tolman (1948) for rats and men.

(*1.*) ‘*The cognitive map is not the most parsimonious explanation*’. This argument is often combined with the statement that such small brains as those of bees cannot support such a memory structure. Parsimony can be understood as a formal criterion and in the case of behavioural biology as an argument for the simplest implementation in neural structures. Both aspects depend on what needs to be explained. The rich body of data which we have collected with the harmonic radar excludes a purely egocentric reference system. Matching of far distance visual cues or local landmarks or odour trails can also be excluded. Arriving at the hive or the feeder can also not result from random searching. Even if we ignore the evidence that bees make decisions according to the expected outcome (see below) and do not take into account any qualitative evaluation of the intended goal we are left with the conclusion that they either perform some sort of long distance vector integration, or they refer to geometric relations of landmarks, best conceptualized as cognitive map. The former is in fact a geometric map, too, so the difference lies only in the procedure how it is established neurally. Thus, there is not a more parsimonious explanation.

Parsimony is a strong argument in the interpretation of experimental data, and has been applied rather strictly in studies of insect navigation (Wehner 1992). However, it should not be overlooked that radical forms of parsimony as applied to behavioural science were (and may still, at least partially, be) a historical burden. New approaches are required to correct for purisms as applied in behaviourism, and too simple assumptions about the brain’s functions in ethology. These ‘cognitive approaches’ (cognitive ethology, psychology, neuroscience) provide us with novel avenues to brain function (Kandel and Squire 1992). It is well possible that the integration of the multiple and complex sensory and procedural neural processes into a common spatial memory with geometric organization (a map) may in fact be more economical and thus simpler for representing sequential experiences during navigation (Griffin 1984).

(*2.*) “*Bees should fly directly home from the release site if they refer to a cognitive map.*” Indeed they don’t. They first perform a flight according to the active state of their working memory. This behaviour is not an argument against a cognitive map because the spatial memory bees need to refer to has been learned during orientation flights, and this memory is obviously not active when they follow their route flights or fly according to the dance information. We argue that only after they have emptied their working memory they can access the remote memory established during orientation flights. It is quite possible that the limited capacity of a small brain is reflected in this particular performance. Storage capacity of working memory was found to be one of the most predictive measures of human intelligence (Baddeley 1986), and working memory span as determined in matching to sample experiments is much shorter in bees than in mammals as long as their hippocampus is functioning (see discussion in Menzel 2009b).

(*3.*) "*Bees should not fly into a region they have not explored, e.g. out on a lake*". Gould and Gould (1982) reported that bees reject dance information which would have brought them out on a lake, thus into an area they are assumed not to have explored. Wray and others (2008) interpreted their data as showing that bees have no problem to fly out on a lake after following a dance, however, they had to use odour marking of the feeding station on a boat, and although they tried to downgrade an odour effect they still could not eliminate the possibility that bees flew out on the lake because of attraction by the odour. In our view, the question whether bees do not accept dance information which would guide them into a white spot of their navigational memory is not resolved yet and needs testing with the harmonic radar. Let's assume for the moment that bees do not hesitate to fly into an unknown area. Does this mean they do not have a cognitive map? Certainly not, because white spots are surrounded by known area, and why should not a bee (like a human) explore the unknown? Indeed, they need to do this in their natural behaviour all the time, because even if they do not follow dance information before they have not explored the landscape the dance will always lead them into regions they have not yet explored fully. Below we shall discuss a model of bee navigation which does not assume complete knowledge of the landscape. According to this model, spots of known areas are connected by a network of long ranging 'gradients', and the area between these spots may well be 'white'.

(*4.*) "*As long as you cannot rotate the landmarks used by bees relative to their sun compass one cannot believe in the cognitive map concept*". We all know from our discussions in science that sometimes abstruse arguments are put up that ask for something impossible. This is such an argument. It has its rootes in a tradition of experimentation in which the experimenter controls for all possible parameters, varies just one, and finds that the animal performs according to the hypothesis behind just that variable. It is then concluded that the animal can do only what was just tested. Navigation does not deal with close-up object recognition. Navigation in bees cannot be tested in a white 1 × 1 m box with three black stripes on the wall. Navigation happens in the natural environment when bees fly over many hundred meters. Thus, experimental manipulations are restricted, but cumulative evidence will either support or weaken a hypothesis, and the concept of a cognitive map is such a hypothesis.

We have argued above that parsimony arguments do not contradict the notion that an overarching, across modality and context including memory structure exists in the bee brain. What could be the structure of such an overarching memory? Vectors are formally the most efficient way of specifying a location (Gallistel and Cramer 1996, Vickerstaff and Cheung 2010, Biegler 2000). If these vectors are anchored to landmarks they provide a geocentric reference frame. Vectors are reported in the waggle dance. Thus, bees appear to take advantage of the formal applicability of such a spatial measure and need to encode only two parameters. This does not mean that all what they are communicating is just distance and direction. The directional component of the communicated vector may be retrieved from the memory of spatial relations to long stretching landmarks (gradients) because these are also defined by their relations to compass directions. Such gradients could compose a memory for a rather simple 'bearing map' as proposed by Jacobs and Schenk (2003). Such a rough bearing map does not require a large amount of neural encoding and storage but would provide a geometric representation of the whole experienced environment at a coarse resolution. Picture memories ('sketch maps' in Jacobs and Schenk 2003 terminology) could exist loosely distributed and only partially connected to each other leaving white spots in between. Way finding (and possibly communication about ways) could therefore consist first in identifying the sketch map of current location, the mental spotting of that sketch map in the bearing map and then the creation of a novel short-cut flight according to the compass direction to the goal as derived from the sketch map. The bee would travel through 'unknown' territory (white spots) whenever she leaves a sketch map memory and has not yet reached another one, but she would not be lost because at any point she has access to the bearing map. If such a scenario would apply bees would dance for a location in a bearing map, and recruits would interpret the message according to such a map. The finding by von Frisch and Lindauer (1954) that extended landmarks can replace access to the sun compass on overcast days has been interpreted as indication for a backup system (Dyer and Gould 1981), but in fact such 'gradients' could provide the primary source of information for navigation and the link to the compass may just be a side effect of learning about such gradients. Since there is no vocabulary for particular gradients in the dance the flight direction has to be encoded into a compass direction.

The sketch map components are related to the properties of the goal, the stimuli characterizing the goal including its location relative to close landmarks as seen from a vantage point, its value and manipulatory properties. These associations would also be retrieved during dance communication, and decisions both by the dancer (how strongly to dance) and the recruit (worth following the message) are based on the expectations created by these associations. These are speculations, but they are addressable by current techniques. At least, navigational memory as used in dance communication does not appear to require a large amount of neural storage capacity to represent the experienced and transmitted information in a geocentric reference frame.

The kind of questions to be asked in the future in navigation and communication studies in honeybees differs from those addressed so far. The sensory-motor routines involved are well-understood, and they have been analysed by asking: "What can the animal do?" Now we need to ask what kind of and how the information is stored in their working memory, how this information is processed and how decisions are being made. We thus will have to analyse the structure of internal representations. Dance communication provides us with a window into these processes, and carefully-designed experiments will allow us to access processes beyond behavioural acts. These operations are far from simple and transcend elemental forms of associations (Menzel and Giurfa 2001). The richness of these operations exists only in animals acting in their natural environment, and the methods are now available for collecting the relevant data. Ultimately, we want to know how and where the bee's small brain performs these operations, but the answer lies in the future.

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Programmed Behaviour, Learning, and Knowing: Caterpillars to Ravens

Bernd Heinrich (Burlington, VT, USA)

With 20 Figures

Abstract

In this essay I trace my research career as I saw it being influenced by mentors and chance events. I see the naturalists' fascination with nature as combining almost all fronts of biology, erasing boundaries, and being the basis of it. Research is driven from passion coming from contact and leading to exploration and paying close attention. In my particular case contact started from collecting beetles, bird eggs and sphinx moths for myself, and ichneumon wasps and later also other insects, birds and small mammals for my father. These activities gave me a grounding in the natural history of organisms, their diversity, beauty and complexity, and that brought wonder. The wonder generated questions, and the questions focused on those where methods led to possible solutions. Methods came by contact with people. Like digging a hole, the wider the reach, the deeper it can be dug; every question of adaptation has various interrelated levels, ranging from the ecological, physiological, behavioural and evolutionary. I never saw any one of them as separate from any other except for practical methodological considerations and the subsequent artificial compartmentalization for simplicity of cogent presentation.

Zusammenfassung

In diesem Essay zeichne ich meine Forscherlaufbahn nach, so wie ich sie sah, beeinflusst von Mentoren und Zufällen. Es ist in meiner Sicht die Faszination des Naturforschers an der Natur, welche fast alle Fronten der Biologie vereint, die Grenzen auslöscht und die allgemeinste Grundlage liefert. Forschungstätigkeit wird getrieben von Leidenschaft, die vom Kontakt mit der Natur herrührt und zur Erkundung und genauen Beachtung führt. In meinem Fall begann der Kontakt mit dem Sammeln von Käfern, Vogeleiern und Schwärmern (Sphingidae) für mich selbst, und Schlupfwespen und später auch anderen Insekten, sowie von Vögeln und kleinen Säugern für meinen Vater. Diese Aktivitäten vermittelten mir einen breiten Zugang zur Naturgeschichte der Organismen, ihrer Vielfalt, ihrer Schönheit und Komplexität, und das führte zum Staunen. Das Staunen führte zu Fragen, und die Fragen wurden konkret, dort wo es Methoden gab, die zu möglichen Lösungen führen konnten. Die Methoden wiederum kamen durch den Austausch mit Leuten. Es ist wie beim Ausheben einer Grube, je weiter sie wird, um so tiefer kann man graben – jede Frage nach Anpassung hat zahlreiche miteinander verbundene Ebenen, von ökologischen, physiologischen und verhaltensbiologischen bis zu evolutionären. Ich habe diese nie als getrennt voneinander betrachtet, außer aus praktischen methodologischen Überlegungen heraus und der daraus folgenden künstlichen Kompartimentierung für die nötige Einfachheit überzeugender Darstellungen.

