

# PRIMATOLOGY

*Theories, Methods  
and Research*



*Emil Potocki  
Juliusz Krasiński  
Editors*

*Animal Science, Issues  
and Professions Series*

NOVA



**ANIMAL SCIENCE, ISSUES AND PROFESSIONS SERIES**

# **PRIMATOLOGY: THEORIES, METHODS AND RESEARCH**

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## **Primateology: Theories, Methods and Research**

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# **PRIMATOLOGY: THEORIES, METHODS AND RESEARCH**

**EMIL POTOCKI  
AND  
JULIUSZ KRASINSKI  
EDITORS**

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# CONTENTS

<b>Preface</b>		<b>vii</b>
<b>Chapter 1</b>	Perspectives in Primate Bioacoustics <i>B. M. Bezerra, A. S. Souto and G. Jones</i>	<b>1</b>
<b>Chapter 2</b>	The Hypothalamic-Pituitary-Adrenal Axis in Nonhuman Primates: Circadian Rhythms of Stress Responsiveness and Aging <i>N.D. Goncharova</i>	<b>29</b>
<b>Chapter 3</b>	Why Apes Point: Pointing Gestures in Spontaneous Conversation of Language-Competent Pan/Homo Bonobos <i>Janni Pedersen, Pär Segerdahl and William M. Fields</i>	<b>53</b>
<b>Chapter 4</b>	Using Sexual Dimorphism and Development to Reconstruct Mating Systems in Ancient Primates <i>Susan Cachel</i>	<b>75</b>
<b>Chapter 5</b>	How Latent Solution Experiments Can Help to Study Differences between Human Culture and Primate Traditions <i>Claudio Tennie and Daniela Hedwig</i>	<b>95</b>
<b>Chapter 6</b>	The Tendency to Make Man An Exception <i>Niccolo Caldararo</i>	<b>113</b>
<b>Chapter 7</b>	Studying Social Development and Cognitive Abilities in Gibbons ( <i>Hylobates</i> spp): Methods and Applications <i>Susan M. Cheyne</i>	<b>129</b>
<b>Chapter 8</b>	Comparing Methods for Assessing Learning and Cognition in Primates <i>Michael J. Beran, Theodore A. Evans and David A. Washburn</i>	<b>153</b>
<b>Chapter 9</b>	Patterns of Daily Movement, Activities and Diet in Woolly Monkeys (Genus <i>Lagothrix</i> ): A Comparison Between Sites and Methodologies <i>M. González and P. R. Stevenson</i>	<b>171</b>

<b>Chapter 10</b>	“How Close Should We Get”– Researchers’ Role in Preventing the Anthropozoonotic Outbreaks in Groups of Free Ranging Chimpanzees and Gorillas <i>Magdalena Lukasik-Braum</i>	<b>187</b>
<b>Index</b>		<b>195</b>



## PREFACE

Primates use four major modes of communication (i.e., visual, olfactory, tactile and vocal), and the ways they communicate depend on restrictions imposed by their habits and habitats. This book discusses past, current and potential future research in the wild and captivity, addressing some of the key questions in primate bioacoustics, identifying gaps in our knowledge, and also describing basic methods and equipment used in the study of primate bioacoustics. Also investigated are the changes of circadian rhythm of the hypothalamic-pituitary-adrenal (HPA) axis activity in nonhuman primates under stress and during aging. This book presents data collected from gibbons in a sanctuary, a rehabilitation center and also the wild highlighting the development of social skills and cognitive abilities. In addition, one of the dominant research areas in behavioral primatology pertains to assessments of the cognitive capacities of various nonhuman primate species. This book outlines studies that compare different methodologies and how those methodologies might contribute to differential learning and cognitive performance. Other chapters in this book examine the cognitive differences between humans and apes, review a powerful experimental methodology to determine the most likely acquisition modes responsible for primate "cultural" patterns, estimate home range use, activity patterns, and diet in woolly monkeys, and discuss the researchers role in preventing disease transmission between humans and apes.

Chapter 1 - Primates use four major modes of communication (i.e. visual, olfactory, tactile and vocal), and the ways they communicate depend on restrictions imposed by their habits and habitats. Primates have varied and complex social systems and vocal communication seems to be an important tool used by these animals to coordinate their sociality. Although vocal repertoires have only been described for approximately 10% of the approximately 645 primate species and subspecies documented so far, vocal communication has received considerably greater attention from researchers than the other communication systems. Previous research on primate bioacoustics has shown, for instance, that knowledge on vocal repertoires may help to: (i) solve taxonomic issues, considering that vocalisations are often species-specific; (ii) improve primate welfare in zoos and laboratories; and (iii) aid surveying primate species in areas where it is difficult to conduct visual surveys. In addition, the physical structure of certain vocalisations can often reveal important information about the caller, such as sex, age, social and behavioural context. Thus, studies on primate bioacoustics clearly generate a greater understanding of primate social ecology and behaviour. In this chapter the authors will discuss past, current and potential future research in the wild and captivity, addressing some of the key questions in primate bioacoustics,



identifying gaps in our knowledge, and also describing basic methods and equipment used in the study of primate bioacoustics.

Chapter 2 - The hypothalamic-pituitary-adrenal (HPA) axis is all-important adaptive neuroendocrine system with the circadian periodicity in the activity. There is some evidence to suggest that the circadian periodicity in functioning of the HPA deteriorates with aging and that these disturbances play an important role in age-related changes of glucocorticoid-sensitive tissue functioning, inadequate reaction to stress and high frequency stress-related pathology in aged individuals. Unfortunately, up to now there have been some unclarities in the character and mechanisms of age-related disturbances in circadian rhythms of corticosteroid production. One of the possible causes of this unsolved problem is the use of inadequate experimental nocturnal models—laboratory rodents—in which the circadian rhythm of the HPA activity is in contrast to that in humans and nonhuman primates.

*The purpose* of this chapter was to investigate changes of circadian rhythms of the HPA axis activity under stress and during aging as well as to evaluate the role of age-related disturbances in melatoninergic and vasopressinergic regulation in their development.

Female *Macaca mulatta* monkeys of 6–8 years (young) and 20–27 years (old) were subjected to acute psycho-emotional stress (two hours immobilization), corticotropin-releasing hormone (CRH) or arginine vasopressin (AVP) injection at 0900h or 1500h on the background of placebo or a pineal tetrapeptide Ala-Glu-Asp-Gly (epitalon) administration (10 µg/animal/day, 10-14 days) as stimulator of the pineal melatonin secretion.

In response to the stress imposed at 1500h, young monkeys demonstrated much higher increase in ACTH and cortisol than to the stress at 0900h. This stress difference attenuates with aging. Compared to old animals, young ones demonstrated much higher responsiveness of the HPA axis to the afternoon stress and a tendency toward lower responsiveness to the morning stress. In response to CRH, young and old monkeys demonstrated the well-defined circadian rhythms in dynamics of ACTH and cortisol. AVP injection did not induce any circadian periodicity in the ACTH and cortisol responsiveness neither in young animals, nor in old ones. However, in response to the afternoon injection of AVP, old monkeys by comparison to the young ones demonstrated lower accretions of ACTH and cortisol without increase in melatonin. The disturbances of the circadian rhythms of the HPA axis responsiveness to AVP and stress were eliminated by epitalon.

Thus, young monkeys showed a circadian rhythm in stress responsiveness of the HPA axis. The rhythm was attenuated in old animals. The age-related changes in circadian rhythms of the HPA stress reactivity were associated with age-related disturbances in melatoninergic and vasopressinergic regulation. The functioning of the HPA was restored by treatment with epitalon.

Chapter 3 - A number of scientists have argued that referential pointing either does not occur among apes or that behaviors in apes which appear as pointing do not have the same underlying psychological mechanisms as pointing in humans does. One prominent argument advanced by Michael Tomasello suggests that cognitive differences between humans and apes preclude declarative or informative pointing in apes.

This study provides evidence that language-competent bonobos, *Pan paniscus*, do indeed point, both declaratively and informatively. Our analysis is based upon data from a video archive of naturally occurring conversations between symbolically competent bonobos and humans. Further, the authors suggest that if pointing is a learned gesture that acquires its meaning in specific communicative interactions in a culture where pointing has a meaningful

purpose, then language-enculturated apes would be expected to point in a way resembling human pointing. An ape not immersed into a culture utilizing index finger pointing, which are the majority of captive apes, would not be expected to exhibit that gesture. Tomasello's argument rests upon questionable empirical evidence, since the apes in the referred experimental studies have not been relevantly reared. By providing evidence that language-enculturated apes do point, the assumptions about the cognitive differences between humans and apes need to be called into question on both theoretical and empirical ground.

Chapter 4 - Male and female interactions are often reconstructed for fossil primates for a number of reasons: To argue that a particular social system is the primitive or ancestral form; to investigate the evolution of mating systems; to examine the potential for infanticide and female counterstrategies; and to study how behaviors like sexual selection and mate choice may have influenced primate speciation. Behavioral reconstruction from fossils is extremely limited. Yet, sexual dimorphism has been used since the 1980s to infer polygynous mating systems in early anthropoids like *Aegyptopithecus*. Rates of growth can be studied from fossil remains using a number of techniques. Despite extensive study, living primates show no good link between degree of dimorphism and social structure. Group composition can be analyzed for fossil primates (including humans) in a few rare cases. In addition to maturation rates in fossils and comparative soft-tissue evidence from living primates, group composition allows a rough outline of social structure to be reconstructed for a limited number of fossil primates. Much more attention has been directed to fossil humans, especially given the existence of multiple hominid species, and sympatry between some early species. The degree of sexual dimorphism in fossil hominids has been used to document hominid status itself and increasing hominization through time, and to infer behaviors such as pair-bonding.

Chapter 5 - Population specific behaviors shown by primates are often regarded as simple forms of culture. In some cases it has been suggested that that the learning processes underlying these primate traditions may be the same as for human culture, namely, process copying (sensu imitation). For example, Mountain gorillas (*Gorilla beringei beringei*) in Karisoke, Rwanda, feed on a diverse range of defended plants by means of complex processing skills. Claims have been made that the required skills are (and must be) learned socially from each other via some form of process copying. However, in general it is often very difficult or even impossible to directly test for underlying transmission processes – especially under field conditions. In this chapter the authors focus on a straightforward and simple, yet powerful experimental methodology to determine the most likely acquisition modes responsible for such primate “cultural” patterns. The underlying idea behind this methodological approach is not a new one: if a population specific behavior represents culture then it should not occur spontaneously in naïve individuals exposed to comparable environmental affordances / constraints. Even rare instances of the same behaviour appearing in only a few naïve individuals (or even in individuals of a related species) should be taken as strong evidence against the cultural hypothesis. In this chapter the authors discuss selected publications as well as previously unpublished data of our own that has applied this methodology. The authors conclude that in general it is premature to put any population specific behavioral patterns in primates into the cultural category. Instead these behaviors seem bound and restricted by “zones of latent solutions”, i.e. the solution space set by the general physical cognitive abilities of a given species.

Chapter 6 - The authors are all familiar with the old saws the authors hear in the press of how special man is, he is the only animal to build houses, change the landscape, have

agriculture, make war. These have all long been shown false, in his delightful 1974 book von Frisch demonstrates the vast number and variety of structures animals of all kinds build and Vander Wall (1990) shows the diversity of food preparation and storage in animals, while E.O. Wilson (1975) and Chavin (1968) describe insect agriculture and warfare. Nevertheless, I am often surprised by the propensity of journalists to magnify any discovered difference between *Homo sapiens* and some other animal as a universal example of man's special place in nature. Even more disappointing is when other scientists display the same tendency. This essay will address a number of areas of *Homo sapiens*' biology and behavior in regards to distinctions with all other animals, the "special place" idea. First I will discuss ideas put forward concerning man's special biology that were argued to place us in a separate taxonomic relation. Secondly I will cover arguments that our biochemistry and molecular chemistry set us off from all other species and finally I will address the areas of behavior and sociality.

Chapter 7 - Social development and cognitive abilities in wild gibbons has received very little attention due to the difficulties of habituating enough animals for a large-scale study. Data from gibbons in captive situations (zoos, sanctuaries and rescue centers) can provide insight into the development of both social skills between individuals, and the development of cognitive abilities within the individual. Gibbon behavior in captivity has correlates to gibbon behavior in the wild and can be used to infer why certain aspects of social or cognitive behavior are seen in the more demanding and complex wild environment. I will present data collected from gibbons in a sanctuary (UK), a rehabilitation centre (Indonesia) and the wild (Indonesia) highlighting the development of social skills and cognitive abilities. Data were collected in a variety of ways and I will discuss the methods and their applicability under different conditions. Data will be presented on object manipulation and tool use and will challenge the assumptions that gibbons are inadequate tool users among the apes. I will also challenge the notion that gibbons have poor social interactions in the wild. The study of social development at all ages can shed light on how gibbon groups maintain their cohesion, not only when traveling but also how the pair bond between the adults is formed and sustained. By using both direct tool manipulation tests and non-invasive behavioral observations by studying gibbons in a variety of captive and wild situations, the authors can begin to answer more questions about the development of social behavior and its function as well as gaining insight into the problem solving and cognitive abilities of the smallest ape. With increased understanding of the development and presentation of cognitive abilities, the authors are in a better position to aid gibbons in rehabilitation and reintroduction programmes and to understand more about these apes in the wild.

Chapter 8 - One of the dominant research areas in behavioral primatology pertains to assessments of the cognitive capacities of various nonhuman primate species. Experiments in this area have shown that primates have many skills that approximate those found in humans. These tests include both manual and computerized assessments, and often the format in which tests are presented can impact the learning and behavioral responding that are produced by subjects. In this chapter, the authors outline two case studies that compare different methodologies and how those methodologies might contribute to differential learning and cognitive performance. In the first, rhesus monkeys responded during a learning task using either joysticks or touch-screens. The task assessed whether the monkeys responded according to stimulus-response associative processes or by using more relational rules about the task. Performance was similar using both input methods and suggested a more associative

response pattern. In the second case, chimpanzees and monkeys learned to sequence stimuli using either a computerized task or through selection of three-dimensional stimuli presented in a manual test. Here, the manual test produced faster acquisition and better performance than the computer task, indicating that in some contexts a hands-on, real world format may produce improved cognitive performance.

Chapter 9 - The authors estimated home range use, activity patterns, and diet in a group of woolly monkeys in Caparú Biological Station (Colombia) during 12 months. These patterns were correlated with fruit supply and compared with previous information reported for woolly monkeys. The comparison shows that the daily distance travelled and home range size were negatively correlated with fruit production. However, woolly monkeys seem to show different ecological strategies depending on the fruiting patterns at each study site. In general, woolly monkeys consume alternative resources (leaves or arthropods) when fruit supply is low, but at Caparú woolly monkeys did not decrease daily path length during periods of fruit scarcity as they do in other places. The activity patterns and diet composition seem to differ among populations, but part of the differences may be explained by the use of dissimilar methodologies. In general, studies which record behaviour by scan sampling tend to overestimate conspicuous behaviours such as movement and fruit feeding, and underestimate less conspicuous behaviours such as resting. The majority of comparative studies recommend the use of both continuous and instantaneous observations on focal individuals.

Chapter 10 - Chimpanzees and gorillas are the closest relatives of humans living on the Earth. Due to this fact they are susceptible to most of human infectious diseases, but the outcome of infection is often very different than in humans.

Chimpanzees can be infected with the HIV virus, but they never develop the actual disease. Opposite situation happens with some other human viral diseases. Common Flu, Metapneumovirus or Respiratory Syncytial Virus, which in post-infant humans are rarely considered the serious diseases, have been recorded to be fatal when transmitted to Great Apes.

In various countries in Africa researchers have witnessed numerous outbreaks of infectious, mostly respiratory diseases in ape communities, which could be traced back to humans as the source. Often most of the ape group would be affected with mortality reaching over 20%.

Gorillas in Rwanda are visited daily by the KARISOKE research team and by the trackers and tourists, which on average adds up to 2000 human visits to each gorilla per year. The numbers of respiratory cases monitored/treated by the Mountain Gorilla Veterinary Program team are at the very top on the list of the infectious diseases affecting gorillas in Virunga NP.

According to the field experience from 3 East African countries, researchers can play positive or negative, but always significant role in following the preventive visitation rules themselves and assisting the National Park offices in doing the same for the tourist visits.



*Chapter 1*

## **PERSPECTIVES IN PRIMATE BIOACOUSTICS**

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### **ABSTRACT**

Primates use four major modes of communication (i.e. visual, olfactory, tactile and vocal), and the ways they communicate depend on restrictions imposed by their habits and habitats. Primates have varied and complex social systems and vocal communication seems to be an important tool used by these animals to coordinate their sociality. Although vocal repertoires have only been described for approximately 10% of the approximately 645 primate species and subspecies documented so far, vocal communication has received considerably greater attention from researchers than the other communication systems. Previous research on primate bioacoustics has shown, for instance, that knowledge on vocal repertoires may help to: (i) solve taxonomic issues, considering that vocalisations are often species-specific; (ii) improve primate welfare in zoos and laboratories; and (iii) aid surveying primate species in areas where it is difficult to conduct visual surveys. In addition, the physical structure of certain vocalisations can often reveal important information about the caller, such as sex, age, social and behavioural context. Thus, studies on primate bioacoustics clearly generate a greater understanding of primate social ecology and behaviour. In this chapter we will discuss past, current and potential future research in the wild and captivity, addressing some of the key questions in primate bioacoustics, identifying gaps in our knowledge, and also describing basic methods and equipment used in the study of primate bioacoustics.

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## INTRODUCTION

Communication is very important in many interactions among animals such as aggression, predation, feeding, playing and mating (e.g. Marler, 1961; Shettleworth, 1998; Strier, 2003). Each primate species has its own repertoire of communication signals and the use of it will depend on the restrictions imposed by the habits and habitats of the species (Napier & Napier, 1996; Corewyn, 2003; Krebs & Davies, 1996; Bradbury & Vehrencamp, 1998; Brumm et al., 2003). Animal communication signals are defined as any act or structure that modifies the behaviour of receivers. Signals are used to communicate about anything of importance and bring advantages to the signaller or their kin (Harvey & Greenwood, 1978; Bradbury & Vehrencamp, 1998; Maynard Smith & Harper, 2007; Hailman, 2008). The signal can either carry information about the signaller or about the external world (Maynard Smith & Harper, 2007).