1. Beginnings

I have been fascinated by living things ever since I can remember. That interest led to curiosity about natural processes that centred on problems or questions that seemed possibly to

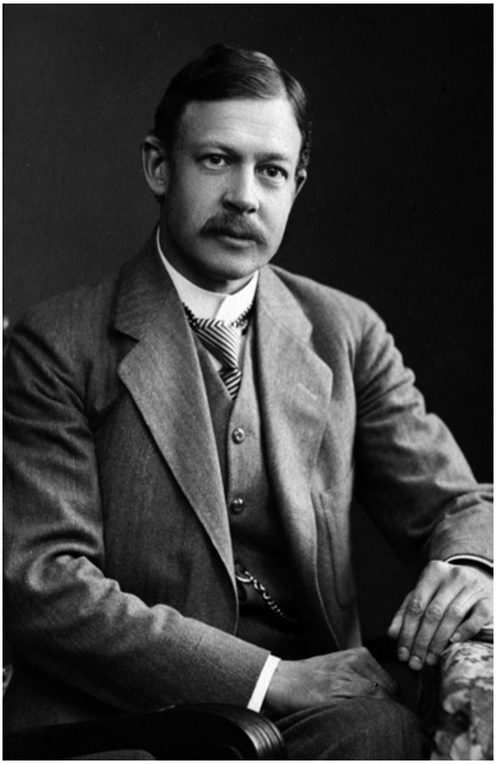

Fig. 1 Richard Heymons (1867–1943), of the Humboldt Museum (*Museum für Naturkunde Berlin*). (Senckenberg Deutsches Entomologisches Institut Müncheberg, Portrait Collection, PSlg 1715)

answer. The specific route I took probably evolved mainly from many chance encounters with different people, animals and methods. I cannot here sketch a map that might serve as a guide to future biologists because the terrain they face will likely be much different from what I encountered. Instead, I will describe how I ended up in behavioural science in the hope that it might encourage others to make their own way as well, and to enjoy a happy and productive journey. I am especially glad to give this account in this venue of the Humboldt University, because ultimately my journey began here through my father. I also want to acknowledge the honour of a Humboldt Fellowship at both Berlin and Marburg that got me back in contact with some of my roots.

Early parental influences were a strong factor in my trajectory. My grandfather was a physician in Berlin, and my father, Gerd H. Heinrich, made connections at the Humboldt Museum (*Museum für Naturkunde Berlin*) and followed the then-dominant Victorian trend of biology, which was collecting. Documenting life's diversity was then the obviously productive and adventurous activity of any student of Life. It was the beckoning mission taken

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Fig. 2 A sample plate illustrating some of the new Ichneumoninae, from Gerd Heinrich's *Die Ichneumoninae von Celebes* (1934). Shown are three species, with femals at left and males at right. ►

Mitteil. a. d. Zool. Museum in Berlin. Band 20.

Tafel 8.

Berntsch pinx.

Heinrich: Ichneumoninae von Celebes.

by Alexander von Humboldt and other explorers, including Charles Darwin. It led not only to taxonomy but later to the pillar of biology, the 'theory' of evolution that connects all of biology into a coherent whole. Collecting as a hobby has long been the first introduction to biology to many blossoming biologists, and I believe it could still be now.

I do not think that my father, a youth 100 years ago, saw much that was practically doable in biology beyond classification. He saw taxonomy as a means of reaching to the horizons of the unknown, both intellectually and physically. When his boyhood collecting of local beetles, bird's eggs, butterflies and small birds and mammals had served to familiarize him with the ecology, behaviour and diversity of animals, he (as most others of similar background) started to look for further challenges. He told me how he had frequently visited the Humboldt Museum and approached a Professor Richard Heymons (Fig. 1), an entomologist, to ask what group of animals might have the most fascinating biology and might also be the least known. The answer he got was: the Hymenoptera. And so, at age 17, his life trajectory was set, and deliberately so, even as he almost immediately became a soldier in World War I (and later in World War II as well). He decided to try to make his collecting 'count' by focusing on the presumed least-known, the Ichneumoninae, which are parasites of Lepidoptera. They became his passion and he would later finance his ichneumon-collecting to Persia, Burma, Celebes, Angola, Tanganyika, and Mexico by piggybacking it onto that of birds and small mammal (which were financed by museums). This endeavour became almost certainly only possible to him because of a lucky connection (which I describe in detail in my book, *The Snoring Bird* [2007]) to Erwin Stresemann of the Humboldt Museum. Stresemann would become his mentor, patron, colleague in ornithology and a life-long friend. Before my father died at age 84 in the USA in Maine, he had described over 1,479 new species of Ichneumons (Fig. 2), and discovered nearly a dozen new species of birds. Although he had attended some lectures at Humboldt University, he had never completed studies for an undergraduate degree (the wars had intervened) and he remained with his ichneumon wasps for the love of them, an amateur without a secure position.

I grew up in isolation from professional biologists but had the advantage that my father's collecting gave me an early foot-hold into the field. Collecting was something I could *do*, and therefore did, maybe because there was no extraneous 'entertainment' in the Hahnheide forest where we lived in a small hut (still standing!) for six years. Since the age of five he took me collecting ichneumons into the nearby woods, both in summer and winter. In the winter we hacked into rotting stumps and peeled up layers of moss to search for insects, and even then at age five I started a beetle collection. I would not have believed how young it started for me, except that I found proof in a poem by Dr. Walz, a dentist friend from Trittau. His handwritten poem documented me finding an especially rare ichneumon that he wanted. I thought I recalled finding it under green moss by a stream-bank, and was recently able to find the precise specimen (in the Munich *Staatsmuseum* which now houses his collection) as identified by the dated label on which he had attributed the find to "B. Heinrich," instead of the customary G. Heinrich. The same poem (written in the fall of 1945) also mentioned a *Carabus* beetle that I was very keen to have. (I have here drawn both. See Fig. 3 and 4.)

As a note I had scribbled to my father near that same time suggests, I had a strong fascination with animals, but at first saw biology mainly through his eyes, as synonymous with taxonomy. I was encouraged to become an ichneumon collector to continue the 'tra-

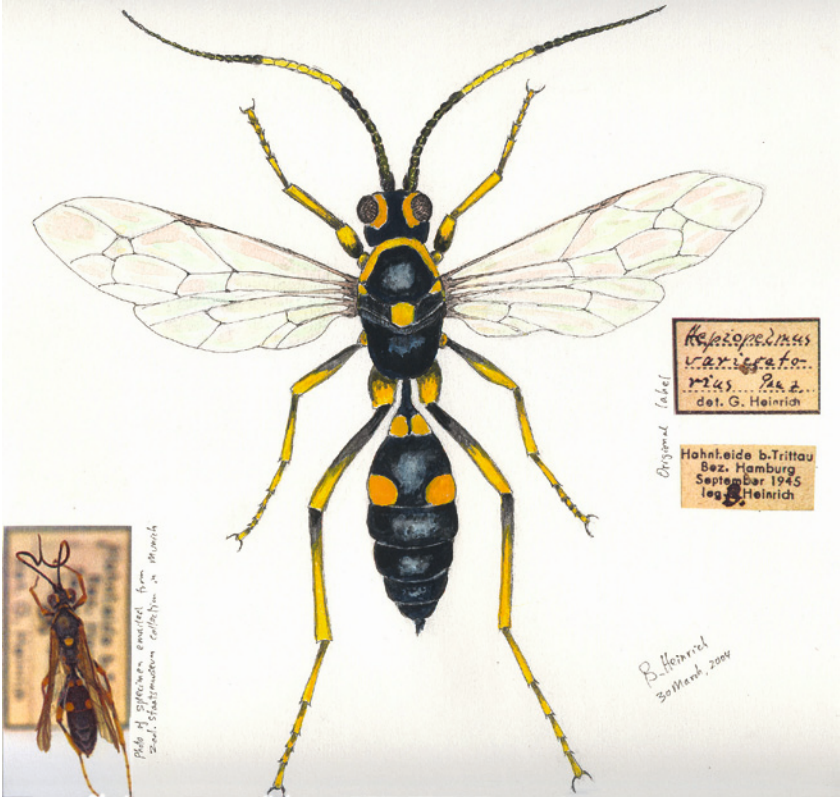

Fig. 3 *Hepiopelmus varigatorius*, a species my father desired that I by luck found in hibernation under moss in the Hahnheide forest (near Hamburg) at age five (from my sketch of the specimen now in the Munich *Staatsmuseum*). Note date and name of collector on label photograph.

dition' he hoped he had started, but he told me to take up a practical profession, namely medicine, to finance travel and collecting in foreign lands. A life in Biology, I was told, didn't buy bread.

By almost bizarre twists of fate I enrolled at the University of Maine and without any money to finance an education. As one of the means of earning money I trapped weasels (for fur and for a professor's research). Along the way in my first year there I caught other small mammals and told a professor of Wildlife Ecology, Malcolm COULTER, about it, and he encouraged me to write up my results and observations. I did so, and thus had my first "scientific paper" in a small local natural history journal (HEINRICH 1961). It was a small step, but it gave me encouragement and courage in my studies. I completed my undergraduate degree in biology, as a "pre-med", after having started in forestry which I had envisioned to be something like ecology is now. I took a year "off" to join my father and mother in their last "expedition," which was to Tanzania collecting birds for Yale University's Peabody Museum. Both the expedition to the tropics and the University experience

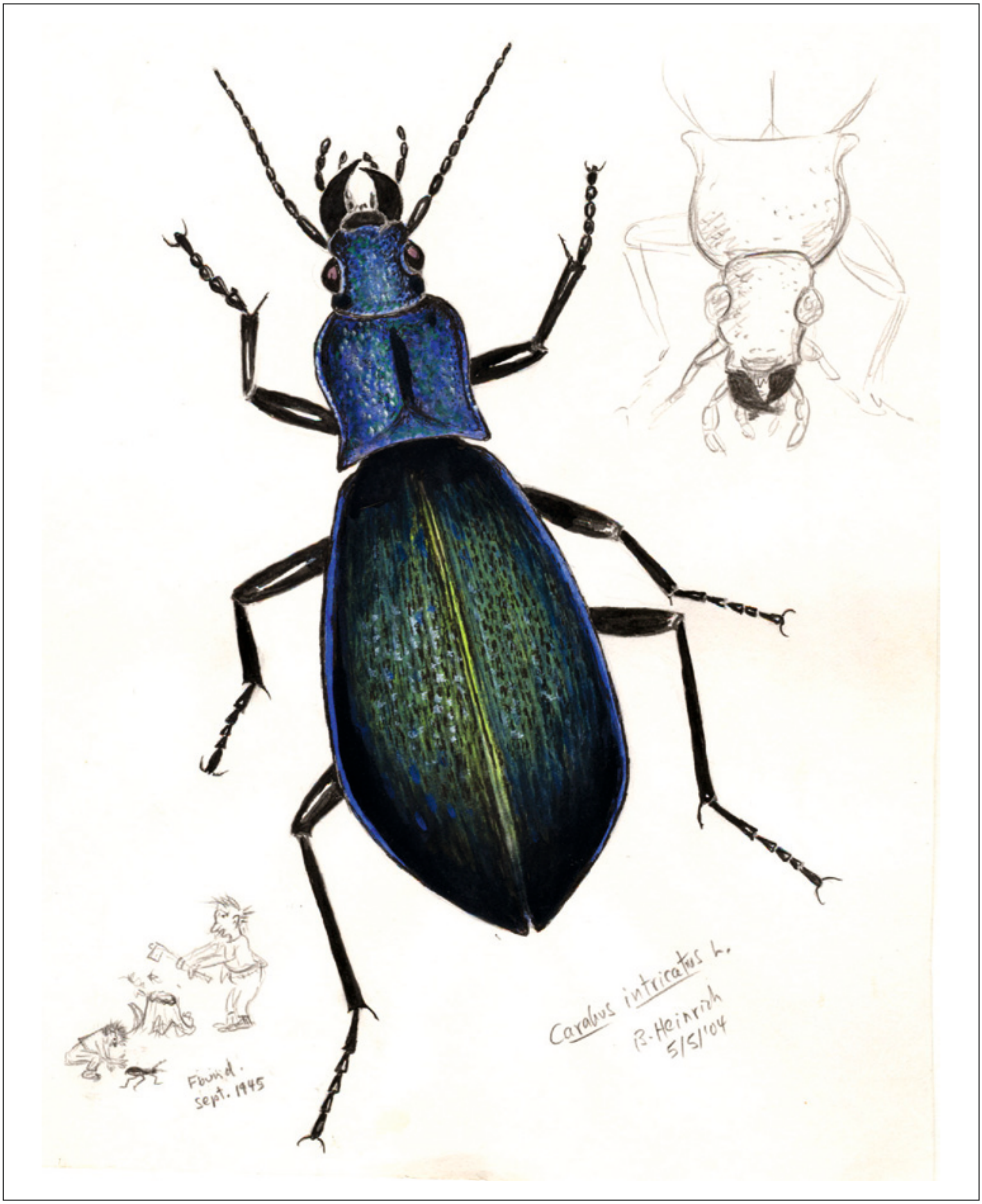

Fig. 4 *Carabus intricatus*, one of the species in my beetle collection that I also found in the Hahnheide at near the same time.

changed everything for me. I was introduced to the then still very current excitement of James D. WATSON and Francis H. CRICK's breakthrough to their "Discovery of the Secret of Life." Collecting and taxonomy had then almost immediately become relegated, as I had heard, to "stamp collecting."

2. Graduate School

Starting out in America, we had not a dime to spend on education, and to pay for my undergraduate college expenses and tuition I had to do more than trap weasels. I worked during my studies at odd jobs, including work in campus kitchens, and in a lab washing glassware in the laboratory of cell biologist James R. Cook (Fig. 5). 'Dick' Cook was a quiet, unassuming man, who loved to fish for trout and hunt ducks, and he recognized both my passion for science and the outdoors. After a while he had me helping him maintain his protozoan (*Euglena gracilis*) cell cultures, monitoring growth curves, doing enzyme and protein assays, and also radio-carbon labelling of cells. He took me on fishing excursions, and during the long car rides we discussed his research. He made the-to-me wild suggestion to stay on with him for a masters degree in cell biology.

The experiences with Dick Cook, a man I admired and respected, felt like lids had been lifted from my eyes. I soon saw biology less as taxonomy but more as lab exercises of finding and solving interesting physiological mechanisms. 'Field work' seemed to become devalued because it purportedly didn't provide experimental controls. I indeed stayed to get a masters degree with Cook, and we published three papers in cell biology (see Cook and Heinrich 1965, Heinrich and Cook 1967). A new and to me exciting world seemed to have opened. However, when he encouraged me to apply to other universities to work for a PhD, as he stated "to broaden your horizons", I was summarily rejected. In interviews I had tried to tout my broader, natural history, interests, and in retrospect believe I was discounted if not dismissed because of them. Indeed, in one interview at a minor college the professor told me the interview was over, after announcing in apparent horror: "You are a Natural-

Fig. 5 James R. Cook, of the University of Maine.

ist!" Dick Cook, on the other hand, must have written me a very strong letter of recommendation when I later applied to the hallowed halls of UCLA (University of California Los Angeles), because I was not only admitted (without any interview) but also offered a full research fellowship, to follow a PhD program in molecular biology.

Not long after I had started, Gunther Stent, then at the California Institute of Technology, lectured and published a book (Stent 1968) and a paper in the already then premier journal *Science* (Stent 1968) proclaiming far and wide that the end had been reached in molecular biology; that everything important had been learned and was done. It seemed to him that after his famous work on phage DNA, the party was over scarcely after it had begun. Indeed, I was working with DNA and felt the same thing already four years earlier. I was extracting DNA with very cumbersome and crude tools and basically getting very frustrated in trying to separate the chromosomal from the mitochondrial and chloroplast DNA's, which I needed to do just to "get my feet off the ground" on the project I envisioned to do. My major professor (serving as Department Chairman at the time) spent no time in the lab and so I was on my own. I floundered on for a full year and ended up doing a small study on the induction of chloroplasts in the protozoans that I was familiar with. I submitted it to the *Journal of Cell Biology*, and it was sent back to me – rejected. I became deeply distressed, and even came down with painful possibly psychosomatic symptoms. I thought I had come to the end of the line, because there seemed to be no more meaningful research in sight. But perhaps luckily, or in desperation, I then stumbled into another camp.

3. First Behavioural Biology

I loved being outdoors in contact with animals in natural ecosystems, and therefore went to talk with Professor George A. Bartholomew who had a lab in the basement of the Biology building. 'Bart' would prove to have as great an influence on me as Dick Cook, but in a different way. Bart was more formal and would not have been distracted by fishing for little trout. He was focused on the ecology and physiology of desert vertebrate animals and on running his 'stable' of numerous graduate students. He was so "serious" he even refused to admit women, because he reasoned that they would marry and have kids and then their education, and his efforts, would have been "wasted." He was not eager to take me on, either, maybe because I was a proven failure in a lab from his Department competitors, the molecular biologists upstairs.

Bart's students went out into the local deserts to look for reptiles and birds to try to solve the problems of heat and water balance they faced there. They then brought the animals back into the lab to study them under controlled conditions to find out how the animals solved problems faced in the rigors of the physical environment. The solutions almost always involved a tight coupling between physiology and behaviour. Bart was naturally sceptical in taking me on, and after I shyly talked with him, and only briefly, he told me to come back to see him in six weeks to discuss six potential problems I might like to solve. Time was short, because unbeknownst to me, he was about to depart on a one year sabbatical leave to Australia and New Guinea.

I had never been in a desert, and eagerly went into the nearby Mojave and Anza Borrego deserts to familiarize myself with these to me new environments, and to find and watch animals and ponder about them. But I ended up spending even more time in the library reading research papers. Those six weeks were probably the most intense, and productive, of my entire career as a biologist. I became oriented about what was known, and indeed managed to pose six questions that I thought were worthy. (It was not wasted time; I would eventually, in the next two decades, publish on all six of my proposals.)