The communication system of primates is represented by complex and varied signals such as vocalisations, facial expressions, tail wagging, genital displays, fur coloration, tongue flicking, piloerection, body postures, various odours, grooming and tactile stimuli. These signals can be classified into four major categories of communication: vocal, visual, olfactory and tactile. These categories are used alone or in combination, and their usage is an extremely important prerequisite for maintaining the complex social structure that primates possess (Marler, 1965; Bastian, 1965; Strier, 2003). Fundamentally, the ability to communicate comprises the capacity to: (i) produce the correct signal; (ii) signal in the correct context; and (iii) respond correctly to the signal (Maynard Smith & Harper, 2007).

In this chapter we will conduct a brief overview of the four modes of communication used by primates. We will focus on vocal communication, discussing research in the wild and captivity. We will address some of the major questions being asked in primate bioacoustics, identifying gaps in our knowledge and also briefly describing important methods and equipment used for studies on primate bioacoustics, the science of sounds produced by or affecting the behaviour of living primates.

## Visual Communication

There are three main categories of visual communication: (i) postures and body movements, (ii) piloerection displays and (iii) facial expressions (Moynihan, 1967). Body postures are common in all primates (i.e. monkeys, apes and prosimians), unlike facial expressions, which are restricted to monkeys and apes (Strier, 2003). *Cebus* species, for example, have a range of different facial displays used in visual communication (Figure 1) (e.g. De Marco & Visalberghi, 2007). Some visual signals are often displayed together with other communication signals (Bastian, 1965; Ghazanfar et al., 2002; Ghazanfar & Logothetis, 2003). For instance, common marmosets, *Callithrix jacchus*, are very territorial (e.g. Stevenson & Rylands, 1988) and during intergroup encounters they perform piloerection and display inflated genitals (Figure 1), together with a range of threatening vocalisations (Stevenson & Poole, 1976; Stevenson & Rylands, 1988; Bezerra & Souto, 2008). During play behaviour (Figure 1), common marmosets use visual communication (e.g. facial expressions) associated with vocal communication (e.g. uttering moaning calls) and tactile communication



(e.g. touches, hugs and soft bites) (Stevenson & Poole, 1976; Stevenson & Rylands, 1988; Bezerra & Souto, 2008). It is not easy to study visual communication, because the identification and classification of signals is not always simple. Various morphological and chromatic features involved in animal visual communication are expressed constantly (e.g. patterns of fur coloration), independent of the signaller's motivational state or environmental conditions, unlike, for example, acoustic signals which are usually produced under specific circumstances and by organs whose primary function is the production of these signals (Rosenthal & Ryan, 2000).



(a)



(b)



(c)



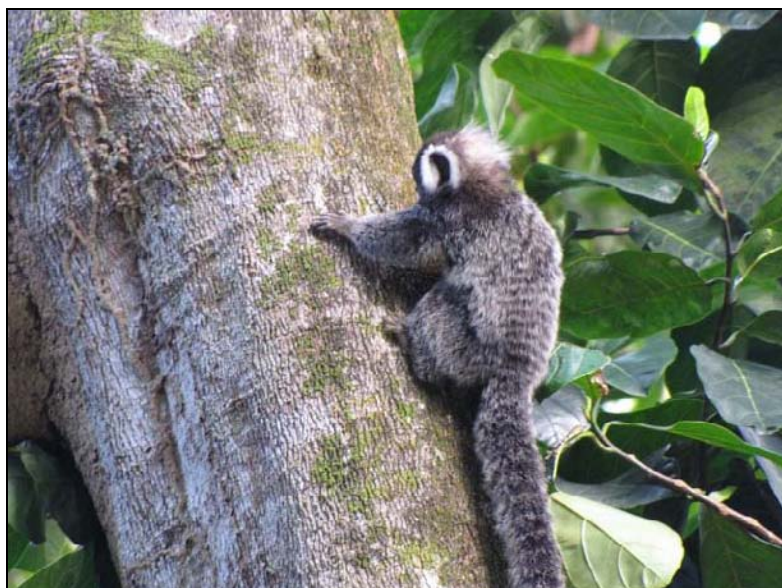
(d)

Figure 1. Visual communication: (a) common marmosets are showing off inflated genitals during an intergroup encounter (Photo: Souto); (b) a common marmoset's facial expression during social play; (c and d) facial expressions by *Cebus xanthosternos*, the golden-bellied capuchin (Photos: Bezerra).

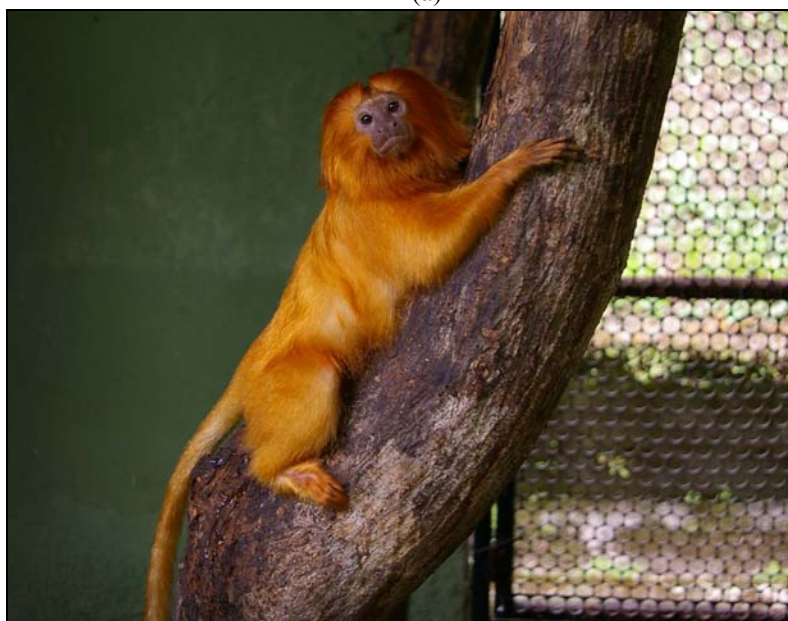
## Olfactory Communication

The study of olfactory communication is still in its infancy. Unlike visual signals, chemical signals do not rely on light for their perception, they remain effective even in the absence of the signaller and the information encoded is usually long-lasting without the need for frequent signal emission (e.g. Smith, 2006). Although chemical signals have little role in long distance communication in primates (Marler, 1965), they have important functions in, for example, intergroup resource defence, in advertising individual quality and competitive

ability, and in individual recognition (Halpin, 1986; Porter, 1999; Heymann, 2006). Common marmosets and golden lion tamarins, *Leontopithecus rosalia rosalia*, for instance, have specialized scent glands on their chests, suprapubic and/or anogenital areas and use these to produce secretions for marking objects (e.g. Stevenson & Poole, 1976; Epplé, 1970; Epplé, 1972; Kleiman, 1983; Lazaro-Perea et al., 1999, Figure 2a and b). These chemical signals are known to carry an olfactory signature in common marmosets (Smith 2006).



(a)



(b)

Figure 2. (a) Wild common marmoset engaged in scent marking behaviour (Photo: Souto); (b) Captive golden lion tamarin engaged in scent marking behaviour (Photo: Bezerra).

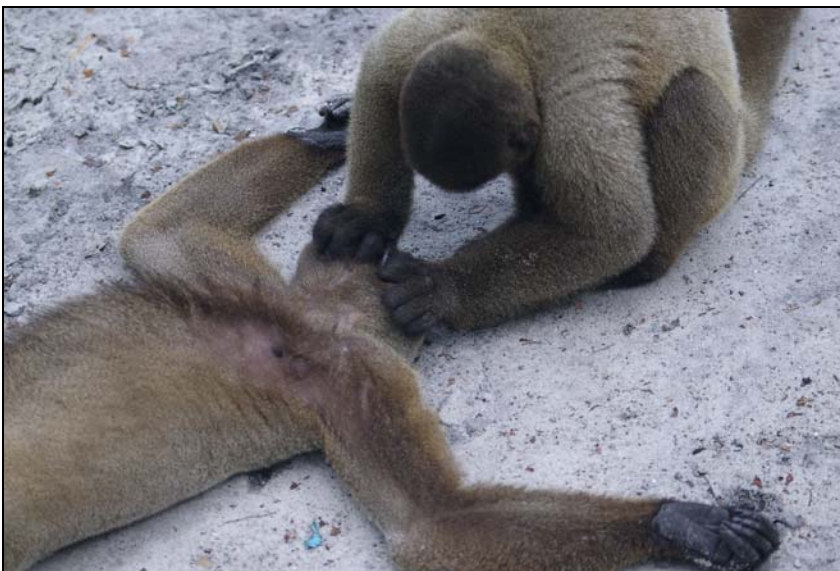


## Tactile Communication

In contrast to the other communication modalities, the signaller has to be in physical contact with the receiver during tactile communication. This communication system is often associated with close distance social activities, especially social grooming (Marler, 1965). woolly monkeys, *Lagothrix lagothricha*, common marmosets and several other primate species use both their hands and mouths during social grooming (Figure 3; e.g. Kavanagh & Dresdale, 1975; Stevenson & Poole, 1976 Alonso & Langguth, 1989; Digby, 1995). In common marmosets, social activities, including grooming, comprise 44% of their behavioural time budget (e.g. Digby & Barreto, 1996), showing how important tactile communication is for this species.



(a)



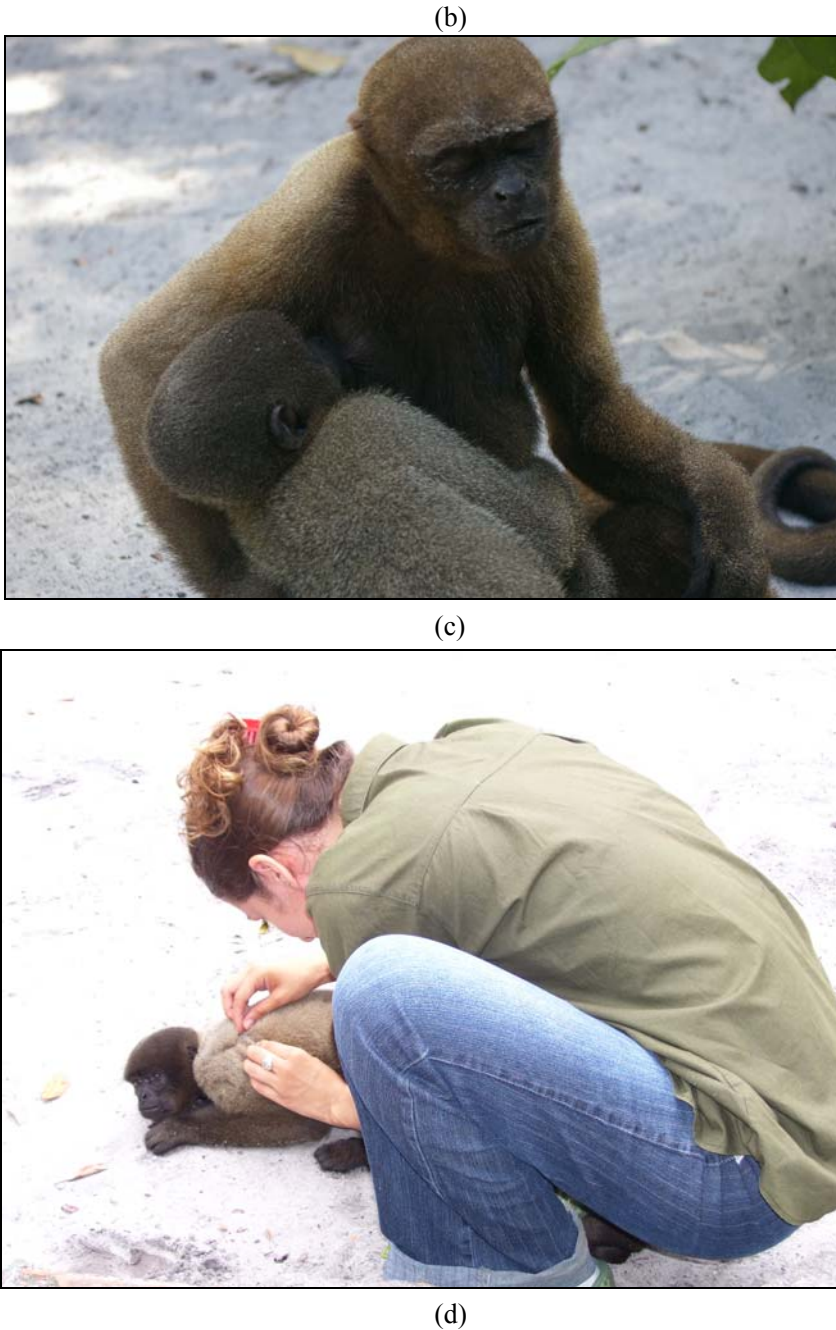


Figure 3. Examples of tactile communication: (a) adult common marmosets engaged in social grooming (Photo: Souto); (b) woolly monkeys also engaged in social grooming; (c) female woolly monkey nursing infant (Photos: Bezerra); (d) Inter-specific grooming (Photo: Souto).

## Vocal Communication

Primates often have varied and complex social systems and vocal communication seems to be an important instrument used by these animals to coordinate their sociality, especially for arboreal primates, due to the poor visibility within their habitats (Altmann, 1967; Owings & Morton, 1990; Yamamoto, 1991; Geiss & Schrader, 1996; Napier & Napier, 1996; Prescott, 2006). Acoustic signals can often function over further distances than other communication signals (e.g. Rosenthal & Ryan, 2000) and their propagation in habitats where primates exist is influenced by factors such as frequency of the vocal signal, height of the sound source, atmospheric and micro meteorological conditions and even time of day (Ingard, 1953; Marten et al., 1977; Waser & Waser, 1977; Morton, 1975; Waser & Brown, 1986; Brown & Waser, 1988; Laron et al., 1997; De la Torre & Snowdon, 2002; Hayes & Huntly, 2005; Sugiura et al., 2006). Investigating how animals cope with sound distortion, for example, is important if we are to create a greater understanding on the evolution of animal communication (Bradbury & Vehrencamp, 1998). Furthermore, in general, understanding the vocalisations of primates is an important step towards a better understanding of their behaviour, sociality and ecology.

Although we only have vocal repertoires described for about 10% of the approximately 645 primate species and subspecies documented so far, vocal communication had received considerably greater attention from researchers than the other communication systems (Tomaselo & Call, 1997; Gouzoules & Gouzoules, 2007). This is probably because vocal signals are far more straightforward to analyse and easier to quantify than are visual, tactile and olfactory signals (Egnor et al., 2005). Furthermore, acoustic signals are more easily identifiable than other communication signals (e.g. Rosenthal & Ryan, 2000). In general, knowledge on acoustic repertoires may help us to (i) solve taxonomic issues, considering that vocalisations are often species-specific (e.g. Jones et al., 2000; Struhsaker, 1970; Quris, 1980; Hodun et al., 1981; Haimoff et al., 1982; Snowdon et al., 1986; Zimmermann, 1988; Courtenay & Bearder, 1989; Hohmann, 1989; Snowdon, 1993); (ii) improve primate welfare in zoos and research laboratories (e.g. Boinski et al., 1999; Dawkins, 2003; Dawkins, 2004; Hewson, 2004; Cross & Rogers, 2006; McCowan & Rommeck, 2006); (iii) and help surveying primate species in areas where it is difficult to conduct visual surveys (e.g. Casting et al., 1997; Bezerra et al., 2008). In addition, knowledge of primate acoustic signals may help us to address fascinating questions such as: do primates have language or dialects? Do they emit 'honest' signals of quality, or can they deceive? Do vocal signals carry information on primate emotional state? Is there vocal learning among primate species?

Recordings of vocalisations and playback experiments on primates were made first in captivity in 1890 (Garner, 1891; 1892; and see Radick, 2007). Garner was a pioneer in the study of primate bioacoustics and the creator of a new method for its study, i.e. using a phonograph (see Radick, 2005; Radick, 2007). Thanks to the bioacoustics studies on wild and captivity that followed the ones made by Garner, we now know, for instance, that structure and/or usage of primate vocalisations are influenced by factors such as phylogeny, body weight, sex, age, dominance rank, social and behavioural context, time of the day and environmental conditions (e.g. Marten et al., 1977; Gautier & Gautier-Hion, 1982; Inoue, 1988; Hauser, 1993; Hammerschmidt et al., 1994; Laron et al., 1997; Weiss et al., 2001; Miller et al., 2004; Hayes & Huntly, 2005; Scott et al., 2006; Bezerra et al., 2009b). Studies in

captivity are ideal for hearing faint and subtle calls, whereas clear knowledge of the natural frequency and usage of calls is more likely to be achieved in the wild (Bearder, 2007).

Although primatologists often focus their studies on particular calls from particular species, inter-specific comparisons of acoustic repertoires should be more explored as they can allow assessment of hypotheses associated with general evolutionary principles (Bradbury & Vehrencamp, 1998; Gros-Louis et al., 2008). For instance, according to McCombe & Semple (2005), evolutionary increases in vocal repertoire size among non-human primate species are associated to increases in both group size and degree of social bonding. The vocal repertoires of primates are usually associated with behavioural context and the vocalisations can even be conditioned and uttered under voluntary control (e.g. Sutton et al., 1973; Cheney and Seyfarth, 1990; Di Bitetti, 2003). For example, vervet monkeys, *Cercopithecus aethiops*, Diana monkeys, *C. Diana* and Campbells' monkey, *C. campbelli*, produce different predator alarm calls depending upon the type of predator that has been seen, which result in predator-specific behavioural responses by the social group (Struhsaker, 1967; Cheney & Seyfarth, 1990; Zuberbühler, 2000b). Similarly, common marmosets emit predator-specific calls, one for aerial and one for terrestrial predators, and also produce a distinctive mobbing call (Bezerra & Souto, 2008; Bezerra et al., 2009a). Common marmosets also produce calls that are frequently uttered in other specific situations such as play (i.e. the 'moaning' call) and submissive interactions (i.e. the 'submissive cry') (e.g. Epplé, 1968; Bezerra & Souto, 2008). Two nocturnal primates, large-eared greater bush babies, *Otlemur crassicaudatus*, and southern lesser galagos, *Galago moholi*, have a rich repertoire of calls associated with situations of potential danger (Bearder, 2007). Cotton-top tamarins, *Saguinus oedipus* produce short, high pitched calls during foraging, which seem to be related to individual food preferences (Roush & Snowdon, 1999). Infants of the pygmy marmoset, *Cebuella pygmaea*, emit babbling calls that consist of an immature version of the vocal signals produced by adults (i.e. call structure encodes information about the age of the caller), and babbling calls are often used in social interactions. The infants that use this vocalisation more frequently are also those that are more often carried by older group members (Snowdon, 2001). Information about the age and gender of a vocalising animal, as well as a close consideration and careful monitoring of the behavioural, social and environmental context of the vocalisation, are essential prerequisites for ascertaining the function of specific vocalisations (McLanahan & Green, 1977; Bearder, 2007).