I was accepted into the lab. Although no definite project was yet chosen for or by me, I decided to make probes into several of them to see how things went. After all, I presumed I would have to make a unique strictly original discovery of a new mechanism in biology, and how could one predict where something might still be left undiscovered? All my projects concerned insects, and so Bart suggested I get Professor Franz Engelmann, a German transplant, as co-chairman. Franz was (and still is) an insect endocrinologist, and he insisted, since all graduate students had a teaching assignment as a requirement, that I be his teaching assistant in his insect physiology course. I knew almost nothing about the topic, but it was a wise choice, because I now had reasons to learn insect physiology.

The first question that I chose for a PhD research project, because I felt it was interesting and doable, concerned caterpillars. I had since I was eight years old been fascinated by caterpillars and hunted them every summer in Maine. I usually raised numerous kinds in part as a means to get sphinx moths in pristine condition to pin in my collection. The Maine summers are sometimes cool and always moist, so I was surprised to find the caterpillars of a large sphinx moth (*Manduca sexta*) in the searing summer heat of the Mojave Desert. It seemed to me that they should shrivel up and dry in the hot dry and often windy desert air. They were the same species that I had found in Maine on tomato plants in the garden. Here in the desert they fed on Jimson weed (*Datura*), whose leaves were the only visible source of moisture around (Fig. 6).

Fig. 6 *Manduca sexta* caterpillars in the Mojave desert on Jimson weed, where often several individuals must compete for limited food resources. The leaves also serve as sun shades.

The only advice that I recall Bart having given me in picking a PhD problem to solve was to "keep it simple – it will get complicated soon enough." Perfect. I would simply find out if the sphinx moth caterpillars ate more leaf to keep themselves hydrated in the desert heat. Bart had a temperature-controlled room at my disposal where I could control the temperature by the turn of a dial, and he had an electro-balance with which I could measure and record "instant" weight loss to a hundredth of a milligram. Incredibly precise weight loss data as a function of temperature was very easy to get.

As predicted, complications started soon enough. It turned out, of course, that humidity varied with temperature, and I learned various ways to control it as I kept the caterpillars in large glass containers (jars). But the caterpillars' water loss shot up enormously as soon as they started to move, and they always moved around unless they were perched on their food. Of course then the presence of leaves messed things up considerably because they give up moisture. But I needed the leaves there to be able to measure how much they ate. Tobacco leaves had a much higher water content than Jimson weed leaves so would they eat a lot more Jimson weed in more dissipating conditions and less juicy tobacco leaves in the cold? But on the basis of what? Then it turned out the moisture content of the leaves varied with temperature as well. OOPS! – maybe the nutrient content would vary, too? I was morphing from a botanist to a biochemist, assaying not only water contents of leaves but also sugar and protein contents, and then of course having to keep track of amount of leaf tissue eaten (area, wet weight and wet), all as a function of weight gain or loss of the caterpillar. Sometimes they did eat more in the heat, but then they gained more weight, too. So, did they eat more as a result of water balance, or did they grow faster simply because they ate faster because they were warmer? Then, during the pre-molt period, water loss suddenly took a plunge – so the overall equation was very much dependent on the age and size of the caterpillar as well. The seemingly 'simple' question of trying to determine if they ate to stay hydrated got too complex for my comfort level. I had worked for a year or more on the project and got reams of physiological data, but disappointingly it did not reveal a new mechanism. The caterpillar's solution seemed to simply involve a multi-factored complexity of interactions, none of which could stand on their own as something new to biology. I was disappointed and dropped this project because I felt it was not leading to anything "clean" enough to publish. On the other hand I got lucky, because a small digression of my attention to the feeding *behaviour* proved to be simple, transparent and direct.

I was impressed how these caterpillars could consume an entire leaf that was several times longer than their body without moving from the spot while they were perched under it and using it as a solar umbrella. The feeding behaviour looked almost like they 'knew' what they were doing during their elegant leaf handling that seemed worth investigating, and I presumed it was based on some simple innate 'rules'. And all I had to do was show what those rules were. I tried to discover them experimentally by using the leaves of another food plant (tobacco grown in the Botany Department greenhouse). Tobacco has very large broad leaves, and by altering leaf shape (with scissors) from broad to long and narrow, for example, it was easy to see how the variations of leaf shape affected leaf-handling behaviour and from that derive the rules of the feeding behaviour (Fig. 7).

I completed this work in around a week, and it resulted in my first paper on animal behaviour, which was eventually accepted for publication in *Animal Behaviour* (Heinrich 1971). This seemed much too simple work for a PhD thesis, but the moths that then emerged from the caterpillars provided the break-through for finding a novel mechanism that I hoped for.

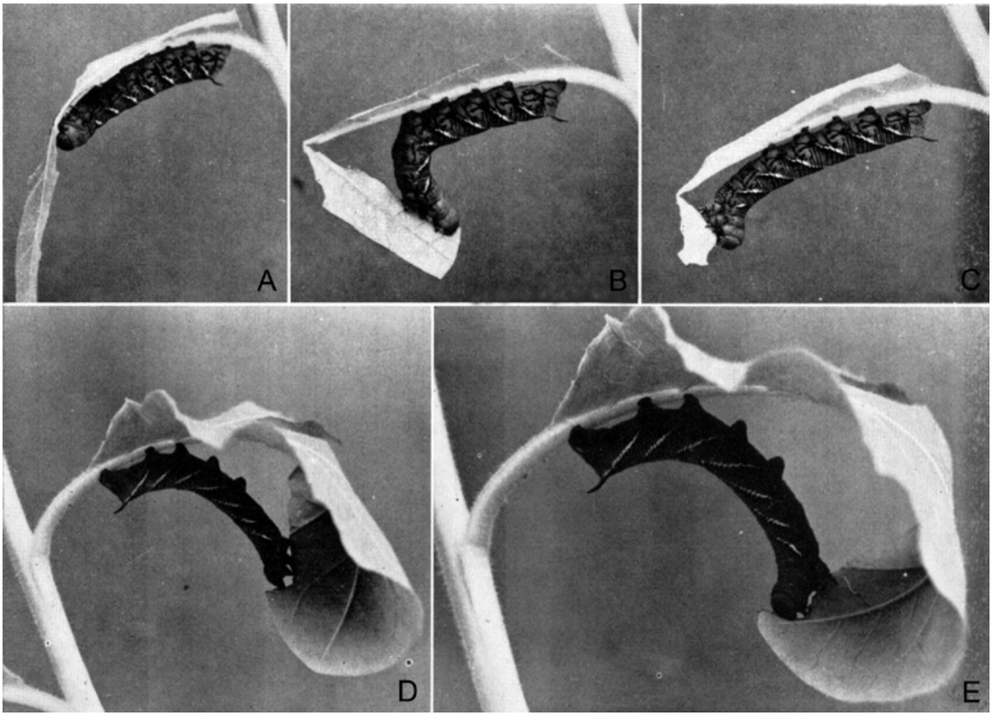

Fig. 7 Feeding sequence of a *Manduca sexta* caterpillar on (*A–C*) an unaltered large leaf (of tobacco) *versus* on (*D–E*) an artificially long pinnate leaf. In both cases the caterpillar does not move from the spot yet consumes the complete leaf (Heinrich 1971).

4. Breakthrough

Everyone (without exception) in Bart’s lab used thermocouples and measured body temperatures. I had measured the thoracic temperature of the sphinx moths, *Hyles* (formerly *Celerio*) *lineate* as they flew and hovered in front of tubular red flowers in the Anza Borrego desert of California (Fig. 8). It was a cool evening shortly after sundown, near 10 ºC. I had also seen these moths fly at mid-day in sunshine, at or above 30 °C. Under both situations their thoracic temperatures were nearly identical – about 43–44 ºC. The moths were continuous flyers – they did not stop and start to heat up and cool down and thus regulate their body temperature by behaviour. Thoracic temperature could therefore not be just a product of the amount of heat generated by flight exercise. They ‘must’ have an unknown mechanism! I knew I had hit on an enigma and that there was no published explanation for my observations. I was wildly excited and switched immediately from all of the other projects I was dabbling in (mostly honeybee swarm thermoregulation, tiger beetle heat avoidance and reflectance of heat from them, and caterpillar feeding and water balance) concentrated on this one. It was an ideal experimental project, because I could formulate numerous alternative hypotheses from the insect physiology I had learned, and there were discrete and elegant tests that would differentiate them.

Fig. 8 My watercolor of *Hyles lineate* sphinx moths foraging for nectar from Belloperone flowers in the Anza Borrego desert of California.

After less than about six months I had the answer to "the moth problem", and it went against the grain on everything that had been published of insects in general and in sphinx moths. Their metabolic rates (oxygen consumption) in free flight were independent of air temperature, contrary to what had been assumed in some papers that came out at the same time using tethered animals. Instead, the moths faced a problem of overheating from their flight metabolism, and they got rid of excess heat – enough to stabilize thoracic temperature – by shunting it into and then out of their abdomen which essentially served like the radiator of a car operating in the heat. Thanks to my previous natural history interests, which involved making a collection of the different species of sphinx moths in part derived from collecting and raising caterpillars, I had been guided to a lucky break. My breakthrough now launched me as a 'physiological ecologist', and on the basis of my first 'job seminar', that I gave at the University of California at Berkeley I was hired to fill their Insect Physiology position.