Even though studies suggest that some calls encode very limited information (e.g. Owren & Rendall, 2001), others have shown that the structure of certain vocalisations (i.e. number of syllables, syllable duration, inter-syllable interval, frequency structure, the number of harmonics in the vocalisation and the interval between harmonics) can reveal significant aspects about the caller, such as sex, social group, population, age, social and behavioural context, and even an individual signature (e.g. Green, 1975; Pook, 1977; Green, 1981; Jones et al., 1993; Norcross & Newman, 1993; Schrader & Todt, 1993; Geiss & Schrader, 1996; Norcross et al., 1999; Ghanzafar & Hauser, 2001; Rukstalis et al., 2003; Roian Egnor & Hauser, 2004; Terry et al., 2005; Scott et al., 2006; Ey et al., 2007; Bezerra & Souto, 2008). Playback experiments showed that female squirrel monkeys, *Saimiri sciureus*, and Japanese macaques, *Macaca fuscata*, for instance, recognize their infants by vocalisations, thus, confirming that vocal signatures can have functional significance (Symmes & Biben, 1985; Shizawa et al., 2005). As in any bioacoustics study, evidence for vocal signatures can only be



confirmed from playback studies, and not solely from statistical analyses that show differences in vocal structure.

The ‘trill’ call (Figure 4a) of common marmosets is a short distance contact call that seems to carry information about the age of the caller (Bezerra et al., 2009b), whereas ‘phee’ calls (Figure 4b), a long distance contact call, are believed to carry an individuals’ vocal signature (e.g. Jones et al., 1993). Sex-specific vocal profiles are less expected in species with little sexual dimorphism (Gautier & Gautier-Hion, 1982; Scott et al., 2006), like common marmosets, for example. As for age-differences in vocalisations, they are believed to be the result of a mixture of factors such as the length of folds, size and shape of vocal tracts, physiological and morphological changes over time, and behavioural experience (Snowdon, 1988; Elowson et al., 1992; Pistorio et al., 2006; Ey et al., 2007; Bezerra et al., 2009b). Experiments and observations conducted with several primate species (e.g. observing natural vocal development and restricting auditory experience by deafening, isolation or cross-fostering) showed that although experience plays a major role in the ontogeny of call usage and comprehension, it plays a small role in call production by primates (see Roian Egnor & Hauser, 2004; Maynard Smith & Harper, 2007).

Dominance rank, an important aspect of many primate societies, influences hormone levels, behaviours and sociality (e.g. Saltzman et al., 1996; Abbott et al., 2003; Pistorio et al., 2006) and consequently affects vocalisation usage and structure as well. It is known that many primate calls have a specific context, and also possess the potential for honest signalling (e.g. Gouzoules & Gouzoules, 2002). For instance, studies suggest that differences in vocal structure within and between species are related to body size or weight (e.g. Gouzoules & Gouzoules, 1990; Hauser, 1993). However, some primate species are also capable of deceiving through vocalisations. For example, bonnet macaques, *Macaca radiata*, utter loud predator alarm calls when they are chased by dominant males of the troop. The dominant aggressors then flee, even though there are no predators around (Sinha, 2003). Deceptive behaviour has been observed in many other primate species such as black lemurs, *Eulemur macaco* (Genty & Roeder, 2006), squirrel monkeys, (Anderson et al., 2001), capuchin monkeys (Mitchell & Anderson, 1997; Fujita et al., 2002), and rhesus monkeys, *Macaca mulatta* (Santos et al., 2005). Deceptive communication may have evolved where there is a high predictability in an animal’s answer to signals (Gouzoules & Gouzoules, 2002).

Like human infants, cotton-top tamarins and possibly other primate species are capable of encoding some of the statistical regularities existent in language-like auditory sequences (Conway & Christiansen, 2001). However, they appear to be limited in their capacity to learn and represent the hierarchical structure of sequences, which may help to explain why non-human primates do not have a human-like language (Conway & Christiansen, 2001). Although rarely observed, some primate species seem to present dialects and accents. For instance, after studying fourteen groups of pygmy marmosets, across five populations in northeastern Ecuador, De la Torre & Snowdon (2009) reported population differences in the structure of two vocalisations, the trills and ‘J’ calls. Mitani et al. (2005) found population differences in the structure of a long distance call, known as the pant hoot, of chimpanzees, *Pan troglodytes schweinfurthii*, living in Tanzania. Furthermore, geographically distant populations of Japanese macaques also present variations in the structure of ‘coo’ vocalisations (Green, 1975).

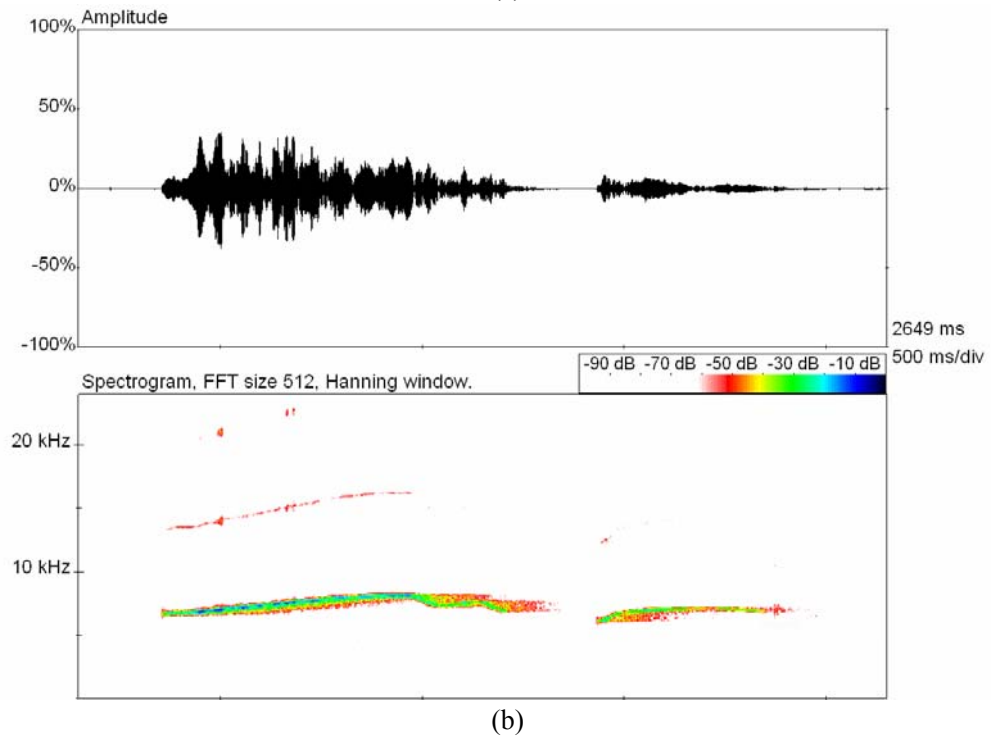
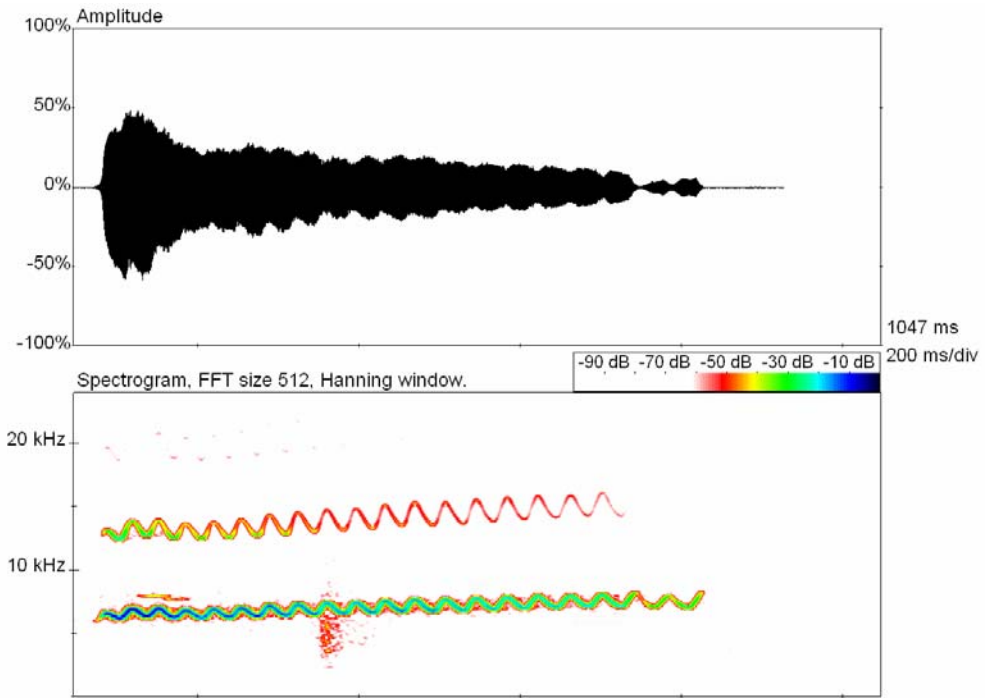


Figure 4. Spectrogram and waveform of a 'trill' call (a), a close contact call of common marmosets; and a 'phee' call (b), a long distance contact call of common marmosets.

Although the first playback experiment was conducted in the 1890s, the act of reproducing a sound to a primate and observe its response was only performed again by researchers in the late-1970s (Radick, 2005). After that, various studies using playback experiments were conducted with wild and captive primates, helping to reveal important aspects of their communication, cognition and ecology. Understanding primate communication is the way to begin understanding their cognitive skills and information-processing systems (Strier, 2003). For example, the famous playback experiments made by Cheney & Seyfarth on vervet monkeys showed how these animals classified and recognized different types of predators (Cheney and Seyfarth, 1990). Playback experiments on putty-nosed monkeys, *Cercopithecus nictitans stampflii*, and Diana monkeys showed that the former offer antipredation benefits to Diana monkeys. The latter recognize, and respond to, the predator-specific alarm calls of putty-nosed monkeys (Eckardt & Zuberbühler, 2004). Moreover, playback experiments revealed that captive cotton-top tamarins do not distinguish between vocalisations of predators and nonpredator mammals, which can have serious implications for reintroduction of these animals to the wild, for example (Friant et al., 2008).

## METHODS/EQUIPMENT IN PRIMATE BIOACOUSTICS

The collection and analysis of animal vocalisations has been used in the, identification of species, populations and individuals, for playback experiments, for attracting and trapping animals and even for deterring pests (e.g. Jones et al., 2000; Struhsaker, 1970; Quris, 1980; Hodun et al., 1981; Haimoff et al., 1982; Snowdon et al., 1986; Zimmermann, 1988; Courtenay & Bearder, 1989; Hohmann, 1989; Snowdon, 1993; Casting et al., 1997; Boinski et al., 1999; Dawkins, 2003; Ranft, 2004; Dawkins, 2004; Hewson, 2004; Cross & Rogers, 2006; McCowan & Rommeck, 2006; Bezerra et al., 2008). When recording animals, it is important to always identify the species, habitat type, the behavioural and social contexts of vocalisations, the date, time and weather conditions (Lehner, 1996). Research on primate bioacoustics is carried out using equipment and techniques that often have to be adapted to the primate species, environmental conditions and aims of the study. Below we give a brief overview about some of the essential equipment used in primate bioacoustics research, and point out the importance and difficulties involved in choosing the equipment with the highest quality and fidelity.

### Microphones

Sound is basically a form of wave motion in which a pattern of pressure is propagated through an elastic medium (Speaks, 2005). Microphones will convert the acoustic signal (sound pressure) into an electric signal (Bradbury & Vehrencamp, 1998). Microphones can be dynamic or condenser. Basically, unlike dynamic microphones, condenser microphones have a wide and relatively flat frequency response, and are powered by an external power. The condenser microphone consists of a “metal plate and a thin membrane of plastic (called a diaphragm) on which a fine layer of metal has been deposited” (Bradbury & Vehrencamp, 1998). The diaphragm changes the capacitance between the metal plate and itself and both

end up acting as electrodes. Dynamic microphones have a diaphragm connected to a mobile coil that produces voltage when air passes moving the coil between the poles of a magnet (but see Ballou, 2002). Microphones can vary in their directional characteristics (e.g. they can have omni-directional, cardioid or supercardioid polar patterns). Omnidirectional microphones are sensitive to sounds in all directions, whereas cardioid and supercardioid microphones are most sensitive to sounds in front of them (e.g. Lehner, 1996). Cardioid microphones (shotgun microphones) are the ones commonly used in primate bioacoustics research (Figure 5) and they must have a relatively flat frequency response (usually ranging between 40-20,000 Hz) for use in bioacoustics studies on primates. A good cable to connect the microphone to the recording device is necessary. The cable choice will depend on the microphone and recorder output/input connections. Parabolic reflectors attached to microphones provide a higher degree of directionality. However, they can sometimes distort the frequency response of the microphone system. The parabolic reflector is only effective at wavelengths shorter than the diameter of the dish and only larger dishes are recommended for primate studies (Geissmann, 2001; Geissmann, 2003), which makes the reflector difficult to carry in habitats such as densely vegetated tropical rain forest.

## Recorders

Once the microphone converts the sound pressure into an electrical signal, it should then be recorded. Having good headphones attached to the recorder is very useful to monitor the sound while recording it. Furthermore, obtaining a recorder with a relatively broad and flat frequency response, usually within the range 40 Hz to 20 kHz is important for primate studies. In the past sound recorders were analogue (e.g. Sony Professional Walkman cassette recorders). Although these devices are rugged and still appropriate for field use most new devices available are digital. Indeed, recordings can be made directly to a laptop computer, although such equipment is cumbersome and can be difficult to use in the field. Recordings can be done in many different formats (e.g. wav, mp3, mp4), although it is important to make the recordings in an uncompressed format (e.g. wav), so that information loss from the acoustic signal is minimised. Solid-state card recorders are now the most used type of recorder for primate research (Figure 5). They record the sound straight to CompactFlash (CF) memory cards, and have no moving parts (which means less energy draw on batteries), no machine noise to interfere with recordings and fewer parts that can jam, bend or break (e.g. Runstein & Huber, 2005). The sampling rate used in digital acquisition of sound must be at least twice the highest frequency in the signals being recorded so that aliasing is avoided. A sampling rate of at least 44 kHz is appropriate for most primate vocalisations.

For many years tape-recordings and reel-to-reel tape recorders were very popular in primate bioacoustics research. However, these analogue recorders often introduced recording speed errors and degrade the acoustic signals by adding hiss, distortion and/or alterations in frequency response (Geissmann, 2001; Geissmann, 2003; Ranft, 2004). Tapes also can break and may degrade when stored in the lab for long periods. On the other hand, analogue machines are usually very good at coping with extreme field conditions (e.g. the high humidity typically found in tropical forests inhabited by primates).



Figure 5. Recording system used by Bezerra: a solid-state card recorder (Marantz PMD670) is connected to AKG K44 headphones and to a Sennheiser ME68 microphone with a K6 powering module (Photo: Souto).

DAT (Digital Audio Tape) recording systems followed the analogue recorders. The frequency response of DAT recorders allows very good recordings from low frequency signals to up to 22 kHz and the recording system prevents tape noise and non-linear frequency response. However, they are very sensitive to humidity and thus, are not very reliable in the field (Geissmann, 2001; Geissmann, 2003). Other technologies such as some MiniDisks (MD), digital compact cassette (DCC) and MP3, tried to get into the market on primate bioacoustics research, however, these recording devices are not recommended, because the sound data are compressed and may result in the loss of important information about the physical structure of the calls (Geissmann, 2001; Geissmann, 2003). Also, many recording formats such as DAT are in danger of becoming obsolete and lack long-term support in case of equipment failure. MP3 players that also allow the recording of uncompressed sound at high sampling rates are highly portable and have potential use for bioacoustics studies. It is vital that recording equipment includes a 'line in' socket and that recording levels can be adjusted manually.

## Speakers

It is worth considering the size, weight and type of battery when choosing a speaker/amplifier for playback experiments. The frequency response is also important, and the playback system should have a frequency response that does not substantially alter the power spectrum of the recorded call. In the field it is always useful to use equipment that is small and not very heavy (e.g. Figure 7). Saul Mineroff Electronics, Inc. provides a good portable field speaker (Model: SME-AFS) that has its own volume control/amplifier. It can be

carried easily in the field and is very useful to survey species through playback of calls. We used this speaker recently to conduct playback experiments in the Amazon black-water flooded forest, Igapó forest, to survey a rare shy primate, the golden-backed uacari, *Cacajao melanocephalus ouakary* (Figure 6). Other speakers used in primate playback experiments have included Toshiba SS-A1W, Nagra DSM; Anchor AN-256; Anchor mini-vox PB-25; Sony SRS; Advent AV570 (e.g. Gebo et al., 1994; Hauser, 1998; Zuberbühler, 2000a,b; Gil-da-Costa et al., 2002; Yorzinski & Ziegler, 2007; Lameira & Wich, 2008). It is also important to pay attention to the amplitude of playback systems, so they are representative of the signal strengths used by the study species in nature. Inexpensive sound pressure meters can be purchased to estimate the amplitudes of both emitted signals and playback sounds in primate bioacoustics studies. For studies of sound intensities, condenser microphones with flat-frequency responses, such as those made by Bruel and Kjaer and Larson-Davis are recommended, and these can be calibrated with a sound pressure meter calibrator.



Figure 6. SME-AFS Portable field speaker (Saul Mineroff Electronics, Inc) (Photo: Bezerra) used for playback experiments conducted in the Igapó forest. The arrow points the speaker positioned on the camouflaged canoe (Photo: Almeida T).

## Sound Analysis

We use sound analysis software to display the physical features of acoustic signals graphically. Software can generate waveforms of the signal (showing the amplitude of the signal over time, Figure 4a-b top) and spectrograms, where the vocalisation is graphically represented as frequency against time (Omedes Regas 1983; Owren & Linker 1995; Figure 4a-b bottom). Waveforms are especially useful to determine whether the signal is overloaded by the use of too high recording levels. Overloaded signals have clipped waveforms (flattened on top), and overloaded signals often include spurious harmonics. Power spectra are useful to determine which frequencies contain most energy in calls. A range of software devoted to the analyses of animal vocal signals is available, with some programmes available for free (e.g. SYRINX-PC sound-analysis Software; Sound Analysis Pro; Sound ruler) and others commercially available (e.g. Signal and RTS; Avisoft, Raven and BatSound). The images in Figure 4 were made using BatSound 3.31 computer software (Pettersson. Elektronik AB, Sweden).

## Choosing the Right Equipment

Any scientific equipment must be as precise as possible. Researchers commonly rely on the technical data sheet provided by the manufacturers to choose between competing products. These data are assumed to be reliable and are often copied to the material and methods section of a paper to justify the use of a particular device. However, researchers who look for information elsewhere face sometimes conflicting specifications, a factor that confounds the process of choosing between products and might reflect on the final quality of the research. We have recently faced a dilemma when acquiring a microphone, commonly used in bioacoustics investigations. We were confronted with the data sheet provided by the company manual, and a review carried out by Schoppmann (1999). Eleven directional microphones were compared in this review. While the manufacturer of the microphone claims a frequency response of 40-20.000 Hz (+/- 2.5dB), the test detected losses of more than 6 dB at frequencies below 200 Hz and of 15dB at 20 kHz. In the review, none of the eleven microphones presented a flat response at frequencies up to 20 kHz (we consider here a flat response when the gain or loss does not exceed 3 dB), but some microphones that are relatively unknown to the scientific community presented losses of less than 9 dB. What we have to consider here is the possibility that we are not having access to unbiased technical data concerning the devices we chose to use in our investigations. We suggest that the researchers who have access to technical labs carry out comparative tests on such devices and publish their findings in scientific journals. This seems to be the best alternative to help colleagues in their decision-making and also in improving research quality.

## Experimental Design

When doing playback experiments, two important points should be considered, pseudoreplication and experiment execution (McGregor, 2000). Although nowadays researchers are more aware of those points, in the past years many of them fell into pseudoreplication when trying to maximize the level of replication of their experiments (Hurlbert, 1984; Heffner et al., 1996; McGregor, 2000; Kroodsman, 2001). Pseudoreplication is defined by Hurlbert (1984) as “the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent”. Pseudoreplication must be considered during the design stage of an experiment, and the questions to be addressed must be clearly defined at this stage too (McGregor, 2000). In order to avoid pseudoreplication in playback experiments one must have multiple stimuli to represent a class of stimuli (e.g. having different recordings of one particular call type, and depending on your aims, uttered by different individuals). Researchers are encouraged to increase independence by using stimuli a minimum number of times possible, and if signals are reused, an average of the responses should be obtained to generate a single data point as the response to that particular stimulus (Kroodsma, 2001). Replication must also be considered at the level of the receiver: in an ideal playback experiment, both the stimuli and the test subjects should be different individuals or recordings of individuals. This will generate true replication, which is essential if we aim not to have limited or invalid conclusions (Heffner et al., 1996). For experiment execution, it is important to consider a time interval between playback trials (e.g. 48 hours), so that



habituation to the stimuli does not become a problem. Also, one should remember that the sound pressure levels of the stimuli must be calibrated using a realistic sound pressure level meter to match with that of the natural stimuli levels. Video recording the responses of the animals and having them individually identified is also ideal, though it is not always possible in free-living primate research due to fieldwork constraints (e.g. level of habituation and habits of the animals, and difficult access to natural environments). Schlupp (2000) and McGregor (2000) show detailed information on several issues regarding experimental analysis (e.g. number and types of response measurements, how responses should be treated and how to interpret lack of response).

## PRIMATE BIOACOUSTICS & CONSERVATION

Collections of animal sounds may also serve for education, entertainment and nature conservation (Alström & Ranft, 2003; Ranft, 2004). The use of sound collections for these purposes is represented by playing the audio files in museums and zoos, in teaching institutions, websites, television and radio programs, and in audio publications (Ranft, 2004). Bioacoustics can provide a great tool to help surveying animals, including endangered primate species. The technique has proven to be efficient with a range of species, such as, golden-backed uacaris, *Cacajao melanocephalus ouakary* and common marmosets (e.g. Bezerra et al., *in prep*), cotton top tamarins and golden-handed tamarins, *Saguinus midas* (Urbani, 2006; Savage et al., 2008), red titi monkeys, *Callicebus discolor* (Darcier et al., 2008), howler monkeys, *Alouatta palliata* (Estrada, 1982), northern muriquis, *Brachyteles hypoxanthus*, capuchin monkeys, *Cebus nigrinus*, southern masked titi monkeys, *Callicebus nigrifrons* and buffy-tufted-ear marmosets, *Callithrix aurita* (Melo et al., 2005).

Furthermore, as the structure of vocalisations in primates can show vocal signatures (e.g. vervet monkeys, Cheney & Seyfarth, 1982; Japanese macaques, Symmes & Biben, 1985; and Shizawa et al., 2005;), recording individuals may also represent non-invasive alternative marking technique to invasive techniques such as tattooing and tagging (see Terry et al., 2005). Vocal signatures can also help researchers conduct long-term monitoring of individuals within a population (e.g. Scott et al., 2006; Eschmann et al., 2006). Braune et al. (2008) show the relevance of communication calls for species recognition and discrimination in cryptic species of primates. Cryptic species are defined as species that are reproductively isolated, but which are morphologically very similar. Many cryptic species were (and probably still are) incorrectly classified under one species name (Bickford et al., 2006; Braune et al., 2008). Braune and colleagues found differences in the physical structure of advertisement calls of Malagasy mouse lemurs (the grey mouse lemur, *Microcebus murinus*, the golden brown mouse lemur, *M. ravelobensis*, and the Goodman's mouse lemurs, *M. lehilahytsara*), previously considered to be the same species (i.e. *M. rufus*). These Malagasy mouse lemurs responded significantly stronger to conspecific than to heterospecific advertisement calls, supporting that specific differences in signalling and recognition systems may work as a premating isolation mechanism, contributing to reproductive isolation among these cryptic species.

Bioacoustics therefore allows non-invasive biodiversity investigations, including the monitoring and discrimination of individuals, populations and species. Thus, it is an

extremely promising route for application in conservation and management plans of many primate species (McCowan & Rommeck, 2006).

## **FUTURE DIRECTIONS**

Worryingly, more than 45% of the primate species/subspecies so far documented are threatened with extinction (Mittermeier et al., 2007; Primate Specialist Group, 2008) and a great deal of basic research still needs to be conducted in primate bioacoustics. Looking ahead, we feel that one very important next step is to conduct more basic research on primate vocal communication (i.e. description of vocal repertoires and behavioural context of calls) so that consequently, we can have (i) an increase in the knowledge of primate communication and use it in comparative studies, (ii) a powerful tool for welfare, conservation and taxonomy, (iii) and have researchers using the vocal repertoires as a playback tool when surveying their primate species.

Although more research still needs to be conducted before aspects of vocalisations can be integrated into standard animal welfare assessment procedures, it is important to consider the potential use of vocalisations for this purpose. They are easily quantifiable (e.g. measurements of call physical features and rate of usage) and they may reflect the inner states of the animals (e.g. Hewson, 2004). Also, vocalisations can be used as indicators of behavioural patterns and may be useful to monitor social communication and dynamics in several species, including primates (e.g. rhesus macaques, McCowan & Rommeck, 2006). This can be very useful for veterinary medicine. In addition, the use of music to promote welfare in captive and domesticated animals and to gain insights into the evolutionary origins of human sound preferences, for example, has started to gain research credibility (e.g. Izumi, 2000; McDermott & Hauser, 2004; Patterson-Kane & Farnworth, 2006; McDermott & Hauser, 2007). Thus, bioacoustics associated with animal welfare is another area to be exploited.

Finally, investigating the perception and social usage of calls in non-human primates in a comparative fashion, might represent a good way to understand factors behind the evolution of language and speech, and also consequently, provide significant insights into the neurobiology of speech (Ghazanfar & Hauser, 1999; Wang, 2000). For example, although the vocal spectra of many non-human primates often occupy much higher frequency ranges than that of humans (Wang, 2000), some species of adult non-human primates, like humans, exhibit a right-ear bias for processing conspecific calls (e.g. Hauser & Andersson, 1994; Ghazanfar & Hauser 1999). According to Wang (2000), there are three main factors that may bias cortical responses to vocalisations: evolutionary predisposition, developmental plasticity, and experience-dependent plasticity in adulthood. Furthermore, there are many acoustic signals used by humans that have comparable simplicity, in terms of production, to non-human primate acoustic signals (e.g. laughs, moans, shrieks, cheers and infant utterances) (Bastian, 1965). In addition, music seems to be the earliest and universal form of human communication, and the loud calls of Old World monkeys and apes are candidates for models of a precursor of human singing (e.g. Geissmann, 2000; Tecumseh Fitch, 2006; Masataka, 2009). Geissmann suggests that the loud calls of early hominids (like the territorial and alarm calls of non-human primates) possibly were the basis from which human singing and, ultimately, music evolved. Comparative and developmental

data can raise important questions concerning underlying mechanisms that shape vocal plasticity, both peripherally and in the central nervous system (Roian Egnor & Hauser, 2004). This makes the neuroethology of vocal communication in non-human primates a potentially fascinating area for prospective research.

## CONCLUSION

Primates often live in complex societies where olfactory, visual, tactile and vocal communication is important. Although vocal communication has been investigated extensively by primatologists around the world, a great amount of bioacoustics research still needs to be conducted if we are to understand the potentially rich and informative vocal repertoires used by majority of the primate species and subspecies currently recognized. Primate bioacoustics is a research field known for more than a century, but it is clear that it has become an important research area for primatologists only in the last 30 years or so. Studies conducted so far have already revealed many important aspects of primate behavioural ecology, welfare, society and cognition. The great potential for future studies makes this a very promising research area.

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*Chapter 2*

## **THE HYPOTHALAMIC-PITUITARY-ADRENAL AXIS IN NONHUMAN PRIMATES: CIRCADIAN RHYTHMS OF STRESS RESPONSIVENESS AND AGING**

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### **ABSTRACT**

The hypothalamic-pituitary-adrenal (HPA) axis is all-important adaptive neuroendocrine system with the circadian periodicity in the activity. There is some evidence to suggest that the circadian periodicity in functioning of the HPA deteriorates with aging and that these disturbances play an important role in age-related changes of glucocorticoid-sensitive tissue functioning, inadequate reaction to stress and high frequency stress-related pathology in aged individuals. Unfortunately, up to now there have been some unclarities in the character and mechanisms of age-related disturbances in circadian rhythms of corticosteroid production. One of the possible causes of this unsolved problem is the use of inadequate experimental nocturnal models—laboratory rodents—in which the circadian rhythm of the HPA activity is in contrast to that in humans and nonhuman primates.

*The purpose* of this chapter was to investigate changes of circadian rhythms of the HPA axis activity under stress and during aging as well as to evaluate the role of age-related disturbances in melatoninergic and vasopressinergic regulation in their development.

Female *Macaca mulatta* monkeys of 6–8 years (young) and 20–27 years (old) were subjected to acute psycho-emotional stress (two hours immobilization), corticotropin-releasing hormone (CRH) or arginine vasopressin (AVP) injection at 0900h or 1500h on the background of placebo or a pineal tetrapeptide Ala-Glu-Asp-Gly (epitalon) administration (10 µg/animal/day, 10-14 days) as stimulator of the pineal melatonin secretion.

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In response to the stress imposed at 1500h, young monkeys demonstrated much higher increase in ACTH and cortisol than to the stress at 0900h. This stress difference attenuates with aging. Compared to old animals, young ones demonstrated much higher responsiveness of the HPA axis to the afternoon stress and a tendency toward lower responsiveness to the morning stress. In response to CRH, young and old monkeys demonstrated the well-defined circadian rhythms in dynamics of ACTH and cortisol. AVP injection did not induce any circadian periodicity in the ACTH and cortisol responsiveness neither in young animals, nor in old ones. However, in response to the afternoon injection of AVP, old monkeys by comparison to the young ones demonstrated lower accretions of ACTH and cortisol without increase in melatonin. The disturbances of the circadian rhythms of the HPA axis responsiveness to AVP and stress were eliminated by epitalon.

Thus, young monkeys showed a circadian rhythm in stress responsiveness of the HPA axis. The rhythm was attenuated in old animals. The age-related changes in circadian rhythms of the HPA stress reactivity were associated with age-related disturbances in melatonergic and vasopressinergic regulation. The functioning of the HPA was restored by treatment with epitalon.

## INTRODUCTION

Circadian rhythmicity in activity of different physiological systems ensures adaptation of an organism to daily variations of environmental light. The HPA axis is all-important adaptive neuroendocrine system with the circadian periodicity in the activity with highest level in humans and diurnal animals in the morning and the lowest one—in the evening and night hours [9, 20, 21, 27, 30, 31, 34, 48, 69, 80]. The HPA axis is the major regulator of stress responses and sleep-wakefulness rhythm in mammals [9, 13, 39, 62–65, 67, 77]. Appropriate regulation of the HPA axis is essential for health and survival [8, 13].

Of the key factors in the HPA axis are CRH and AVP that are synthesized mainly in the paraventricular nucleus (PVN) of the hypothalamus in response to signals from the primary endogenous pacemaker, the suprachiasmatic nucleus (SCN), or in response to the stress; adrenocorticotrophic hormone (ACTH), synthesis of which in the anterior pituitary is regulated by CRH and AVP; and glucocorticoids [mainly cortisol (F) in humans and laboratory primates and corticosterone in rodents] synthesis of which in the adrenal cortex is regulated by ACTH. Glucocorticoids bind to glucocorticoid receptors to mediate the peripheral stress response and also feedback to the central nervous system to modulate further activation of the HPA axis [39, 63, 65].

There are the reasons to believe that the circadian periodicity in the functioning of the HPA axis in humans and nonhuman primates deteriorates with aging [6, 16, 19, 20–22, 25–27, 30, 31, 35, 48, 65, 69, 71, 72] and that these disturbances play an important role in age-related changes of glucocorticoid-sensitive tissues functioning, inadequate reaction to stress and high frequency stress-related pathology in aged individuals [7, 9, 11, 16, 27, 31, 32, 33, 65, 71].

Circadian periodicity is characteristic not only for basal levels of ACTH and corticosteroids in peripheral blood [6, 16, 20, 22, 30, 31, 34, 48, 69, 80] but, apparently, and for magnitude of their rise in response to the acute psycho-emotional stress imposed at various times of day [12, 15, 23, 29, 33]. At aging, smoothing of circadian rhythms in stress responsiveness of the HPA axis was observed. Additionally, in the afternoon time, the stress responsiveness of young animals was found to be higher in comparison with old animals,

while in the morning time, on the contrary, the stress responsiveness of old animals was found to be essentially higher or trend towards being higher [23, 29, 32, 33]. The age-related changes in the circadian rhythm of stress-responsiveness of the HPA axis may be important factors in the deterioration of reliability of the antioxidant enzyme system in erythrocytes and of oxygen transport to tissues under stress conditions [23, 32, 33]. The decrease of F secretion in response to acute stress in the afternoon and, on the contrary, its increase in the morning may lead to detrimental effects of glucocorticoids on cognitive function [56].

In connection with the above-stated, a correction of age-related changes of circadian rhythmicity of the HPA axis in basal conditions and also under stress could be the important chain of gerontoprotection and prophylaxis of age pathology. Unfortunately, mechanisms of age-related disturbances in circadian rhythms of corticosteroid production are still far from being clear. One of the possible causes of this problem is the use of inadequate experimental nocturnal models—laboratory rodents, in which the circadian rhythm of the HPA activity is in contrast to that in humans and nonhuman primates [9, 45, 46, 76]. Moreover, primates essentially differ from rodents in hormonal regulation and they are unique in dehydroepiandrosterone sulfate secretion [24, 40, 60]. Therefore, the use of nonhuman primates should be more preferable than use of rodents as experimental models in age-dependent changes in biological rhythms and ways for restoring the age-related circadian endocrine dysfunction research.

One of the most perspective approaches in this direction, probably, is study of a role of age-related disturbances in melatonergic and vasopressinergic regulation of the HPA axis in their development. Really, an important role of age-related changes of pineal melatonin secretion in development of age-related alterations of circadian rhythm of F secretion was demonstrated [26, 27, 31, 48, 51, 80]. Additionally, an important role of AVP in the transmission of controlling influence from the SCN on circadian rhythm of glucocorticoid secretion was shown [10, 45, 46].

The purpose of this chapter is to review mechanisms of age-related changes in the reaction of the adrenal cortex to acute psycho-emotional stress imposed at different times of day, namely, to elucidate a role of age-related disturbances in melatonergic and vasopressinergic regulation in their development and develop possible approaches for correction of the age-related circadian adrenal dysfunction on the model of female rhesus monkeys. We have found, for the first time, that age-related changes in circadian rhythms of the HPA stress reactivity are associated with age-related disturbances in melatonergic and vasopressinergic regulation and that a synthetic pineal tetrapeptide Ala-Glu-Asp-Gly (epitalon) is a promising factor for restoring the age-related circadian endocrine dysfunction of primates.

## MATERIAL AND METHODS

A series of experiments was carried out to solve the above-mentioned problems. Twenty-two young adult (6–8 years) and twenty-nine old (19–26 years) healthy female rhesus monkeys were used in the experiments. The animals were kept in open enclosures or cages designed for group housing in the monkey colony of the Research Institute of Medical Primatology, Sochi, Adler, Russia. During the observation period they were kept in individual cages under conditions of controlled temperature (20–25°C) and controlled illumination



(from 0600h to 1800h). Body weight of the animals ranged from 4.4 to 6.8 kg. The mean body weight of the young group was  $5.10 \pm 0.15$  kg and of the old group  $5.6 \pm 0.20$  kg. All experiments were carried out in the period June–September when ovarian cycles are not typical for female rhesus monkeys. The animals were fed pellets prepared by the Institute according to the technique of the firm “Altromin” (Lage, Germany). The pellet diet was complemented with bread, boiled eggs, and fresh vegetables and fruit. Water was available *ad libitum*. Before the experiments, the animals were adapted to living in metabolic cages and to the procedure of bleeding for at least four weeks.

## The Experiment 1

The first experiment was aimed at studying the HPA axis responsiveness to acute psycho-emotional stress in different age animals. Animals of both age groups ( $n = 8$  for each age group) underwent an acute stress procedure: moderate restraint in a metabolic cage for two hours. Restraint was achieved by using a conventional squeeze board to press the animal to the front wall of the metabolic cage. The body and extremities of the animal were not tightly immobilized. Animals were subjected to the stressor two times, once at 0900h and once at 1500h, at a 2-week interval. The animals were fasted overnight. Blood samples were taken before immobilization (0), at 15, 30, 60, and 120 min during application of the stressor, and at 240 min, i.e., two hours after termination of the stressor. Besides blood samples were taken at 24 hours after the onset of immobilization.

## The Experiment 2

Five young and 5 old healthy female rhesus monkeys were subjected to CRH administration (Sigma, intravenously in the dose of  $1 \mu\text{g/kg b. w.}$ ) in the different time of a day—at 0900h and 1500h. The animals were fasted overnight. Blood samples were taken before administration of CRH (0), and at 15, 30, 60, 120, 240 min and 24 hours after the administration. The intervals between the injections were 2 weeks.