As I already mentioned, my previous interests in the sphinx moths had been restricted to netting various species at night at lights or while they were hovering during feeding at

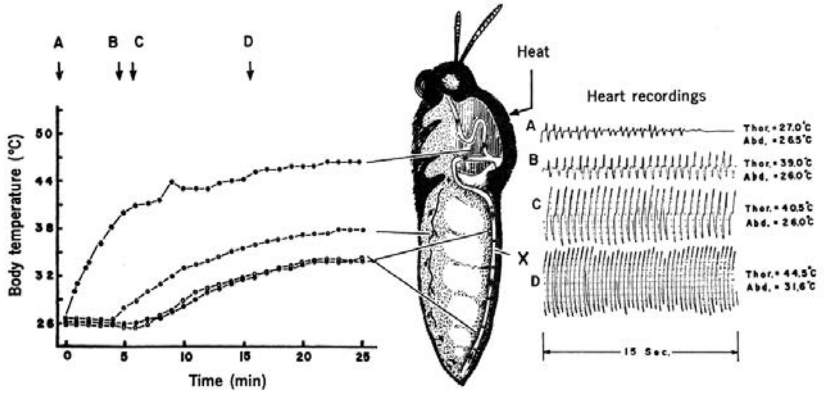

Fig. 9 Body temperatures and abdominal heart activity simultaneously recorded with body temperature at four different locations in a tethered *Manduca sexta* moth whose thorax is being artificially heated (Heinrich 1970a).

flowers, or raising them from caterpillars. After having the adults there was little more to do except pin and spread them; I was constrained by methods, but Bart's lab almost immediately opened several new doors through oxygen analysers, thermocouples, recorders, oscilloscopes, means to control air humidity and temperature-controlled rooms. I could now measure body temperature in the field and in the lab, and record it continuously under controlled conditions, and associate it with metabolic rate and heart activity. Muscle contractions, wing-beat rate, metabolic rate and heart behaviour might all have been 'physiology' before, but now I could reduce or correlate them with discrete movements *within* the animal, and they were then actually details of behaviour that was normally not accessible to the naked eye (see Fig. 9 and 10). That said, relevant methods did not always involve new exotic instrumentation.

Fig. 10 The *Manduca sexta* moth specimen from the above data set. Because of my elation at the moment I cut the wire leads and tied them with a red ribbon.

Indeed, one of my proudest experiments resulted from a nudge by Franz Engelmann. The method involved little more that a fine 'thread' (a strand of my hair) and a needle. I had told Franz about my heat dissipation discovery, but to my disappointment then he was sceptical and said: "To prove it you have to eliminate the mechanism and then see if its presumed effects are gone." Since insects don't need a heart for cellular respiratory exchange like we do, I simply tied off the dorsal vessel ('heart') of moths and that almost immediately resulted in the definitive proof: elimination of body temperature regulation. A quick succession of two papers in *Science* (Heinrich 1970a, b) resulted, which I then followed up with the supporting data in more detail later.

5. Follow-ups

The moths' natural behaviour when they were collecting nectar or flying from flower to flower had suggested where to look for the underlying physiological mechanisms making the behaviour possible. But if the hovering of the moths explained the behaviour of their heart pulsations and the consequent heat loss and body temperature, then that also prompted the question of what an insect like a bumblebee did that *landed* on flowers.

Difference in foraging behaviour pointed to alternative physiological mechanisms, as well as to questions of ecology and evolution where the 'methods' of answering them become accessible by considering the diversity of animals and their natural history. Thus, without any conscious effort, I found myself becoming a student of behaviour who was sandwiched between 'physiology' at one end and ecology and evolution at the other end.

Although all my papers are connected ultimately to the first one on the sphinx moths, a perusal of my literature citations would likely seem to be a wild perhaps incoherent jumble. To me, they seem connected because I followed the animal to wherever it led. Most studies followed linearly related from a previous question, but others resulted from tangential observations. For example, I spent many hours in a hide in the woods waiting for ravens to show up at a bait and while there noticed a nearby red squirrel bite into sugar maple twigs and then move on without having eaten anything. But the next day it was back, and I watched it again and began to see a pattern. These 'on the side' observations became interesting and led to a publication of these animals (*Tamiasciurus hudsonicus*) making 'trap-lines' of bite-marks that result in sap flow on warm days, which then evaporates and leave sugar. The squirrels then harvest the sugar or sugar syrup (Heinrich 1992). The raven study continued, but such forays could potentially become roots or others side-branches. The main trunk developed on its own accord from the material as it became available. I would now like to show some of the connections that developed from the caterpillar feeding behaviour and moth physiology to the eventual testing of the 'intelligent' behaviour of ravens.

Insights come from seeing contrasts to expectations, which are inferences drawn from broad experience. My side-project with the sphinx moth caterpillar feeding behaviour had come from my expectation that these larvae would have simple innate rules of adaptive behaviour. In the Mojave Desert these animals fed on widely-scattered Jimson weed plants, which should select for efficient use of these potentially hard-to-reach food resources. Indeed, I found as expected that the caterpillars did not only chew away the leaf tissue closest in front of them so that the rest would drop off the plant. Instead, they fed more systemati-

Fig. 11 An underwing moth (*Catocola* sp.) caterpillar in the act of discarding the remains of a large basswood (*Tilia* sp.) it had just fed from. The caterpillar will then hide by remaining hidden and not moving the rest of the day. Some feed only at night.

cally, and even though a leaf might be long and narrow they did not eat simply the part of the leaf where they were perched so that the rest dropped off. Instead, they bent leaves to then feed to the tip and then back from there. When they met resistance to the bending they bit into the leaf, which at that point was the central rachis of the leaf, and then the leaf again bent easily and they could continue to feed. No wastage of food resulted.

With the above experience as a background I was therefore shocked several years later to notice partially-eaten leaves on the forest floor – leaves that had apparently been deliberately discarded; they had been clipped off by having their tough petioles severed (Fig. 11). This observation then led to a hypothesis that birds hunt for highly cryptic and hence edible caterpillars, like I always did, by keying in on their conspicuous feeding damage. I speculated that caterpillars that are vulnerable to bird predation either minimize the conspicuousness of feeding 'tracks' by paring leaves down rather than making conspicuous holes and tatters, remove themselves from leaves after feeding and not being able to finish them, or they "cover their tracks" by removing leaf remnants. In the resulting study to test these ideas in the field (Heinrich 1979c), colleagues and I captured chickadees and tested this hypothesis in an aviary (Heinrich and Collins 1983). We showed that these birds not only easily distinguish the different leaf shapes of different tree species, they also distinguish the feeding damage of non-palatable caterpillars (who are 'messy' feeders) and palatable caterpillars (who pare leaves down smoothly and thus making their feeding less obvious). Subsequent studies with blue jays in the laboratory confirmed these findings (Real et al. 1984).

The sphinx moth thermoregulation study also opened to me a new vista on the stage of behaviour and comparative physiology, and I eagerly jumped on. First, honeybees, apparently because they are pre-adapted to make honey by evaporating diluted nectar, accomplish heat loss by the behaviour of wagging their tongue as they extrude honey-stomach contents. On the other hand, they can conserve heat when they perch and would otherwise cool, in part by a counter-current heat exchanger in the abdomen. Since the sphinx moths are large in size and are primarily of tropical distribution, their physiology for active heat dissipation made sense. But what about some of the much smaller noctuid moths that are fly in the winter (apparently to escape the heavy bird predation in the summer) (Fig. 12)? What about others, like geometrids, that are very small and therefore could generate only negligible elevations of muscle temperature? I turned to both groups (Heinrich 1987), find-

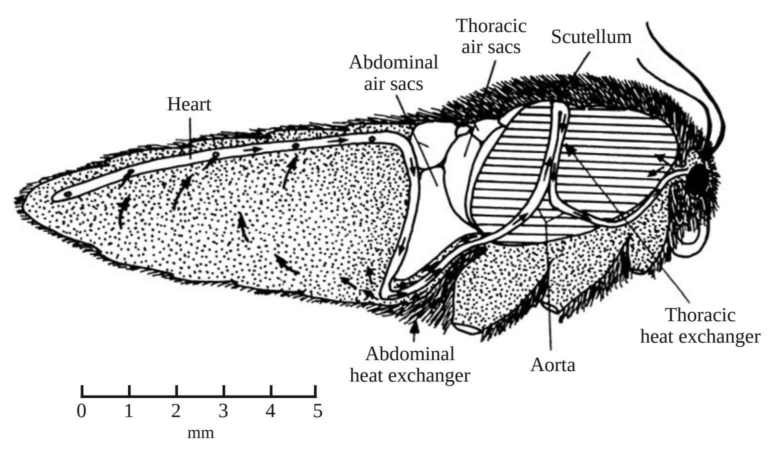

Fig. 12 Diagrammatic representation of a noctuid winter moth anatomy showing two countercurrent heat exchangers, one in the thorax reducing heat loss from the head, and another in the petiole reducing heat loss to the abdomen (Heinrich 1987).

ing to my surprise that while a high muscle temperature is proximally both a consequence and a requirement for vigorous flight exercise, it is not necessarily ultimately so since some geometrid moths can fly with a muscle temperature of 0 °C (Heinrich and Mommsen 1985). A regulated high muscle temperature is an evolutionary consequence of adaptation to the muscle temperature experienced during sustained activity (Heinrich 1977), as was revealed by an overview of the insects (Heinrich 1993).