## The Experiment 3

The same animals, which were used in the experiment 2 (5 animals for each age group) were subjected to AVP administration (Sigma, intravenously in the dose of  $1 \mu\text{g/kg b. w.}$ ) in the different time of a day—at 0900h and 1500h. Blood samples were taken before administration of vasopressin (0), and at 5, 15, 30, 60, 120, 240 min and 24 hours after the administration. The intervals between the injections were 2 weeks.

## The Experiment 4

### *The Experiment A*

Five young adult and eight old healthy female rhesus monkeys were used in this experiment. To study role of melatonin in regulation of the circadian rhythm of stress-responsiveness of the HPA axis four old animals were subjected to epitalon administration (10 µg/animal per day at 0900h–0930h during 14 days, intramuscularly). *Epitalon* (tetrapeptide Ala-Glu-Asp-Gly) was synthesized on the basis of amino acid analysis of epithalamin (pharmacopoeia drug, the peptide extract from the cattle pineal gland) in the St. Petersburg Institute of Bioregulation and Gerontology, RAMS (St. Petersburg, Russia) [49]. It was showed that the epitalon or epithalamin administration caused the increase in the basal evening and night melatonin level in old monkeys [26–28, 31, 48] and aged humans [31, 50]. The other 4 old animals and also 5 young animals were injected with a placebo (0.9% solution of NaCl in water). On the seventh and fourteenth days of epitalon or placebo administration the animals were exposed to 2-hour immobilization at 0900h and 1500h, respectively (see the experiment 1). Blood samples were taken before restraint (0), at 15, 30, 60, 120, 240 min and 24 hours after onset of restraint.

### *The Experiment B*

Four old healthy female rhesus monkeys were subjected to epitalon administration (10 µg/animal per day at 0900h–0930h during 10 days, intramuscularly) and the other 4 old animals and also 4 young animals were injected with placebo (0.9% solution of NaCl in water). On the seventh day of epitalon or placebo administration the animals were exposed AVP administration (Sigma, intravenously in the dose of 1 µg/kg b. w.) at 1500h. Blood samples were taken before administration of AVP (0), and at 120, 240 min and 24 hours after the administration.

All blood samples (at each time point 2.5–3.0 ml) were taken from the cubital or femoral vein with EDTA as anticoagulant and immediately centrifuged at 2000g at +4°C. Plasma was stored at -70°C. ACTH and melatonin in the plasma was determined no later than 1 month after the sampling of blood. Plasma melatonin levels were measured before injection of AVP (0), and at 120, 240 min after the injection (see the experiments 3 and 4B).

Concentrations of ACTH, F, and melatonin were measured by the immunoenzyme assay using the ELISA kits: DSL, Texas, USA for ACTH and AlcorBio, Saint-Petersburg, Russia for F. The concentrations of melatonin were measured by the immunoenzyme method with preliminary purification of the hormone on chromatographic columns using the ELISA kits: IBL, Germany. The intra- and interassay variation coefficients for all hormones did not exceed 10 and 15 %, respectively.

The experimental values are presented in the tables and figures as means ± SEM. Statistical tests for circadian and age effects were performed using one and two-way analysis of variance (ANOVA) followed by post hoc significant difference (HSD) test for paired comparisons [43].

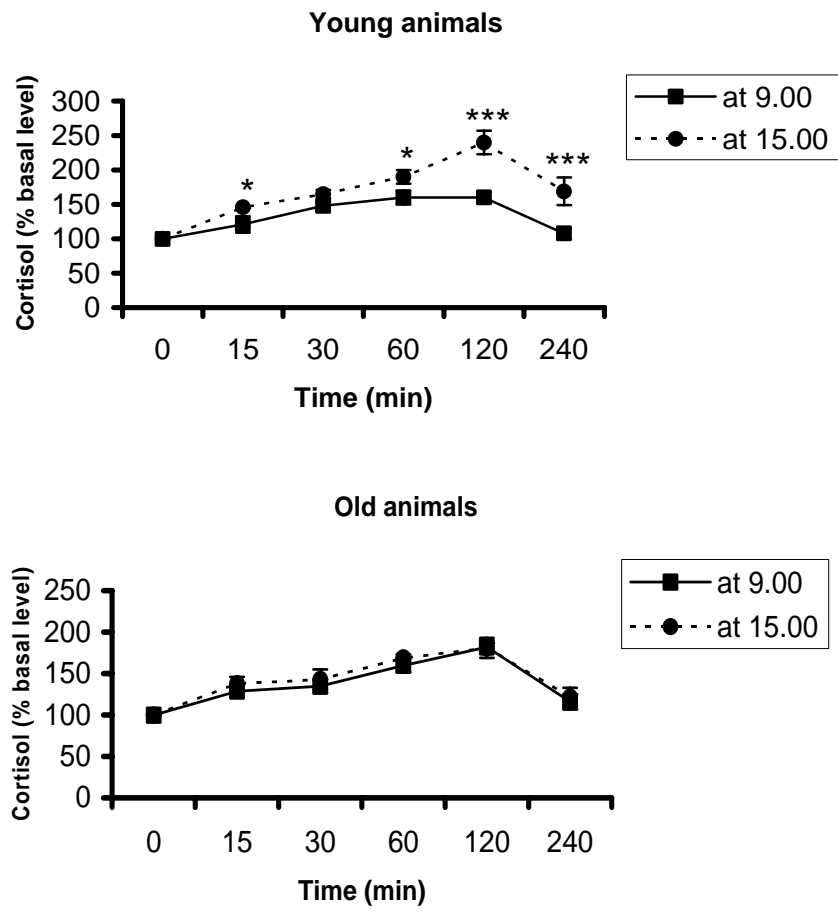


Figure 1. Dynamics of plasma cortisol concentration in young (n = 8) and old (n = 8) rhesus monkey females in response to stress imposed at different times of day (mean ± SEM).

\* P < 0.05; \*\*\* P < 0.001 vs the immobilization at 0900h.

Results

*Activity of the HPA axis in female rhesus monkeys of different age under conditions of acute moderate psycho-emotional stress imposed at different times of day*

We detected that, in young animals, the increase of plasma F level 120 and 240 min after the stress imposed in the afternoon (1500h) was significantly higher than the increase in response to stress imposed in the morning (0900h) (Table 1). This difference was detected nearly at all time periods (15, 60, 120, and 240 min) after the beginning of the immobilization experiment when expressed in relative units (Figure 1).

However, no statistically significant differences were detected in the similar experiments with old animals. The data presented in Table 1 and Figure 1 show that the increase of F after the stress imposed at 1500h was not different from the increase of F after the similar stress

imposed at 0900h. It means that the difference in the reaction of the adrenal cortex to stress that was conditioned by the time of day is flattened with aging.

**Table 1. Dynamics of plasma cortisol concentration in young (n = 8) and old (n = 8) rhesus monkey females in conditions of stress imposed at different times of day (mean  $\pm$  SEM)**

Age groups	Time of Day	Time after onset of restraint, min					
		0	15	30	60	120	240
		Cortisol concentration, nmol/l					
6–8 y. o.	9.00	840 $\pm$ 40	1020 $\pm$ 80	1248 $\pm$ 60	1380 $\pm$ 80	1380 $\pm$ 50	910 $\pm$ 6
	15.00	736 $\pm$ 30 P<0.05	1080 $\pm$ 17	1180 $\pm$ 60	1400 $\pm$ 80	1770 $\pm$ 80 P<0.01	1250 $\pm$ 90 P<0.05
20–27 y. o.	9.00	810 $\pm$ 66	1044 $\pm$ 80	1080 $\pm$ 70	1300 $\pm$ 80	1470 $\pm$ 80	940 $\pm$ 90
	15.00	740 $\pm$ 70	1020 $\pm$ 50	1060 $\pm$ 17	1250 $\pm$ 80	1340 $\pm$ 80 P <sup>1</sup> <0.01	900 $\pm$ 50 P <sup>1</sup> <0.01

P vs at 9.00

P<sup>1</sup> vs the relative values (at 15.00) in young monkeys

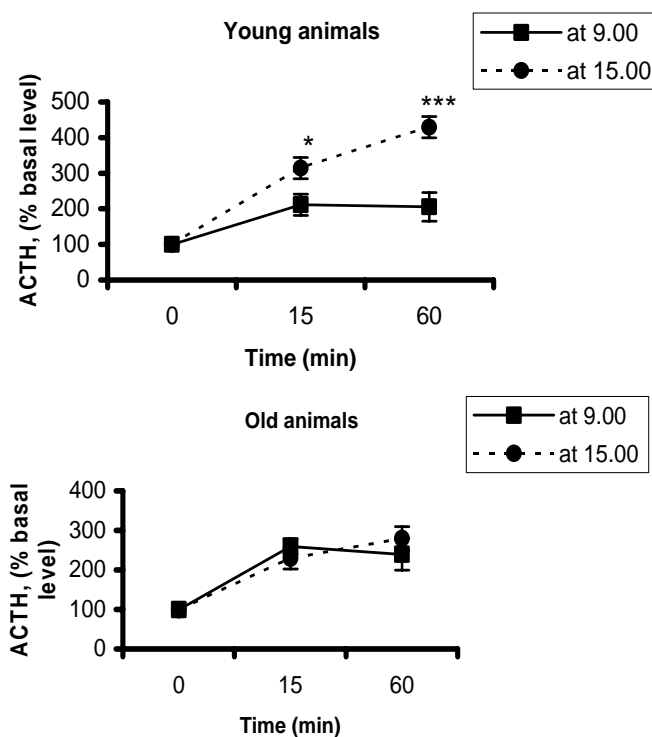


Figure 2. Dynamics of plasma ACTH concentration in young (n = 8) and old (n = 8) rhesus monkey females in response to stress imposed at different times of day (mean  $\pm$  SEM).

\* P<0.05; \*\*\* P<0.001 vs the immobilization at 0900h.

**Table 2. Dynamics of plasma ACTH concentration in young and old rhesus monkey females (n = 8 for each age group) in conditions of stress imposed at different times of day (mean  $\pm$  SEM)**

Age groups	Time of Day	Time after onset of restraint, min		
		0	15	60
		ACTH concentration, pg/ml		
6 – 8 y. o.	9.00	16.0 $\pm$ 2.7	34.0 $\pm$ 7.0	33.0 $\pm$ 7.0
	15.00	20.0 $\pm$ 2.0	63.0 $\pm$ 4.0 P<0.01	86.0 $\pm$ 4.0 P<0.05
20 – 27 y. o.	9.00	24.0 $\pm$ 5.0	63.0 $\pm$ 9.0 P <sup>1</sup> <0.05	58.0 $\pm$ 4.0 P <sup>1</sup> <0.05
	15.00	18.0 $\pm$ 3.6	41.0 $\pm$ 8.0 P <sup>1</sup> <0.05	51.0 $\pm$ 5.3 P <sup>1</sup> <0.001

P vs at 9.00

P<sup>1</sup> vs the relative values (at 9.00 or 15.00) in young monkeys

The data presented in Figure 2 and Table 2 show that in the case of young animals, the increase of ACTH in the same blood samples after the immobilization stress imposed at 1500h was also significantly higher comparing with its levels after the stress imposed at 0900h, as it detected in measurements of the F levels. Again, in the similar experiments with old animals, no significant differences in the stress-induced increase of ACTH levels depending on the time of day were detected. It means that the difference in the reaction of the anterior pituitary to stress that was conditioned by the time of day is flattened with aging in the same manner as the reaction of the adrenal cortex.

Additionally, we have discovered that young animals, in comparison with old animals, demonstrate a higher responsiveness of the HPA axis to stressors in the afternoon time but a tendency toward a lower response to stress in the morning time. It is confirmed by the data presented on Tables 1, 2 and Figure 3. The increase of F and ACTH levels in response to immobilization at 1500h for young animals is significantly higher when compared to the data for old animals (120 min and 240 min after the beginning of immobilization for F, Table 1, Figure 3, and 15 min and 60 min for ACTH, Table 2). In addition, the increase of ACTH in response to the immobilization at 0900h (Table 2) was statistically significantly higher for old animals comparing to the young ones (15 min and 60 min after the beginning of immobilization).

It is of interest to underline that for animals of the both age groups, the extent of increase of ACTH was higher than that of F. For example, the maximum increase of the ACTH level was calculated to be 430  $\pm$  30% (from its basal level) for young animals and 280  $\pm$  30% for old animals, while the maximum increase of F was calculated to be 240  $\pm$  17% for young animals and 180  $\pm$  12 % for old animals.

Plasma F and ACTH levels returned to baseline values 24 hours after stress imposed at 1500h (740  $\pm$  20 nmol/l and 18.0  $\pm$  2.0 pg/ml for F and ACTH, respectively) and at 0900h (835  $\pm$  30 nmol/l and 16.5  $\pm$  2.0 pg/ml for F and ACTH, respectively) for young animals as well as at 1500h (760  $\pm$  50 nmol/l and 18.0  $\pm$  1.5 pg/ml for F and ACTH, respectively) and 0900h (820  $\pm$  50 nmol/l and 22.0  $\pm$  3.0 pg/ml for F and ACTH, respectively) for old animals.

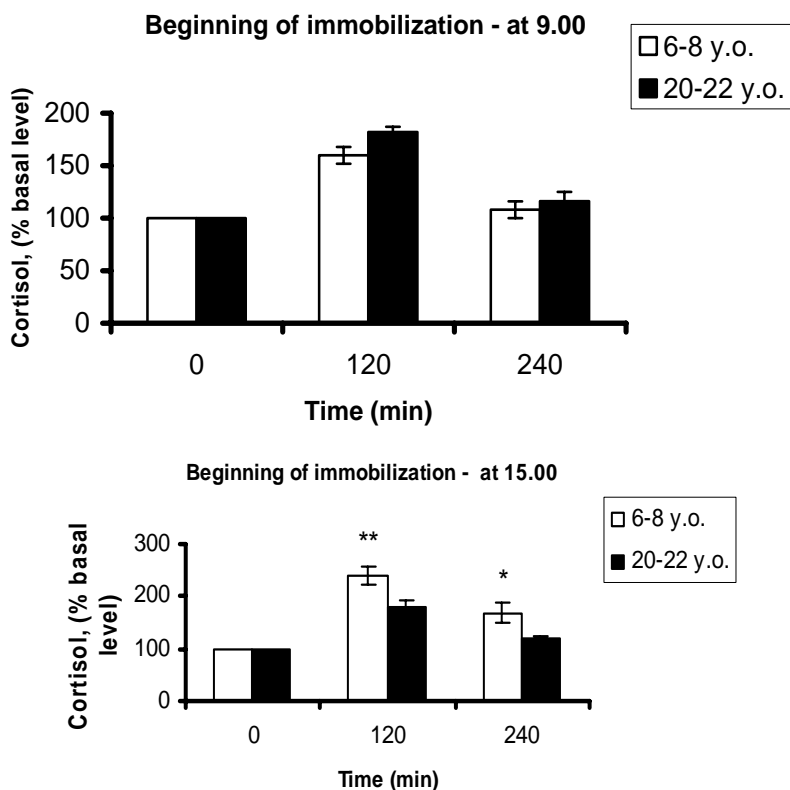


Figure 3. Dynamics of plasma cortisol concentration in young ( $n = 8$ ) and old ( $n = 8$ ) rhesus monkey females in response to stress imposed at different times of day (mean  $\pm$  SEM).

\*  $P < 0.05$ ; \*\*  $P < 0.01$  vs the old animals.

**Table 3. Dynamics of plasma cortisol concentration in young and old rhesus monkey females ( $n = 5$  for each age group) in response to CRH administration ( $1 \mu\text{g/kg}$  b. w., i.v.) at different times of day (mean  $\pm$  SEM)**

Age groups	Time of Day	Time after onset of restraint, min					
		0	15	30	60	120	240
		Cortisol concentration, nmol/l					
6–8 y. o.	9.00	845 $\pm$ 50	950 $\pm$ 40	1010 $\pm$ 60	1030 $\pm$ 40	1110 $\pm$ 30	930 $\pm$ 50
	15.00	776 $\pm$ 70	1040 $\pm$ 80	1170 $\pm$ 90	1420 $\pm$ 90 $P < 0.01$	1490 $\pm$ 90 $P < 0.01$	1110 $\pm$ 110
20–27 y. o.	9.00	830 $\pm$ 40	950 $\pm$ 60	1020 $\pm$ 50	1060 $\pm$ 60	1100 $\pm$ 90	830 $\pm$ 80
	15.00	760 $\pm$ 90	1110 $\pm$ 90	1240 $\pm$ 50	1550 $\pm$ 80 $P < 0.01$	1270 $\pm$ 80	850 $\pm$ 100

$P$  vs at 9.00 (circadian differences)

The finding, that the diurnal age-related changes in the levels of F and ACTH in response to the stress are similar, testifies that the age disorders in the hypothalamic-pituitary chain of the HPA axis disturb the circadian organization of the adrenal function.

To study the possible mechanisms of age-related disturbances in the stress-reactivity of the hypothalamic-pituitary chain of the HPA axis we performed functional tests with CRH and AVP administration at different times of day (at 0900h and at 1500h).

***Activity of the HPA axis in female rhesus monkeys of different age under conditions of CRH administration at different times of day***

We detected that in young animals the increase of plasma F level 60 and 120 min after CRH administration at 1500h was significantly higher than the increase in response to CRH injection at 0900h (Table 3). Old monkeys also demonstrated the well-defined circadian rhythms in dynamics of the F plasma level in response to CRH administration (Table 3).

Plasma F levels returned to baseline values 24 hours after CRH administration at 1500h ( $800 \pm 700$  nmol/l) and at 0900h ( $840 \pm 45$  nmol/l) for young animals as well as at 1500h ( $790 \pm 60$  nmol/l) and 0900h ( $840 \pm 50$  nmol/l) for old animals.

These data testify that responsiveness of the pituitary-adrenal axis to CRH both in young and old *Macaca mulatta* monkeys undergo the circadian periodicity with higher level in the afternoon time and lower one – in the morning hours.

***Activity of the HPA axis and pineal gland in female rhesus monkeys of different age under conditions of AVP administration at different times of day***

A test with the administration of AVP did not reveal any circadian changes in the reaction of F neither in young animals, nor in old individuals (Table 4). There were no evident diurnal changes in the reaction to AVP and in the levels of ACTH neither in young, nor in old animals (Table 5). However, young monkeys demonstrated higher increase of F and ACTH levels after AVP administration at 1500h than old ones to identical challenge (Table 4, 5).

We detected a slight increase of melatonin level 240 min after AVP administration in young animals (Table 6). In the same time in old animals the melatonin level not only did not increase, but even shown a trend toward reduction. Different directivity in character of the changes of melatonin level in response to AVP injection in young and old animals led to appearance of the marked age-related differences in melatonin levels 240 min after AVP administration, that is at 1900h ( $P < 0.01$ ) (Table 6). The tendency to increase of plasma melatonin level in young animals after AVP administration rather reflects physiological rise of melatonin secretion in this time of day, than influence AVP.

The results of functional tests with CRH and AVP show that the revealed age-related changes in the circadian rhythms of the HPA axis stress responsiveness, perhaps, are conditioned by the decrease of AVP contribution to stimulation of the HPA axis under stress in the afternoon and in the evening time in old monkeys.

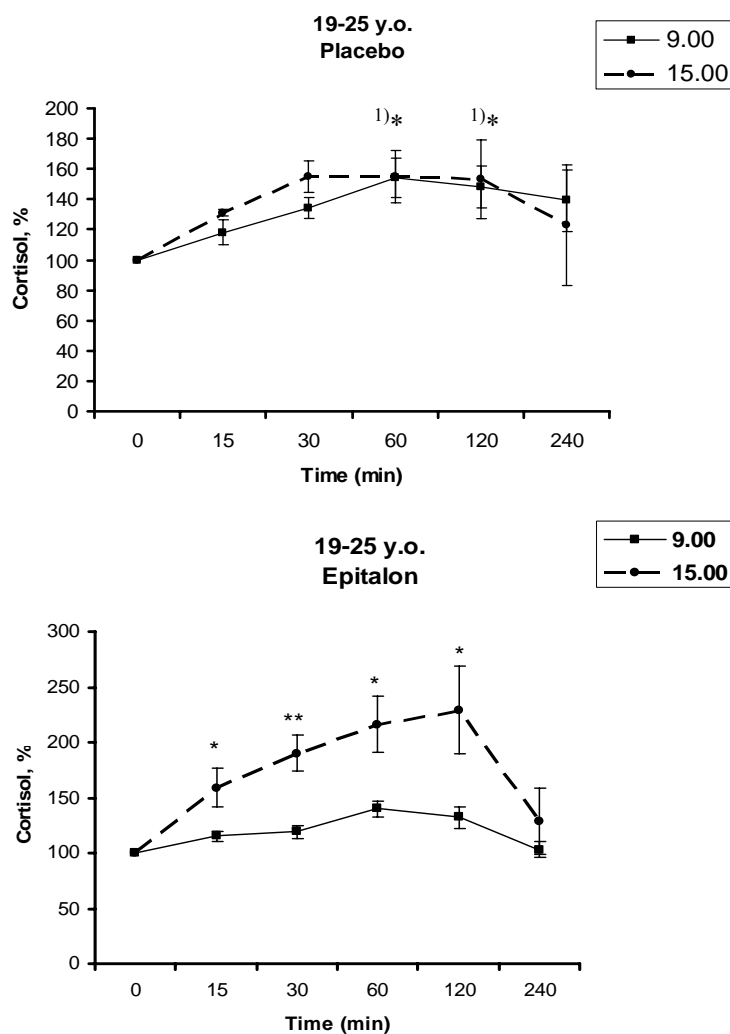


Figure 4. The dynamics of plasma cortisol level in response to stress imposed at 1500h and 0900h on the background of epitalon (10 µg/animal per day during 14 days, i. m.) or placebo administration in old rhesus monkey females (n = 4 for each group) (mean ± SEM).

\*  $P < 0.05$ ; \*\*  $P < 0.01$  circadian differences; <sup>1)\*</sup>  $P < 0.05$  vs the relative values in monkeys with epitalon.

Taking into consideration the fact, that the most evident disorders in the adrenal cortex were found 120 and 240 min after the stress exposure or AVP injection at 1500h, i.e. the evening hours (1700h and 1900h), and also that in this time of day plasma melatonin level begins to rise in young animals (see Table 6), may was expected that age differences in reactions of the HPA axis on stressful influence and AVP injection can be conditioned by age-related differences in melatonin secretion in this time of day. So, possible was expect that administration of epitalon which has a beneficial regulatory role on the pineal gland function in old nonhuman primates and humans [26–28, 31, 48, 50] could restore both melatonin plasma level and stress responsiveness of the HPA axis in old monkeys.



**Table 4. Dynamics of plasma cortisol concentration in young and old rhesus monkey females (n = 5 for each age group) in response to AVP administration (1 µg/kg b. w., i. v.) at different times of day (mean ± SEM)**

Age groups	Time of Day	Time after onset of restraint, min					
		0	15	30	60	120	240
		Cortisol concentration, nmol/l					
6–8 y. o.	9.00	820±60	870±60	1140±90	1120±30	1310±50	960±60
	15.00	760±60	800±16	960±60	1100±50	1410±30	990±50
20–27 y. o.	9.00	820±80	850±50	1100±30	1150±60	1190±50	1020±90
	15.00	780±50	1010±50	1110±30	1200±50	1200±80*	840±30*

\* P < 0.05 age-related differences

***Activity of the HPA axis in female rhesus monkeys of different age under conditions of acute moderate psycho-emotional stress imposed at different times of day on the background of epitalon and placebo administration***

### **Experiment A**

The results of the experiment demonstrated that in control old animals there were no circadian variations in the F responsiveness to acute stress (Figure 4) while in old animals, injected with epitalon, the well-defined circadian rhythm in the reactivity of adrenal cortex to stress was found (Figure 4). It was similar to that of the F stress responsiveness in young animals, injected with placebo (Figure 5). In response to the epitalon administration, the old animals demonstrated increase of plasma F 60 and 120 min after the beginning of stress at 1500h in contrast to the control old ones (Figure 4), that, in turn, led up to leveling of age differences in stress reactivity of the adrenal cortex in the afternoon.

### **Experiment B**

In the other experiment with epitalon (4 old monkeys) and placebo (4 old and 5 young monkeys) administration it was revealed that single injection of AVP in the same dose, as in experiment 3, was accompanied by increase of melatonin level 240 min after the injection both in the young control animals and in the old ones on the background of epitalon administration (Table 7).

**Table 5. Dynamics of plasma ACTH concentration in young and old rhesus monkey females (n = 5 for each age group) in response to AVP administration (1 µg/kg b. w., i. v.) at different times of day (mean ± SEM)**

Age groups	Time of Day	Time after onset of restraint, min			
		0	15	30	60
		ACTH concentration, pg/ml			
6–8 y. o.	9.00	14±2	57±20	105±50	70±30
	15.00	18±3	92±30	110±30	69±19
20–27 y. o.	9.00	20±10	41±10	50±20	18±04
	15.00	16±6	31±9	40±09 *	12±08 *

\* P < 0.05 age-related differences

**Table 6. Dynamics of plasma melatonin concentration in young and old rhesus monkey females (n = 5 for each age group) in response to AVP administration (1 µg/kg b.w., i. v.) at 1500h (mean ± SEM)**

Age groups	Time after AVP administration, min		
	0	120	240
	Melatonin, pg/ml		
6–8 y.o.	7.8±1.8	5.0±0.7	10.5±1.8
21–26 y.o.	5.1±1.0	3.9±1.2	3.6±0.9**

\*\* P < 0.01 age-related differences

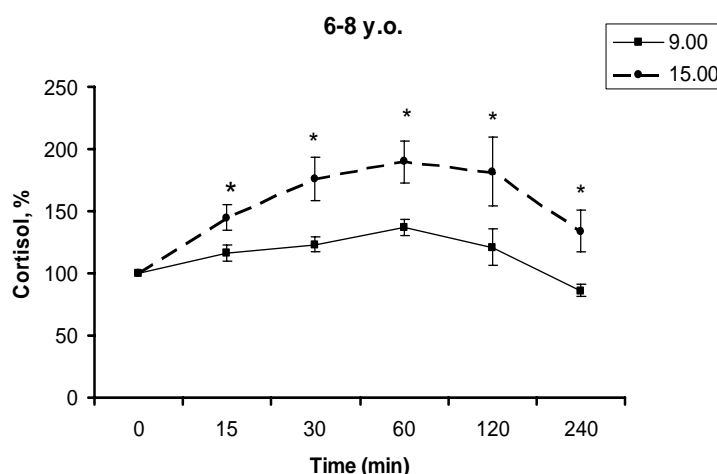


Figure 5. The dynamics of plasma cortisol level in young rhesus monkey females (n = 5) in response to stress imposed at 1500h and 0900h on the background of placebo administration (mean ± SEM).

\* P < 0.05 circadian differences.

**Table 7. Dynamics of plasma melatonin concentration in young and old rhesus monkey females (n = 4 for each group) in response to AVP injection at 1500h (1 µg/kg b.w., i. v.) on the background of epitalon or placebo administration (mean ± SEM)**

Age groups	Time after AVP administration, min		
	0	120	240
	Melatonin, pg/ml		
6–8 y.o. (placebo)	7.8±1.8	5.0±0.7	12.5±1.5
21–26 y.o. (placebo)	5.3±1.0	3.9±1.0	3.6±0.8**
21–26 y.o. (epitalon)	8.0±2.5	5.6±1.6	15.0±4.5 <sup>1)*</sup>

\*\* P < 0.01 - age-related differences; <sup>1)\*</sup> P < 0.05 – vs old animals with placebo.

**Table 8. Dynamics of plasma cortisol concentration in young and old rhesus monkey females (n = 5 for each group) in response to AVP injection at 1500h (1 µg/kg b.w., i. v.) on the background of epitalon or placebo administration (mean ± SEM)**

Age groups	Time after AVP administration							
	0		120 min	240 min		24 h		
	Cortisol							
	nmol/l	%	nmol/l	%	nmol/l	%	nmol/l	%
6–8 y.o. (placebo)	964±50	100	1660±120	172±10	1320±170	137±16	880±110	91±9
21–26 y.o. (placebo)	838±40	100	1250±60 *	149±8	875±70 *	104±7	640±80	76±9
21–26 y.o. (epitalon)	805±100	100	1375±170	171±4 <sup>1)*</sup>	1110±150	138±10 <sup>1)*</sup>	675±85	84±8

\* P < 0.05 age-related differences; <sup>1)\*</sup> P < 0.05 vs old animals with placebo.

The injection of AVP led up to elevation of F concentration in young animals and in old ones of both groups (Table 8). However plasma F level was significant lower in old control animals in comparison with young animals 120 and 240 min after AVP injection (Table 8). The old animals administered with epitalon demonstrated a tendency towards an increase of plasma F level in comparison with the old control animals in response to AVP injection when expressed in absolute values and significant elevation of F when expressed in percent of basal level (Table 8).

The data of these experiments in addition to the results of the experiment 3 point to a possible role of melatonin in regulation of stress responsiveness of the HPA axis and elucidate a possible way for correction of the age-related disturbances in the responsiveness of the HPA axis to acute stress by treatment with epitalon.

## CONCLUSION

### **Activity of the HPA Axis under Conditions of Acute Moderate Psycho-Emotional Stress Imposed at Different Times of Day**

The responsiveness of the HPA axis of young rhesus monkey females to moderate acute restraint stress exhibits the pronounced diurnal changes. In response to the stress, the increase of plasma F concentration in the afternoon was significantly higher compared with the accretion of F level in the morning. These differences were observed regardless of whether the values were measured in absolute or relative units (see Table 1, Figure 1). The direct underlying cause of a circadian rhythm in stress responsiveness of the adrenal cortex is due to higher stress responsiveness of ACTH in the afternoon compared to the morning (see Table 2, Figure 2).

Our data are in agreement with the clinical data that sensitivity of the HPA axis to different stimulus is higher during evening- and night-times than in the morning and standard diagnostic tests for the HPA axis function, as a general rule, are carried out in the evening time [20, 68, 70]. Moreover, circadian periodicity in reactivity of the HPA axis to mild psycho-emotional stress with higher responsiveness in the afternoon in comparison with morning time was revealed in young pregnant women [15]. The time-dependent responsiveness of the HPA axis to acute severe restrain stress was observed in male Papio hamadys [12].

However, as is evidenced from our experimental results, old animals, in contrast to young ones, do not exhibit such a phenomenon. Our study showed a reduction in the ACTH and corticosteroid response to restraint stress in the afternoon in old animals compared to young adults (Tables 1, 2, Figure 3). It testifies that the circadian organization of the HPA axis functioning is essentially disturbed with aging. The disappearance of circadian periodicity in the responsiveness of the HPA axis to stress in nonhuman primates with aging was found in our previous papers [23, 29, 31, 33]. In the elderly a flattening of a circadian periodicity in the adrenal response to endogenous ACTH that is characteristic for young individuals was also marked [54, cited in 69].

This apparent contrast with an earlier report that the cortisol response to restraint stress is not influenced by age [59] was likely due to the fact that the earlier study was conducted in the morning and that the 20-minute duration of the stressor was much shorter than the 120-minute duration in this study. Indeed, like the earlier study, our study showed no age effect on cortisol responsiveness in morning tests (Table 1, Figure 3). A significant age effect appeared only at the 120 minute time point in afternoon tests. These findings are consistent with a common observation in aging research that age effects are not as evident in the resting level and initial response of physiological and behavioral measures as in the time course and maximal intensity of response to a stimulus that stresses the system.

## **Mechanisms of Age-Related Disturbances in the HPA Axis Stress Responsiveness: Role of Age-Related Changes of Vasopressinergic and Melatoninerpic Regulation**

Earlier the disturbances in circadian rhythms of the HPA axis functioning were revealed in basal conditions in nonhuman primates [25–27, 30, 31, 35, 48] and humans [6, 16, 19–22, 65, 69, 71, 72]. The disturbances were mainly expressed in reduction of the amplitude of circadian rhythms for plasma F and ACTH levels in old subjects and animals in comparison with young ones in consequence of increase of these hormones levels during late afternoon, evening and night time. The reasons of these differences remain to be elucidated, but it likely age-related changes in the circadian pacemaker of the SCN involves. Really, it is known that circadian rhythms of glucocorticoid and ACTH secretion derives from connections between the PVN and the SCN [10, 38, 58, 73] and that the disorders in the function of the SCN were found in animals and humans with aging [3, 71, 75].

To understand mechanism of the age-related changes in stress-responsiveness of the HPA axis, we organized additional studies. Firstly, we came from the data that diurnal rhythmicity is typical not only for stress responsiveness of F (a representative of final chain of this system, i.e. the adrenal cortex) but also for stress reactivity of ACTH (i.e. the anterior pituitary hormone). Additionally, age-related differences in response to the acute stress are typical both for F, and ACTH. It is of interest to underline that the accretion of ACTH in response to stress in animals of both age groups was higher than that for F (see Table 1, 2 and Figure 1, 2). All this gave us the reasons to suppose that flattening of circadian rhythmicity in the responsiveness of the adrenal cortex to stress in old animals firstly may be caused by disorders in the circadian rhythm of the hypothalamic-pituitary chain of the HPA axis.

On the other hand, it is known that in response to stress, the HPA axis is driven by the release of CRH and AVP from parvocellular neurons of the PVN. These neuropeptides then allow for the release of ACTH from the anterior pituitary [36, 39, 63, 65]. To study the possible mechanisms of age-related disturbances in the stress-reactivity of the hypothalamic-pituitary chain of the HPA axis, we performed functional tests with CRH and AVP at different times of day (at 0900h and 1500h).

Administration of CRH showed a higher reactivity of the adrenal cortex in the afternoon (1500h) when compared to the reaction in morning hours (0900h) both in young and old animals (see Table 3). Thus, the results of functional tests with CRH allow us to make the conclusion that the anterior pituitary responsiveness to CRH in young and old monkeys undergoes the circadian periodicity which is not essentially disturbed with aging. Existence of circadian periodicity in the anterior pituitary responsiveness to CRH is supported by data that CRH is released in a circadian-dependent, pulsatile fashion from the PVN [38, 61].

At the same time, a test with the administration of AVP did not reveal any circadian changes in the reaction of F neither in young animals, nor in old individuals (Table 4). There were no evident diurnal changes in the reaction to AVP and in the levels of ACTH neither in young, nor in old animals (Table 5). However, young monkeys demonstrated much higher increase of F and ACTH levels in response to the AVP administration at 1500h than old ones to an identical challenge (Table 4, 5).

What is a possible mechanism of the decrease of the responsiveness of the anterior pituitary to AVP during aging? Maybe, a reduction of pituitary corticotroph responsiveness to AVP exists in old monkeys in the afternoon and evening time when compared to young

individuals. This can be caused, for instance, by change of the functional state of vasopressin receptors type V1b on corticotrophs, which are enough plastic and after short exposure of AVP *in vitro* are subjected to desensitization of the ACTH response to a subsequent stimulation with AVP [36]. An excessive exposure of AVP on vasopressin corticotroph receptors can exist and in physiological conditions. So, it was expected in old rodents which the increased basal release of AVP within the PVN was revealed in [37, 47]. This is also consistent with the data that in both aged men and postmenopausal women, AVP neurons in the PVN are larger than in young persons and AVP cell size correlates positively with age [41].

The data that in old age the corticotroph receptors to AVP (type 1) are more important for realization of CRH stimulation effects on ACTH secretion than in young age can also be of interest. Thus, treatment with an AVP type 1 receptor antagonist reduces the magnitude of the ACTH response to a CRH challenge in old rats relative to young rats [37].

A reduction of pituitary corticotroph responsiveness to AVP in old monkeys in the afternoon could be also conditioned by age-related changes in circadian rhythm of AVP secretion. As well known, secretion of AVP in the SCN and the PVN in young healthy subjects undergo by the well-defined circadian rhythm with essentially higher level during daytime in comparison with night time [55]. In the same time in old patients with Alzheimer's disease, day- and night-time levels of arginine vasopressin mRNA in the SCN are identical [55].

Thus, disturbances in vasopressinergic regulation of ACTH secretion (and activity of the HPA axis as a whole) formed during aging, apparently, are the important factors underlying arising of age-related disorders in reaction of the HPA axis on acute psycho-emotional stress.

The age-related changes in dynamics of plasma melatonin levels in response to AVP injection were also demonstrated in this chapter. Melatonin level in response to AVP administration increases only in young animals and only 240 min after the challenge (see Table 6). This led up appearance of significant age-related differences in melatonin levels 240 min after AVP administration that corresponded to 1900h of day (see Table 6). It is interesting that the age-related differences in dynamics of F levels in response to AVP injection were mainly revealed in this time of day (see Table 8). These results have served as a starting moment for studying a possible role of age-related changes in plasma melatonin level in pathogenesis of the age-related alterations of the HPA axis responsiveness to AVP and acute stress.