Temperature not only explained the evolved muscle physiology and sometimes also enzyme function, but as it turned out in later studies, it was also correlated with morphological features such as wing size, sexual dimorphism, and the unique circulatory anatomy and pile of some other insects. Other taxa besides moths and butterflies, such as dragonflies (Heinrich and Casey 1978), beetles and bees confirmed these ideas. In dragonflies, for example, some species, the ‘perchers’, regularly stop either to heat up by basking or to prevent overheating. Others, the ‘flyers’ which are principally the larger-sized species that generated high muscle temperature from their flight activity, used their long cylindrical abdomens as heat radiators. ‘Perchers’ were unable to physiologically unload excess heat. And in small northern butterflies who maintained an elevated thoracic temperature primarily by stopping to bask, activity patterns in the field were closely predictable by their thermoregulatory behaviour (Heinrich 1986).

In addition to the patterns and intensity of activity, body mass was important to thermoregulatory physiology and behaviour as well, and no insects vary as much in body mass as beetles. I had perhaps been predisposed to working with beetles, since I had a fairly comprehensive beetle collection by the time I was ten years old. Remembering my year spent in Tanzania helping my father collecting birds and insects, I thought of the giant dung beetles that became entangled in our mist nets whenever a herd of elephants were near. Elephant dung piles also contained thousands of tiny, medium-sized and giant sparrow-weight beetle species. Bart was enthused and I persuaded him to get a grant so we could travel to Kenya to take the body temperatures of dung beetles during continuous free flight, i. e. when they were first arriving at fresh dung. We netted beetles and then with our portable electronic thermocouples measured body temperatures, collecting large amounts of data in a short time. Our results were as I predicted – the small beetles didn't heat up, but the medium-to-large ones all had thoracic temperatures near 44 °C, the upper limit of almost all 'warm-blooded' animals (Bartholomew and Heinrich 1978, Heinrich and Bartholomew 1978). Comparative behaviour would presumably give insights into the evolution of thermoregulation of insects (Heinrich 1972a, b, c) and should be applicable to the evolution of warm-bloodedness from extinct dragonflies to dinosaurs and other animals (Heinrich 1977).

Bees were another natural follow-up for comparisons with moths. Bumblebees had been charismatic to me already during childhood. During my PhD qualifying exams at UCLA I was asked by one of the five professors of my committee: "Why are you in Biology?" I didn't have any logically-formulated 'reason' and so answered from the heart and recounted an-to-me evocative experience while I was probably about ten years old (shortly before we came to America) that must have made an impression because I still see it to this day almost as though it had occurred yesterday. I had stopped on the walk to the grammar school in Trittau (near Hamburg) at a large willow tree growing at the edge of a brook in the Hahnheide forest where we had lived for six years. The tree was in bloom with yellow catkins, and I saw black and orange-colored bumblebees and I heard the tsseeps of wood warblers (*Laubsänger*). I was entranced by the scene of beauty and complexity and stopped, absorbed in it. And since I was still entranced by it two decades later, that was probably why I was interested in and wanted to study Biology.

Although I studied neither bumblebees nor birds for my PhD, they reemerged later. The year or two after my youthful bumblebee epiphany we moved to Maine, and here under the tutelage of backwoods farmers and woodsmen, I was drawn to honeybees through an activity we called 'bee-lining', the finding of wild honeybee nests in hollow trees (Fig. 13). We had found bee trees by tracking bees that had been recruited to baits we provided to bees we had captured at flowers. This activity became my passion. After finding a bee tree we

Fig. 13 Bee lining to find wild bee trees was for me a passion in the fall. Here I am at one end of a line. Harvesting the honey and the bees into a hive.

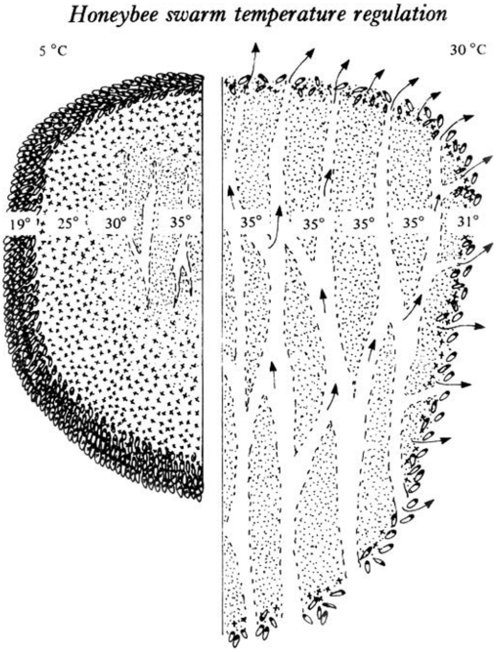

Fig. 14 Diagrammatic representation summarizing social thermoregulatory behaviour of a honeybee cluster. At low temperature the outermost bees crawl in and regulate their temperature above a minimum, and at high temperature the inner overheated bees come out to the periphery creating holes through which heat from the center escapes (Heinrich 1981 a, b).

harvested not only the honey but also the bees, and so I started to keep bees (and still keep two or three hives). Indeed, while at UCLA, one of my side-projects was to find out how the individuals at the swarm centre *versus* those at the periphery are involved in regulating the swarm core temperature as external temperature varies (Fig. 14).

I continued this project after I was hired in the Entomology Department at the University of California at Berkeley (Heinrich 1979 b, 1980, 1981 a, b). But in the meantime, because of a comparison I made of thermoregulation of individual bees with my moths, my main focus had become bumblebees. Bumblebees were interesting because anatomically they are very different from honeybees: they don't have the convoluted coils of the circulatory system in the petiole that I had concluded reduce heat leakage to the abdomen.

6. Bumblebees

The main draw I felt for the bumblebees was initially a question of physiology derived from their behaviour: unlike the sphinx moths which hovered the bees perched on flowers. The most easily and readily answered question was to find out if they stopped heat production when they landed. The problem was that they stopped at a flower only a second or two, which was too short a time to measure appreciable cooling, even if they did stop shivering (Kammer and Heinrich 1972, 1974, Esch et al. 1991). I could, however, manipulate their behaviour: I could induce them to stay for a minute or more by providing flowers in the field with sugar syrup droplets that were thick-enough so that they could not lap them up 'instantly'. Given the timed durations that the bees were detained at flowers, their initial thoracic temperatures, and the easily-determined passive cooling rates (from dead bees) I could then calculate how much they *should* cool in a specific time after they stop heat production after landing (HEINRICH 1972b, c). My results indicated that body temperature did not drop; the bees continued to produce heat by shivering, and at low air temperatures they produced as much heat as they did as a by-product of their flight metabolism (HEINRICH and KAMMER 1973). There was no visible wing movement, but the heat had to be produced by the flight muscles. Here then was a new and interesting question: how did the flight muscles behave to accomplish such prodigious heat production without showing any external evidence of that behaviour? It was at this point that I had sought and found the pleasure of collaborating with two electro-physiologists, Ann KAMMER and with Harald ESCH (a student of Karl VON FRISCH). We deciphered the mechanism of this heat production, which involved complex behavioural interactions of the different up-stroke and down-stroke wing muscles that could only be accessed through electronic eaves-dropping. Anatomical features involved during this shivering that lock the wings dorsally into place and that hide the muscles' movements from visibility from the outside had previously been worked out, but the physiological measurements added the behaviour of the relevant muscles to this externally-seeming lack of behaviour.

Bumblebees have a variety of uses for their flight muscles aside from flight. These include vibrating flowers to shake out pollen, pre-flight shivering and brood incubation. They perch on their brood and produce heat in the thorax. I found, ironically thanks to cues from the moth studies, that they then heat the brood not with the thorax directly but with their abdomen (HEINRICH 1972c, 1974a, b), much like birds heat their eggs (Fig. 15). The 'problem' with this finding is that we showed that virtually all their body heat is produced by their flight muscles in the thorax during shivering such as during pre-flight preparation.

Fig. 15 Photo of *Bombus vosnesenskii* queen in the lab (at University of California) incubating her brood clump with her abdomen.

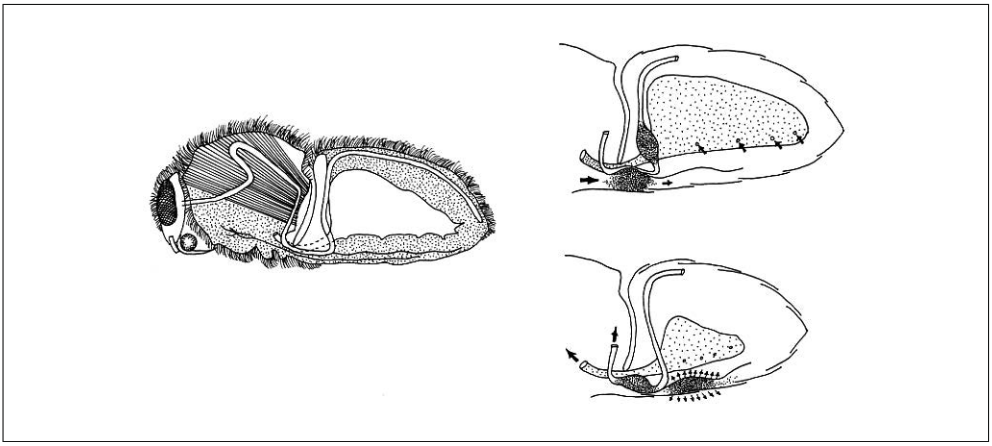

Fig. 16 Schematic sketch of bumblebee anatomy. The two sketches to the right show the respective inspiration of air into the abdomen (*top*) and the contraction of the abdomen (*bottom*) driving the air to the thoracic muscles in the thorax. Congruent with the breathing cycle is shown a bolus of hot blood in the process of leaving the thorax (*top*), and entering the abdomen (*bottom*) in the same instant that the 'cold' blood from the abdomen enters the thorax. In this way the anatomical counter-current anatomy is circumvented by the behaviour of the breathing and heart movements. (Heinrich 1976)

So how can they then heat their brood by contact through their *abdomen*? As previously indicated, honeybees' circulatory anatomy precludes such behaviour, but they don't need it because in the thousands of the colony the relevant space is heated as many bees together form a virtual blanket.