The results of our experiments with administration of epitalon to old animals point to the restoring effect of epitalon both on circadian periodicity of the adrenal cortex stress responsiveness (see Figure 4) and on magnitude of F increase in old animals in response to stress or AVP injection in the afternoon – evening time (see Figure 4, Table 8). Restoration of magnitude of F level accretion in response to an AVP injection was accompanied by increase of plasma melatonin level in old animals up to its level in young animals. Most likely, the increase of plasma melatonin level is caused by restoration of natural circadian rhythm of melatonin secretion as a result of treatment by epitalon than stimulating effect of AVP on activity the pineal gland.

These experimental results are in good agreement with our data published earlier that epitalon administration caused the increase of the basal evening and night melatonin levels in old monkeys [26–28, 31, 48]. Moreover, the other research group demonstrated restorative effect of epitalon on plasma melatonin levels in old people with reduced secretion of

melatonin [31, 50]. However, epitalon had no significant effect upon melatonin secretion by the pineal gland *in vitro* [17].

On a question, whether is restoration of melatonin secretion in old animals the reason of restoration of the adrenal cortex responsiveness on AVP administration, difficultly to answer. There are a data testifying close relationships between secretion of AVP and melatonin. So, some of them point to a role of the pineal gland and its hormone melatonin in regulation of diurnal variations in the AVP secretion [14, 42, 44, 66, 79]. Additionally, the specific membrane receptors for melatonin also as for AVP have been demonstrated in abundance in the SCN and the pituitary [18, 42, 66, 74].

It is impossible also to exclude possible restoring influence of epitalon on the HPA axis function through restoring influence on catecholaminergic nervous ways - the major regulators of activity of the HPA axis, the pineal gland and AVP. For example, it is known, that during aging the brain has a reduced capacity to secrete dopamine and norepinephrine [4, 5, 52, 57] and catecholamine metabolism is disturbed in the hypothalamus and neurointermediate lobe [1, 2, 78]. Additionally, the prolonged administration of another pineal peptide preparation, epithalamin, normalized the levels of various neurotransmitters in the hypothalamus of old mice [53].

Nevertheless, the results of these experiments unequivocally specify the important role of epitalon in restoration in old monkeys both circadian rhythm of stress responsiveness of the adrenal cortex, and reaction of the adrenal cortex to AVP administration. Thus, age-related changes in circadian rhythms of HPA stress reactivity are associated with age-related disturbances in melatonergic and vasopressinergic regulation. Epitalon obviously shows promise as a remedy to restore the age-related endocrine dysfunctions of primates.

In summary, it is concluded: (1) In response to the acute stress, young rhesus monkeys manifested well-defined circadian rhythm of the stress-responsiveness of the HPA axis with the maximum level in response to the stress imposed at 1500h and the minimum level in response to the stress imposed at 0900h. (2) With aging, the circadian rhythms of the stress-responsiveness of the HPA axis were flattened. Growth of plasma ACTH and cortisol levels in response to the stress imposed at 1500h was essentially lower. A tendency to the higher growth of plasma ACTH and cortisol levels in response to the stress imposed at 0900h was demonstrated.

(3) Study of possible mechanisms of age-related disturbances in the stress-responsiveness of the HPA axis revealed that the pituitary-adrenal chain responsiveness to CRH in young monkeys undergoes the well-defined circadian periodicity with higher level in the afternoon time and lower one in the morning hours. Responsiveness of the pituitary-adrenal chain of the HPA axis to AVP did not undergo marked circadian periodicity. (4) With aging, the pituitary-adrenal chain responsiveness to CRH did not change. At the same time the pituitary-adrenal chain responsiveness to AVP administration in old monkeys decreased in comparison with young ones. Perhaps, the age-related changes in the circadian rhythms of the HPA axis stress responsiveness are determined by the decrease of AVP contribution to stimulation of ACTH production under stress in the afternoon and evening time. (5) The pineal gland possibly controls the circadian rhythms of stress responsiveness of the HPA axis and reliability of this regulation decreases with aging. The disturbances of the functioning of the HPA are eliminated by treatment with epitalon.

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*Chapter 3*

## **WHY APES POINT: POINTING GESTURES IN SPONTANEOUS CONVERSATION OF LANGUAGE- COMPETENT PAN/HOMO BONOBOS**

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“This pointing is *not* a hocus-pocus which can be performed only by the soul.”

*Ludwig Wittgenstein, Philosophical Investigations*

### **ABSTRACT**

A number of scientists have argued that referential pointing either does not occur among apes or that behaviors in apes which appear as pointing do not have the same underlying psychological mechanisms as pointing in humans does. One prominent argument advanced by Michael Tomasello suggests that cognitive differences between humans and apes preclude declarative or informative pointing in apes.

This study provides evidence that language-competent bonobos, *Pan paniscus*, do indeed point, both declaratively and informatively. Our analysis is based upon data from a video archive of naturally occurring conversations between symbolically competent bonobos and humans. Further, we suggest that if pointing is a learned gesture that acquires its meaning in specific communicative interactions in a culture where pointing has a meaningful purpose, then language-enculturated apes would be expected to point in a way resembling human pointing. An ape not immersed into a culture utilizing index finger pointing, which are the majority of captive apes, would not be expected to exhibit that gesture. Tomasello's argument rests upon questionable empirical evidence, since the apes in the referred experimental studies have not been relevantly reared. By providing evidence that language-enculturated apes do point, the assumptions about the cognitive differences between humans and apes need to be called into question on both theoretical and empirical ground.

## INTRODUCTION

Gestures are an integral part of human language (McNeil, 2005). They are, in various forms, part of conveying meaning during verbal communication and may even, in the form of sign language, constitute an autonomous fully-fledged language with grammar and other features commonly associated with spoken language. Studies of the vocal repertoire of nonhuman primates have been more abundant than studies of their gestural communication, a situation which has changed in recent years (Byrnit, 2004; Pika, Liebal, & Tomasello, 2005; Pollick & de Waal, 2007; Pollick, Jeneson, & de Waal, 2008; Smith, 2007; Tomasello, 2004). Earlier studies do exist, however (Hewes, 1973; Savage-Rumbaugh, Wilkerson, & Bakeman, 1977). The contemporary rise of interest in primate gestural communication is, among other things, spurred by the resurrection of the idea of a gestural origin of human language (Corballis, 2002; Gouzoules & Gouzoules, 2007; Pollick & de Waal, 2007). However, whereas it is recognized that human gestures, including pointing, may have a broad spectrum of semiotic and communicative functions (Kendon, 2004; McNeil, 2005), there is no agreement as to which of these features may be found in nonhuman primate gestural communication. In particular, it has been argued that indexical pointing does not occur in apes (Butterworth & Grover, 1988; Corballis, 1991; Donald, 1997), while other scholars report observations of pointing in apes (Boysen, Berntson, Shreyer, & Hannan, 1995; Leavens, Bard, & Hopkins, 1996; Savage-Rumbaugh, 1984). These diverging results have spurred discussions of how to interpret ape gestures resembling pointing (Gomez, 2007; Leavens, Hopkins, & Bard, 2005).

Pointing is central from developmental, evolutionary, and comparative perspectives. It is a primordial gesture in human infants, occurring before spoken sentences and closely associated with word learning (Butterworth, 2003). Evolutionarily<sup>1</sup>, it may be related to the origin of reference and deixis<sup>2</sup> which are central features of language. These two perspectives converge in the third perspective, the comparative: humans seem to be the only species utilizing index finger pointing; this behaviour has not (yet) been observed in wild ape populations while it is a widespread behaviour among human cultures. However, some captive apes exhibit a similar gesture, though its semiotic and linguistic status is contested.

Given this background, we will argue that language-competent bonobos, *Pan paniscus*, do point with their index finger and that their pointing exhibits a semiotic and conversational function similar to the function of pointing in human conversation. Further, given their rearing histories, we will argue that we would expect them to do so. However, before the data is presented, a conceptual and methodological discussion of what pointing is and why results from different primate laboratories differ is necessary.

<sup>1</sup> 'Evolution' in this sentence may be cultural or biological, or, as we will argue, a interdependent relation where both forces act to shape each other and a behavior such as pointing.

<sup>2</sup> Deixis is the linguistic feature that words have reference in time, space, or refer to other features, relative to the speaking event between the interlocutors. Pointing can have deictical properties in that it may convey, replace, or specify words such as "here", "there", "her", "that", etc. that only have meaning relative to the situation in which they are used.

## THE COMPARATIVE APPROACH

In a recent publication, “Why don’t apes point?” (Tomasello, 2006), Tomasello makes several important observations concerning the human gesture of pointing. He argues, convincingly, that pointing is not as simple and straightforward a gesture as it may appear to be on casual inspection, but a learned action which functions meaningfully only in sophisticated communicative frameworks.

It is easy to agree with Tomasello on the importance of the comparative method in psychological research, but we want to raise the issue of the correct application of the comparative method. If human cognitive skills to a substantial extent are cultural (Tomasello, 1999), then this should have consequences for the manner in which human cognition is compared with that of other primate species. Can we draw valid conclusions from comparisons of how children and chimpanzees perform on cognitive tasks without ensuring that at least some of the apes in the study have undergone relevant humanlike cultural rearing? If human cognitive skills develop in cultural rearing contexts, can we from the observation that some skills, such as pointing, are found only in the human species, draw the conclusion that the skills are *uniquely* human, in the sense that only humans are biologically adapted for them and capable of developing them? Do we not have to be certain that apes, reared in a cultural context where the behaviour in question has a meaningful function, do not develop that behaviour as well?

Controlling for that possibility is not feasible in most primate laboratories, since apes with relevant humanlike cultural rearing are scarce. But science is a collaborative enterprise and relevantly reared apes exist. Our laboratory at the Great Ape Trust of Iowa (GATI) is known for its human-enculturated and language-competent bonobos Kanzi, Panbanisha and Nyota (Savage-Rumbaugh & Fields, 2000; Segerdahl, Fields, & Savage-Rumbaugh, 2005). By “language-competent” it is meant that these bonobos exhibit receptive competence of spoken English and productive competence through lexigrams - colourful symbols on a keyboard that stand for and function as English words. Due to their upbringing and documented linguistic abilities, they constitute a relevant control group for Tomasello’s conclusions on apes and pointing. In this study we analyze data, in the form of film sequences of spontaneous conversations between humans and bonobos, and argue that these bonobos exhibit the communicative forms of pointing that Tomasello assumes are uniquely human. Thereby, they constitute both a methodological and a theoretical challenge to Tomasello’s experimental methods and results.

We will first discuss an advantage and a disadvantage of the predominant form of comparative primate laboratory, where all human subjects are reared by humans and all ape subjects are reared by apes, and no cross-species rearing is conducted. We argue that Tomasello’s notion of pointing questions his own experimental evidence. If pointing is what Tomasello says it is, the ape subjects that would be expected to point need to have had substantial experience of interactions in a culture where pointing serves a meaningful communicative role. We then present evidence that relevantly reared apes indeed do point communicatively, and conclude that the comparative method needs reconsideration. If primate cognition is shaped by cultural rearing, the appropriate comparative method in psychological research should consist in the systematic comparison of *rearing studies* in different primate species, the human species being one of them.



## On the Advantage and Disadvantage of the Mainstream Primate Laboratory

One of the most instructive aspects of primate cognition research is noticing the things that most ape subjects do not do, but are self-evident for humans. Pointing is perhaps the most striking example. This may explain why it is primarily primatologists, such as Tomasello (Tomasello, 2006, 2008) and Povinelli (Povinelli, Bering, & Ciambone, 2003; Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997), who most dramatically unravel the complex nature of these seemingly self-evident human skills. We do not imply that human skills generally are more complex than chimpanzee skills. Rather, we suggest that many human skills, such as pointing, are more complex than we initially are inclined to *think* they are. We compare certain facts with our initial *view* of them, and note that the primate laboratory often helps us notice otherwise easily unnoticed complexities.

However, this instructive aspect of the primate laboratory is susceptible of becoming an intellectual trap. Although studies of ape cognition can help us see the complex nature of seemingly simple human skills, accumulated experiences of seeing ape-reared apes fail on cognitive tasks where humans succeed easily creates another form of appearance. It produces the impression that skills such as pointing somehow “come naturally” for humans, that we are uniquely biologically adapted for them, while apes lack the requisite biological equipment. Based on contradictory evidence from our laboratory where we observe human enculturated apes daily perform many of the actions that researchers studying ape-reared apes do not find, we suspect that their laboratories, although they help us notice the complex nature of human skills, to a considerable extent also have become intellectual traps. Caught in these traps, we fail to see another significant complexity: the complexity of rearing.

Apes do not, as we will demonstrate in this chapter, lack the biological equipment for communicative pointing, although they may not be as *well*-adapted for it as humans are. From an evolutionary point of view, this statement is plausible. Certain biological traits that we share with the other extant apes, and are part of the cultural development and performance of communicative pointing, both ontogenetically and phylogenetically, can reasonably be expected to have undergone evolution<sup>3</sup> also after the evolutionary pathways of *Pan* and *Homo* split. Therefore, we replace the categorical “adapted or non-adapted” framework of Tomasello’s and Povinelli’s reasoning with a framework of biological continuity, where primates are “more or less adapted” for human cultural skills, such as pointing. Human-reared apes help us explore this biological continuum. They function as correctives to many conclusions drawn from laboratories with only ape-reared apes. They demonstrate the need of talking about animals not only in species categories, but also in cultural rearing categories. The human-reared bonobos in our laboratory, for instance, are so different from bonobo-reared bonobos that we view them as belonging to a bonobo category of their own. We call them *Pan/Homo* bonobos, to emphasize how their intermediary life-ways tease out biological continuities and flexibility that the conventional primate laboratory hides.

Tomasello’s work on cultural cognition (Tomasello, 1999, 2006, 2008), surprisingly, is not cultural. His basic theoretical assumption is that human cognition is cultural in the sense that humans have species-specific adaptations for cognition in the social domain, summarized as *we-intentionality*, and that these abilities are what sets humans apart from other animals.

<sup>3</sup> We will not discuss the exact nature of the selectional pressure or other evolutionary mechanism, as that is outside the scope of the present paper. We do acknowledge, however, the importance of the issue.

Our unique mental abilities created human culture and culture made even more advanced behaviours possible. His overriding research task, therefore, is to identify some hitherto unknown, uniquely human biological adaptation necessary for cultural cognition. His perspective on communicative pointing hence wavers between seeing it as a cultural gesture which might develop also in other primates, if they are relevantly reared, and as a uniquely human gesture which helps us identify skills that separate humans from other apes. Since he is heavily inclined towards the latter position, he underestimates the importance of evaluating if human-reared apes develop communicative pointing. The possibility is ruled out from the onset, since his overriding aim of studying pointing is to explain why only humans have cultural cognition. That makes our data below all the more significant. But before we present these data, we need to explain how Tomasello's valid conclusions about human pointing as a complex communicative gesture conflict with his use of evidence from ape research.

### **Tomasello's Notion of Human Pointing Conflicts with His Use of Evidence from the Primate Laboratory**

Tomasello's immediate aim is to explain why apes do not point; why only humans do it. He chooses to address this problem by comparing apes with human infants. The rationale of this choice, in his own words, is "to avoid the dizzying complexities of language" (Tomasello, 2006 p.507). These complexities, though, seem to be precisely what he needs to highlight in order to illuminate the problem. Throughout the article, Tomasello implicitly portrays human infants, between one and two years old, as the linguistic creatures they already are in the process of becoming when they start to point communicatively. These infants participate in simple conversations where they respond to speech by pointing, where they elicit speech in adults by pointing, and they insist on what they want to communicate about by repeatedly pointing, thereby controlling the conversational topic. The pointing gesture is a communicative action deeply embedded in emerging frameworks of conversational interaction.

A significant part of Tomasello's article is "the hidden object test" where an experimenter hides food or a toy in one of three containers. A "helper" thereafter points to the container where the food or toy is hidden. The chimpanzees subjected to the test did not understand the gesture, but performed at chance level when they tried to obtain the food. Two-year-old human children, on the other hand, understood the communicational cue. And, Tomasello adds, "even prelinguistic human infants of fourteen months of age can comprehend the meaning of the pointing gesture in this situation" (Tomasello, 2006 p. 508).

The fairness of this comparison can be questioned. Two-year-old children already participate in linguistic interactions with adults. In these daily conversations, they often point communicatively and respond appropriately to adult pointing. It is vital to observe this fact about the human test subjects, for it means that they did not have to learn the meaning of the pointing gesture in the test situation (or in the preparations for the test). They were tested "in vitro," in the lab, *but they learned pointing "in vivo," in forms of human life*. The situation for the ape subjects is not comparable. Since they were not raised by humans – who indeed happen to be the only animals yet reliably observed to exhibit index finger pointing – and therefore were not given opportunity to learn pointing *in vivo*, they would, in order to pass the test, have been forced to learn the gesture *in vitro*. They would have to *learn* the gesture in the

situation of being *tested* if they understand it. Would children deprived of close human bonds be able to learn the gesture in that hasty way? It can be doubted. Since that vital question, for obvious reasons, cannot be investigated experimentally, apes raised by speaking and pointing humans become the relevant test subjects.

But what about the “prelinguistic human infants of fourteen months” who understand the pointing gesture in the test? Do they not provide evidence how naturally the pointing gesture emerges in humans? While it may be true that these infants do not utter many words yet, their experiences during the fourteen months that preceded the test differ radically from the apes’ experiences before the test. The children had ample opportunities before the test to learn communicative pointing from role-models with whom they had close bonds. Considering the conversations in which they already have begun to participate when they, by pointing, respond to, or elicit speech, the so-called “comparative method” once again appears to be applied in a manner that does not allow fair comparisons between species. The human infants developed communicative pointing *in vivo*, in their everyday lives, while the chimpanzees were not given that opportunity.

We conclude that when using the comparative method in cognitive and linguistic studies, it is not sufficient to put humans and apes to the same test. An adequate comparison of their skills demands that they have had comparable rearing histories. If we are studying cultural cognition comparatively, the distinction between learning at home and being tested in the lab – vital for cultural psychology (Bruner, 1983) – must be equally applicable to both test groups. For further discussion of how the duality of home and lab applies to work with enculturated apes in our laboratory, and how it accounts for the apes’ humanlike development and test performance, see Segerdahl, Fields and Savage-Rumbaugh (2005) and Fields (2007).