A cursory look at the anatomy indicated that blood and heat flow channels in and out of the bumblebee thorax are in close apposition to each other, thus conforming to a counter-current heat exchanger (Heinrich 1976). It was anatomically very different from that of honeybees but similar to that of noctuid winter moths (Heinrich 1987). As in the latter animals, it 'should' have prevented heat loss to the abdomen! However, in this case my experiments contradicted my expectations; bumblebees could and sometimes did dump much heat into the abdomen. I was very excited by this because it meant there was an enigma: apparently the same anatomy could function to sometimes conserve heat and at other times prevent heat retention or indeed facilitate it. In perhaps one of my fondest discoveries I eventually parsed out the relationships of the bees' breathing movements in relation to heart and ventral diaphragm pulsations, correlated with micro-measurements of heat pulses entering the abdomen, to discover that during that heat transfer to the abdomen the blood shunted through the two channels *alternately* rather than concurrently, thereby eliminating counter-current flow (Heinrich 1976) (Fig. 16). This physiology then gave meaning to the bees' behaviour of perching motionless on top of brood and straddling it tightly with contact of the abdomen, which otherwise made no sense. I would not have discovered this mechanism if it had not been for my previous work on the sphinx moth heat dissipation mechanism during flight exercise. Furthermore, in collaboration with a post-doctoral fellow, F. Daniel Vogt, I enjoyed several expeditions to the Arctic from which we learned that due to the apparent time constraints of the social cycle there the queens even 'incubate' their eggs internally before laying them (Vogt et al. 1996, 1998). These results were surprising since we expected low abdominal temperatures during foraging at near freezing temperatures, since hypothermia is a standard strategy of energy conservation.

My experiment of voluntarily retaining bumblebees on flowers with droplets of sugar syrup to try to answer a physiological question also had behavioural as well as ecological implication. Namely, we found that on some flowers the bees *did* drop their body temperature, provided there was much competition in nectar collecting. It had to do with the amounts of food found, which influenced their willingness to shiver. While foraging on inflorescences with many tiny florets (containing minute food rewards in each) the bees were thus retained because the nectar was dispersed. If the nectar amounts were also small then the bees' body temperatures dropped and did not increase until they were ready to leave to fly to the next inflorescence (Heinrich 1972a, b, c, Heinrich and Heinrich 1983). A new world of behaviour had opened up: foraging behaviour with its underpinnings of energy economy and pollination (Heinrich and Raven 1972). It turned out that floral architecture as well as food rewards manipulated foraging behaviour. I had already measured the energy expenditure of flight and shivering for the physiology work (Heinrich 1975a), and I could apply this to foraging behaviour for the quantification of the energy profits of foraging offered by flowers (availably by determination of nectar volumes using calibrated capillary tubes and sugar amounts by refractometer). This then allowed opening up the foraging behaviour to quantitative investigations and showed that the bees balance their energy budgets during foraging and in many cases achieve a profit margin by specialization. They were 'economists' who balanced their energy budgets by the kind of flowers they visited and how they handled them, and since flowers have evolved specifically to 'manipulate' pollinators' behaviour, that in turn suggested insights into the evolution of flower diversity and blooming phenology (Heinrich 1975b).

Comparative biology gives evolutionary/ecological meaning to both physiology and behaviour. Many solitary bees, for example, were known to be flower specialists who have a short life cycle in synchrony with the flowers of their host plants. Social bees could not afford to be hard-wired flower specialists because the long life cycle precludes restriction to just one kind of flower. They must utilize many kinds of flowers as they come into bloom throughout the season. Yet, many of my bumblebees appeared to be clumsy in the field while visiting flowers with complex morphology. I marked individuals and followed their foraging careers through their lives and under different conditions of food availability in the field and in an experimental 'meadow' with flowers like those in the surrounding fields. I followed the same individuals from their first foraging trips from the colony and until they specialized. One of the most fascinating aspects of this work to me was the individual specialization of the bees (Heinrich 1979a) of any one colony. I wondered how specific skills and specializations were arrived at and sometimes changed, during a bees' foraging career, and how these dynamics related to the overall colony success from an optimal allocation of foraging skills. Again, this work was possible only because of a unique method that had previously been developed and that was commercially available: coloured tags with numbers that could be glued onto the bees' thorax so that individuals could be permanently marked and recognized in the colony and in the field.

7. From Bees to Birds

I was later surprised and delighted to find parallels between the bumblebee economy and that described for humans by Adam SMITH'S "capitalism." Flower handling skill proved to be critical for the hive economy in the bumblebees' northern environment of diverse and highly scattered flowers, whereas communication of distance and direction of food bonanzas by the "dance language", as elucidated by Karl VON FRISCH and Martin LINDAUER and colleagues, was more important than for honeybees generally evolved in more tropical regions where large local food bonanzas, such as flowering trees, are available. Meanwhile, Edward O. WILSON had highlighted the social insects from his taxonomic ant studies that had extended to scent communication for colony integration and foraging. I was stimulated to spend a semester at Harvard in the Museum of Comparative Zoology with WILSON and Bert HÖLLDOBLER, and share an office with Thomas SEELEY who was continuing LINDAUER'S already classic studies of honeybee swarm decision-making. I there wrote my first book, Bumblebee Economics. WILSON had enlarged his ant studies by concentrating on social organization, and he had extended them to taxa throughout the animal kingdom including humans. By comparing bumblebee energetics to Adam SMITH'S economic model I had also extrapolated, but mostly as a heuristic mechanism to teach the unity of the bumblebee system, not to draw ethical or practical conclusions.

At that time in the 1970s the biological atmosphere breathed the theory of kin selection, as formalized by W. D. HAMILTON in the early 1960s, and it was tested and applied to good account to the mystery that DARWIN alluded to and that he thought might prove to be the death knell to his theory of evolution by natural selection. The kin selection hypothesis dramatically rescued it, especially when the haplo-diploidy of the hymenoptera nailed it mathematically (the lack of haplo-diploidy of the termites notwithstanding). In any case, these issues were current and still vigorously debated, and they applied to 'my' bumblebees even though they were clearly social yet specialized individually to maximize individual foraging returns and did not recruit colony-mates to point-sources of food like ant and honeybees did. The explanation seemed to be ecological. In bumblebees, because they are native to relatively open tundra-like habitat where flowers are small and scattered in all directions and each yields very little nectar or pollen, point recruitment would cost time and energy and the energy returns would predictably be less than the investment. On the other hand, honeybees and stingless bees' recruitment can be applied to food bonanzas that yield huge potential returns, by beating the competition, saving time, and reciprocal sharing that all feeds into the hive economy.

It was with these ideas of VON FRISCH'S work on bees and HAMILTON'S on kin selection in mind when I saw a group of ravens at a moose carcass that was almost all covered by brush that I was alerted to an interesting problem. I had since a child had long associations with tame corvids, especially crows, jays and ravens (Fig. 17). The wild ravens in that area of the mountains of western Maine were rare. I knew of only one pair that had nested nearby for years at the edge of a lake. I had never seen more that a family of them together, and that only in the summer. It was October, and the families should since months have been broken up and dispersed; it could hardly be a kin group that was doing an apparent sharing of a huge food bonanza. If it had been ants or bees at a honey-pot I wouldn't have given them a second glance. But ravens? I had heard the commotion from over a kilometre away and had therefore come to investigate. Why were the birds so noisy? Were they recruiting others – who might be strangers? If so, why and how?

Fig. 17 At our Maine farm shortly after we came to America in the spring of 1951. I raised a number of birds as pets, and here with one of my favorites, my crow, Jacob.

The idea of working with such wild wide-ranging birds, who I knew would vanish as soon as the carcass was consumed, were daunting. But I could do one little thing that might be easy to do: record the calls and play them back on a concealed loudspeaker. If I attracted them to the calls then that would show that the calls I heard – the ones that had attracted me to the moose – might also recruit others. In short, such behaviour would constitute recruitment. And if so, the implications seemed astounding since they would phenotypically be sharing, yet necessarily (if evolved) 'selfish'.

My results were positive, as well as negative. Ravens were recruited by the 'yell' calls I had heard (Heinrich 1988), but only if there were ravens already within about a kilometre or two. Yet I knew that the dozen to two dozen ravens at the moose carcass must have come from a considerably farther distance. Was it a stray crowd that had wandered there by chance? Answering this question proved to be one of the for me physically most challenging ones I ever attempted. I would end up needing thousands of pounds of meat/carcasses, something that seemed impossible. But it did become possible because I eventually got a steady flow of meat and dead animals from local butchering places and dairy farms.

Cow carcasses and other huge amounts of meat eventually attracted many ravens (Fig. 18). I became 'hooked' on the magic of these mysterious and extraordinarily shy birds that I eventually came to know intimately from close interactions with many hand-reared individuals. Their mystery deepened when, at some carcasses, I observed fighting. How could there be fighting, if they recruited, as I thought I had proved, many others from a considerable distance?

I knew that, as with the bumblebee and gyrinid beetle studies (Heinrich and Vogt 1980), I needed to identify individuals in order to solve what was becoming an ever-deep-

Fig. 18 A group of ravens, *Corvus corax*, at a skinned sheep carcass in a snowstorm in Maine. Photographed from my blind. This was during my first close look at ravens in the wild from up close (1985).

ening mystery (Fig. 19). I had to capture the birds and mark them. With my bees that step had proved to very simple, and it had been crucial to all the behaviour studies of their foraging behaviour, which included learning, specialization, and sometimes changes of foraging professions. With ravens it seemed to be impossible. But the mystery of their behaviour was too compelling for me to let go.

Leg rings could not be read from a distance and would be of no use for identifying free live birds in the field. But I found that plastic wing tags had worked on ravens in previous studies. There was still the main problem: capturing sufficient numbers of ravens and applying the proven method. Capture seemed impossible in Maine where I found the birds to be extraordinarily shy of humans. Also, I expected the marked birds to disappear almost immediately even if I did manage to catch any and mark them.

I mention here the beginning of these studies only, because the research and the process of it are summarized in two books (Heinrich 1989, 1999 a) and the 32 scientific papers resulting from the studies. It would be tedious here to describe the methods and results of testing six different alternate hypotheses, involving research of birds in the field as well as in a giant outdoor aviary built into the woods (with the help of about a hundred eager volunteers). The whole effort was later greatly amplified especially by the ambitious efforts

Fig. 19 Portrait of raven, showing expanded gular pouch. The snow on the beak is from the bird's making a hole in the snow to hide the meat it has taken from a carcass where it is trying to remove as much meat as possible before the others can, after being recruited there by others.

of two very enterprising and energetic post-doctoral fellows, John Marzluff, who with his wife Colleen came from Arizona and joined up in Maine mainly for field studies, and Thomas Bugnyar who joined me in Vermont to take charge of studies of raven cognition in tame captive birds. Many other wonderful people volunteered their help on part-time bases. Aside from the marvellous post-docs were at one point three students who joined me for a winter in the Maine woods radio-tracking what we thought might be a 'flock' of ravens, but wasn't (Heinrich et al 1994). The romantic setting in the forest in the winter, the physical challenges, and the companionships and teamwork were all memorable. However, above all was the fact that almost every 'answer' led to new questions and surprising revelations. The project with the wild birds became an adventure of a life-time.

The first answer, regarding recruitment in social foraging (Heinrich 1988, Marzluff and Heinrich 1991, Heinrich and Marzluff 1991, Marzluff et al. 1996) involved relatively simple responses, as did the caterpillar foraging that began during my PhD thesis work. In this case, however, 'knowing' what the birds were doing could not be dismissed as a possibility, and that realization then led to questions of 'insight' or problem-solving. It was necessary to find out precisely what they did or could know and why it matters (Bugnyar and Heinrich 2005, 2006). This opened into a new and expanding chapter of studies that is now still being pursued at several levels including the social relations with wolves (Stahler and Heinrich 2002). Ironically for me, as with the unlocking of the sphinx moth physiology mechanism that involved using a length of fine hair, a key method in unlocking whether or not ravens could know, involved a piece of string and a piece of sued (Heinrich 1995a, b, 1999a, b, Heinrich and Bugnyar 2005).

I began this story of biological exploration at the Humboldt Museum about a century ago when Richard Heymons steered my father to the world fauna of the Hymenoptera. Simultaneously, Erwin Stresemann of the same museum made the collecting in the distant tropics possibly by commissioning him to collect birds for this and other major museums of the world. He "opened up the world" to him, and Papa acknowledged him not only as his friend but also his "Gönner" who made things possible. Stresemann's 1939, 1941 publication of the Celebes (Sulawesi) Heinrich collection (in four parts for a total of 461 pages) under commission of the Humboldt and the American Museum of Natural History in New York, has recently been acknowledged (Vuilleumier 2005) to have been the major fodder and basis of Ernst Mayr's work. Celebes is a key island in biogeography because it is in an area of the mixing of the Australian and Indo-Malayan faunas, and Vuilleumier (2005) wrote: "There is no doubt that Stresemann's Celebes monograph is the most significant of his many publications in biogeography." Largely because of the comprehensive bird collection my father made for the Humboldt and American Museum in New York, Stresemann and Mayr (his former student) arguably became the most influential ornithologists and evolutionary biologists of our time. This eventful and at times poignant story I have told in detail in *The Snoring Bird* (2007). I mention it here only to round out my account, by now returning again to the Humboldt.

In 1998 I was in Berlin as a senior Humboldt fellow in the lab of my bee colleague and friend Randolf Menzel. It seemed like an excellent opportunity to visit the Humboldt Museum to see the famous *Archaeopteryx* specimen and look up my father's birds. I especially wanted to see a thrush that Papa had discovered and that Stresemann had allocated to a new genus and named *Heinrichia calligyna*. I was kindly escorted by Dr. Sylke Frahnert, the curator of birds, and she led me into the collections. As I examined the specimens I wondered if it was really a new genus, and how would you know? I also noted that the

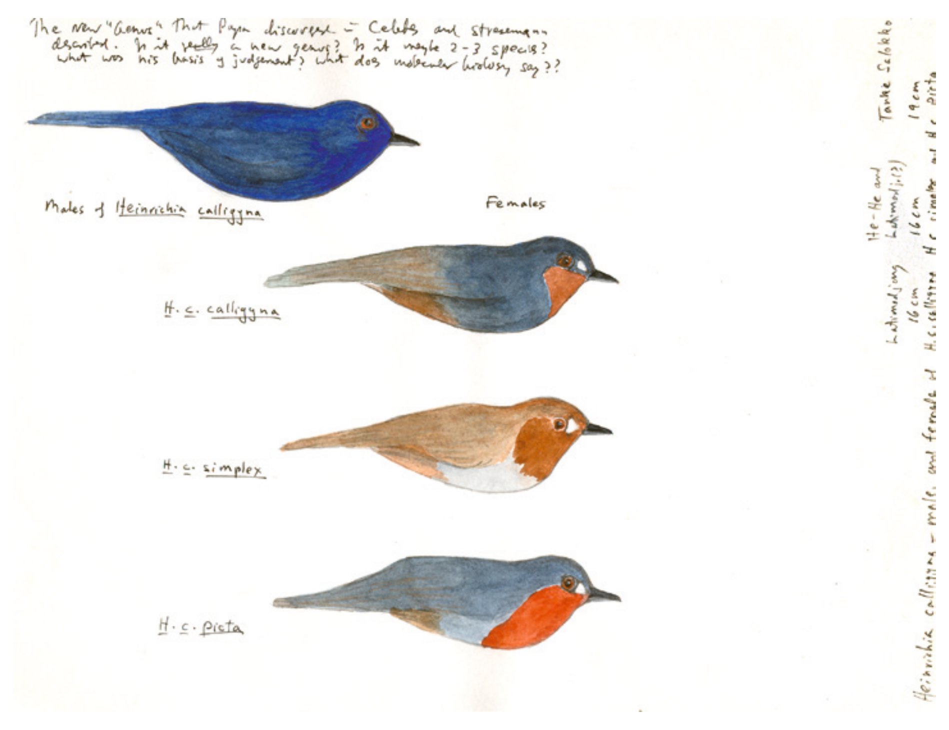

Fig. 20 My color sketch of the *Heinrichia calligyna* (from the specimens at the Humboldt Museum). G. Heinrich collected them in 1930 in Sulawesi, and E. Stresemann named and divided into three subspecies. Is it really a new genus? Are they really different species? Molecular techniques are now bringing possible insights that were not possible before.

birds had come from three different mountain ranges, and Stresemann had assigned them to three sub-species. But there was also a specimen that was on the 'wrong' mountain – or was it misidentified? I wanted to do a watercolour sketch of this bird and so took careful notes, and I noted colour and size differences between the birds (Fig. 20).

I wondered if the supposed one species might actually be two, or maybe three species. Molecular techniques that were unimagined when I was a graduate student were useful in the raven work (Parker et al. 1994) and had become ever-more sophisticated and might now be able to resolve the taxonomy of these thrushes, and Dr. Frahnert secured tissue samples for me from these now over 70 year-old birds from this collection. I located experts whose labs are equipped with the molecular tools to work with this material and to resolve these issues. This work is presently in progress at the Smithsonian Institution in Washington, DC, in the lab of Robert Fleischer and with Ellen Martinsen. Not only is molecular biology not dead, as the then most prominent molecular biologist Gunther Stent had so blatantly claimed in the 1960s, but neither is systematics/taxonomy now, in an age of renewed interest in biodiversity and biogeography, a matter of "stamp collecting" as I had been led to assume when I was a graduate student. Indeed, both molecular biology and taxonomy have and are having a stronger than ever revival, and not only that, they are now bedfellows and have recently become remarkably prolific.

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