## **Evolving Language as the Framework of Pointing**

There is a further reason for questioning Tomasello’s use of the comparative method; a reason which so far has remained implicit in our discussion above. It concerns the role of language for human cognition and, above all, its role for pointing. Tomasello views pointing as a prelinguistic ability that requires the same cognitive makeup as language does. Pointing, for him, is the simplest communicative act that helps us identify the biological adaptations that explain why cultural cognition is uniquely human. However, when human infants point, they typically do so in acquired conversational frameworks. There is not one single observation of any human being who points communicatively but cannot participate in elementary conversational interactions (e.g., who cannot indicate an answer to a question). An infant’s communicative point may be a response to, “Where is ...?” It may elicit, “How beautiful!” Or perhaps the child’s repeated pointing returns the adult to an earlier topic of talk (see Pedersen and Fields (2008) for an account of the language-competent bonobo Panbanisha’s ability to create topical cohesion in conversation with humans). To be meaningful, pointing presupposes an interactive, communicative framework, illustrated by Tomasello with the following example:

“Thus, if you encounter me on the street and I simply point to the side of a building, the appropriate response would be “Huh?” But if we both know together that you are searching for your new dentist’s office, then the point is immediately meaningful. In the object choice

task, human infants seem to establish with the experimenter a joint attentional frame – perhaps mutual knowledge – that “what we are doing” is playing a game in which I search for the toy (and you help me) – so the point is now taken as informing me where the toy is located”. (Tomasello, 2006 p.509)

Tomasello’s approach to cultural cognition is to describe the broader framework – illuminated here with the aid of a conversation on the street – *in psychological terms, as if the framework was independent of language, underlying its emergence*. For instance, instead of saying that apes who do not comprehend pointing fail to do so because they have not been culturally initiated into the linguistic framework where the point could function as an answer to a question, or could clarify an unclear issue, he prefers to say that the apes “do not understand the embedded structure of informing” (Tomasello, 2006 p. 510). The latter, psychologically phrased framework is supposed to underlie and explain the former, more pedestrian conversational framework. We believe that Tomasello is moving in a circle here; that his description of the cognitive framework of the human use of language in actual fact is *a psychologised description of the very linguistic interaction he wants to explain*. For a critique of similar circular explanations of human language use in pragmatics, see Segerdahl (1996), and for a more detailed critique of Tomasello in this regard, see Segerdahl, Fields and Savage-Rumbaugh (2005 pp.183-193). Moreover, it has been argued that pointing by human infants is not necessarily mediated by the mindreading skills that we are able to elicit in humans and therefore commonly associated with referential pointing (Gomez, 2007). Rather than being based on mental abilities for constructing chains of inferences about other’s minds, infant pointing may be rooted in the pragmatics of coordination through communication. According to Gómez, attributing the motivations and mental states adults construct to infants may be imposing a framework on them that does not adequately describe how they develop pointing.

The explanation why apes do not point finally reached by Tomasello is, characteristically, one where the framework that makes pointing meaningful is described in *psychologising* terms, for instance, as “the collaborative joint attentional engagements that create the common communicative ground necessary for pointing to be meaningful in particular contexts” (abbreviating somewhat). This psychologically phrased communicative framework, sometimes described more simply as “we-intentionality,” is supposed to constitute the underlying, uniquely human mental abilities that explain why only humans point and have language.

Tomasello’s example from the streets of a human city is brilliant. It reminds us of the everyday communicational frameworks which make pointing meaningful. But we hold on to the initial pedestrian description of the framework, and question the psychological phrasing of it in the latter half of the quotation as a misleading *repetition* of what was said in the first part of the quotation. Translating the street interaction into psychologising jargon does not produce a scientific hypothesis; it only creates the impression that pointing, to paraphrase Wittgenstein (1953 paragraph 454) is a hocus-pocus which can be performed only by the human soul.

Pointing emerges in human infants together with the ability to participate in simple linguistic communication. It is in the framework of forms of language use that the child understands pointing gestures and points communicatively for others. The “uniquely human” cognitive framework of pointing that Tomasello claims he has disclosed is, in our view,

*acquired everyday language use, disguised in mentalistic jargon as an elusive “mentality” of collaborative we-intentionality.* In order to illuminate this statement empirically, we now turn to the data of bonobo-human conversations, showing the bonobos pointing communicatively at critical junctures in their interactions. The transcripts of the conversations indicate the everyday cultural matrix in which bonobo pointing makes communicative sense, for the bonobos and for the humans with whom they talk.

The above philosophical discussion can be summarized in the following points:

- Since the primate laboratory helps us see how many human skills (e.g., pointing) are more complex than we initially are inclined to *think* they are, primate experimentation goes hand in hand with philosophical inquiry.
- When the cultural complexity of human cognition is taken seriously, it has an important consequence for the comparative method in psychological research: we cannot just put humans and apes to the same test, but must ensure that at least some apes and humans have comparable rearing histories. The home/lab duality must exist in both test groups.
- Research with human-reared apes, whose lives and participation in experimentation exhibit home/lab duality, teases out biological continuities that are hidden in the mainstream primate laboratory. It thereby functions as a corrective to many conclusions drawn from mainstream primate research.
- We must be careful so that we do not produce vacuous explanations of human skills that merely translate what we want to explain into mentalistic jargon, as if the jargon referred to underlying mental states, frameworks and processes.
- There is a need for a renewed study of ape language, since it appears to be the vital factor that must be taken into account in order to understand why relevantly reared apes point communicatively.

And now we turn to ape pointing, as it occurs in the framework of acquired ape language.

## Method and Data Collection

The subjects in this study are the three bonobos Kanzi, Panbanisha, and Nyota. Being born and raised at the Language Research Center, Atlanta, Georgia (LRC), they have been part of language and cognitive research since their birth and continue to be so at their home since 2005, GATI. Kanzi was born in 1980, Panbanisha in 1985, and Nyota in 1998.

These individuals developed linguistic skills through early exposure to a language-enriched environment, in which humans spoke to them in English while pointing to lexigrams on a keyboard. The bonobos have been documented to comprehend spoken English at least comparable to a 2½ year old human child and to use the lexigrams referentially to communicate with their human caretakers. For data and overview of their accomplishments, see (Savage-Rumbaugh & Fields, 2000; Savage-Rumbaugh, et al., 1993; Savage-Rumbaugh & Shanker, 1996; Savage-Rumbaugh, Shanker, & Taylor, 1998). The bonobos were not explicitly trained to point, but developed pointing *in vivo*, by being enculturated into a way of living in which pointing serves a meaningful communicative function. This enculturation

consists of coordination of daily activities through human language and activities mediated by this language.

The data were collected from the video archive now at GATI. The filming was not directed by the researchers, or with a specific research purpose in mind. Rather, the video archive contains film taken by caretakers and research associates as part of the daily routine or by the film company NHK which followed and documented life at LRC for several years. Video footage was obtained from both Atlanta and the bonobos' current Des Moines residence. Thirty-three hours of film from LRC and twenty-five hours of film from GATI were used.

The filming was not controlled for time of day, amount of time with a specific focal individual, or other variables. This makes the data unsuitable for frequency of pointing, but the large amount and distribution of videos make it suitable for the analysis proposed here: the use of pointing in spontaneous conversation. Due to the character of the videos, many aspects of daily life that are unlikely to occur in an experimental set-up have been captured. Pointing as part of a meaningful conversational exchange is one of these aspects.

Film sequences with gestural communication were identified. Those films sequences were then coded for occurrences of pointing, which are a subclass of indexical gestures. An operational definition of "indexical gesture" is: *a gesture that refers to or points something out through a logical or causal resemblance* (Burling, 1999; Pierce, 1991), while pointing for our purpose can be defined as *"the simultaneous extension of the arm and index finger towards a target"* (Povinelli, et al., 2003). We do not require a complete extension of arm and index finger, nor do we exclude that pointing could have other forms than index finger pointing (see discussion below).

These individuals communicate through pointing to lexigrams on their keyboard. Structurally, this is pointing to a proximal object which is touched by the individual. According to Leavens et al. (1996) *"end of digits touching an object"* is a probe rather than a point. Further, due to the symbolic status of the lexigrams, it was decided to exclude instances of bonobos pointing to lexigrams from the data. Including such pointing would involve a discussion about their conversational and semiotic status that is outside the scope of the present paper.

Following the identification of the pointing gestures, they were categorized according to whether it involves a bonobo comprehending or producing a point, the conversational function of the point, as well as whether they fall into the categories indicative or imperative. The two last categories are significant in that Tomasello argues these are the forms not exhibited by apes, particularly the declarative point. Declarative pointing is using the pointing gesture to attract another person's attention to an object, event, or phenomenon, while the imperative point functions as a request. However, pointing may function in a wide variety of conversational settings, and therefore we expanded our categorization of pointing to include other categories of the role of the pointing gesture in the conversations. This will provide the background for arguing that the conversational settings in which bonobo pointing occur question the reasons why, according to Tomasello, apes do not point.

The first category is pointing in response to a question. This includes indicating objects in response to questions such as "Can you find the (noun/proper noun)", "Which one do you want?", "or "Where are the surprises?". The second category includes points that indicate an object or person without a preceding question, such as pointing to a human to take on a role in a game of chase or indicating who should go to the kitchen to find treats. The third category includes instances of pointing that serve to indicate direction or location, such as pointing

where to go or where an object is without being asked first. The fourth category includes requests for food or objects. Tomasello aims to reduce all imperative pointing into this category, but our data shows that imperative pointing gestures may serve many other conversational functions. The fifth category includes the instances where pointing serves to comment on an object or sharing attention and excitement about it. The last category contains the points that serve to change or maintain the activity/topic, such as pointing to the puzzle currently being worked at when a suggestion is made to instead begin on another one.

Our method of collecting and analyzing data, as well as choice of subjects based on their rearing histories, provide an alternative to Tomasello’s use of the comparative method. Our philosophical inquiries are not merely a conceptual exercise, but have consequences for the way we do science.

**Conversational Functions of Pointing**

Below, we summarize the ways these bonobos utilize pointing in the conversational interactions found in the video material. The instances of pointing were categorized both according to their conversational function as well as with regard to the two forms of pointing argued by Tomasello that apes are unable to produce or comprehend.

**Table 1 Summary of our bonobos' pointing in relation to Tomasello's categories.**

	Comprehension of human point	Production of pointing	Imperative point	Declarative point
Total	63	136	103	33
Kanzi	54	58	40	18
Panbanisha	9	71	57	14
Nyota		7	6	1

The pointing gestures of these bonobos are referential. It has been debated how to determine whether a gesture is “truly” referential. Gómez (2007; 2005) discusses whether ape request gestures are appropriately categorized as referential or not. If the criterion is joint attention as evidenced in gaze following, apes do exhibit referential gestures, while, if the criteria is an understanding of the causal role of joint attention, the evidence does not yet allow for a conclusion as to whether they do or not. While Tomasello argues that the results do allow for concluding that “referential” pointing in apes and humans are different behaviours, this statement summarizes, in the words of Gómez, where Tomasello’s research strands: at a conclusion it cannot itself question. However our data allows for a new way of approaching this question, and thereby addressing this conundrum that is difficult to resolve in the framework of the traditional primate laboratory research. Their status as referential was determined in the conversational context, by analyzing the framework in which it occurred and the role it plays in moving the communication forward. Tomasello’s mentalistic framework does not adequately account for the ways the pointing gesture may function in conversations, the roles it may take on.

**Table 2 Summary of some of the conversational functions pointing may take in bonobo-human discourse**

	Kanzi	Panbanisha	Nyota	Total
Indication of person, object, or direction in response to question	18	7	1	26
Indication of person, object	15	19	2	36
Indication of direction or location	8	15		23
Request for object, food, without prior question	8	18	4	30
Commenting, sharing attention and excitement	7	7		14
Maintaining or changing topic or activity	2	4	1	7

While our data does not reveal the frequency of pointing among *Pan-Homo* bonobos, it reveals both the multiple conversational contexts in which pointing occurs as well as how pointing is a gesture used by the bonobos at various stages in their lives within a range of different situations. Indexical pointing is used both by baby Nyota and when he is an adolescent male reaching maturity, by a young Panbanisha being carried through the woods on the shoulders of a human friend and when she is a mature adult exploring the kitchen, indicating her wish to a human. The meaning of the pointing gesture is inherent in the conversational frameworks that constitute a part of these activities. It would be expected that apes who were raised taking part in such activities mediated by language do point. More specifically, this helps elucidate why Tomasello and we reach different conclusions: due to rearing differences, our apes behave differently, and this difference pertains to even complicated behaviour such as pointing.

In the examples referred to above, the bonobos use their forelimbs as a vector indicating direction, item, or person. The conversational framework in which it occurs is what enables the classification of the pointing gestures as imperative or declarative, or as an answer to a question or a change of topic.



## Pointing, a Part of the Game

To see the complex communicative nature of *Pan/Homo* bonobo pointing, we need to study the conversational framework in which the apes point or respond to human pointing. Games are one such framework. The bonobos enjoy role-playing with humans. In this highly collaborative and co-constructed framework, pointing may be used to control the direction of the game and who should play which role. Appendix 2 is the transcript of a conversational exchange between Panbanisha (PB), Sue Savage-Rumbaugh (SSR), and a group of visitors, occurring during a game of “scare-and-chase.”



Photo 1. Panbanisha pointing while she and Sue Savage-Rumbaugh are spending time in the forest. Panbanisha points to a human friend right outside the camera angle right after she used her lexigrams to say where she wants someone to go, the shop. It is interpreted as indicating whom she wants to drive to the shop.

PB points 5 times over the course of the interchange which consists of 14 turns. The interchange is initiated by SSR, who opens up with a question. PB then, in lines 2-3, uses pointing to respond to the question:

1. SSR: DO YOU WANT THE VISITORS TO BE BUNNY
2. PB: (POINTS AT BUNNYS HEAD)
3. PB: (POINTS AT VISITORS)

“Bunny” is a figure of the *Pan-Homo* culture that comes to life through a costume, including a mask that humans (and bonobos) wear for purpose of pretend play. PB points first to indicate the bunny costume, the “what”, and then points to the visitors; the “whom” and “where.” It is interesting that, given how the rest of the conversation unfolds, this conversational turn could both be a confirming answer and a comment on what SSR is

uttering. PB picks up a monster mask and pretends to scare the visitors, a favourite game among the bonobos. The pointing gesture is not a random occurrence but a meaningful utterance, given SSR's preceding utterance and the framework which sets the stage for the conversation.

In line 6, PB points again. This time, the point follows her taking off the monster mask, and her utterance is clearly understood by SSR and the assistant outside the caged room. The assistant follows PB's point with her gaze and SSR initiates that the mask can be given to the visitors whom PB indicated with her point. PB is thereby, through pointing, controlling the game of "chase and scare" and indicating whom she wishes to see playing which role. The humans are in this case interpreting PB's point as meaningful and PB's subsequent behaviour confirms that interpretation. In this way, the meaningfulness of the point is a co-constructed event, both in this specific case and likely during ontogeny. These advanced skills emerged because during the infancy of these bonobos, human adults with a high social status interpreted their utterances, including pointing, as meaningful. Tomasello implicitly acknowledges that this is the case for the dyad of human parents and children in his examples of children using pointing and being responded to. Only because adults respond appropriately does the pointing gesture develop and only because they receive a response to their pointing are the human children subsequently able to create expectations and react to the lack of an appropriate response. Tomasello's chimpanzees were not reared this way and it is therefore not surprising that their pointing behaviour did not develop the same way as it does in human children or the bonobos of our study.

In line 10, PB uses her pointing gesture to support SSR's suggestion of who should wear the mask from line 9. This control of the syntax of the game is carried on to line 13 where PB by pointing indicates a change.

12. Female visitor: (PUTS ON THE MASK – PRETEND TO SCARE)

13. PB (POINTS TO MALE VISITOR)

14. Male visitor: (PUTS ON MASK, PRETENDS TO SCARE, PB MOVES CLOSER)

Panbanisha uses her pointing gesture to initiate changes in how the game is carried out, to indicate when it is time for the participants to change roles. Tomasello and others might object that Panbanisha is simply pointing imperatively, merely to ensure that a particular person wears the mask. The data, however, show that Panbanisha points cooperatively at critical junctures in the conversational interaction; her points function as answers to questions and are vital to collaboratively staging the joint activity of "chase and scare". She waits for the request of her point to be carried out while the mask is being transferred to the visitors and reacts in line 13 when her request is being carried out, seemingly changing her mind. This means that imperative gestures by Panbanisha can be referential and fulfil a range of conversational functions at least if they take place in a meaningful situation that is based upon coordination through communication.

## Tomasello's Five Claims

Tomasello lists five reasons for why apes presumably do not point. These reasons are based on the elements of “we-intentionality”, the cultural cognition that supposedly separates human and nonhuman primates. These are 1) apes lack understanding of communicative intentions, 2) apes do not participate in joint attentional engagement as common communicative ground within which deictic gestures are meaningful, 3) apes do not have the motives to help or share, 4) apes are not motivated to inform others of things because they cannot determine what is old and new information for them, and 5) apes cannot imitatively learn communicative conventions as inherently bidirectional coordination devices with reversible roles (Tomasello, 2006 p. 516). Below, these claims are discussed in light of our data.

The data in appendix 3, conversation 2, makes Tomasello's first claim dubious. In this conversation, SSR uses speech and pointing to explain to Kanzi (KZ) where his bowl is.

1. SSR: kanzi can you find your bowl? Where's your bowl? see if you can find it, it is behind the keyboard
3. KZ: (KANJI TURNS AROUND)
4. SSR: your bowl is hiding behind the keyboard
5. KZ: (KZ GRABS THE KEYBOARD, THERE IS ANOTHER KEYBOARD BEHIND IT)  
(...)
9. SSR: you want them to -see your bowl it is right under there (POINTING TO THE SECOND KEYBOARD)
10. KZ: (GAZE FOLLOW POINT)
11. SSR: look see it see it
12. KZ: (GETS UP AND GETS THE BOWL)

As situated in a meaningful context, KZ's reactions in line 3, 5, 10, and 12 show that he interprets SSR's utterances as communicative, as providing him with information he is lacking. More precisely, he understands the communicative intention behind her utterances. This situation illustrates what Tomasello, in the second claim describes as absent in ape behaviour: participation in joint attentional engagement as common communicative ground within which deictic gestures are meaningful". SSR's gestures are deictic, indicating the “over there” in line 9, and the direction of “look” in line 11. This corresponds to what we saw in the previously examined conversation where PB indicates the “where” and the “who” through pointing, thereby employing her gesture in a deictic way. Such behaviour is deemed sufficient to ascribe reference to infant gestures and, as a matter of consistence, same criteria should be applied to apes.

In conversation 1, appendix 3, KZ utilizes SSR's point to be indicating the “over here” of SSR's speech. Kanzi understands SSR's communicative intention and more specifically, a deictic gesture. Noteworthy is that the pointing gesture is used to construct the blanket as having a different function than ordinarily. Normally KZ sits on blankets but in this case, SSR wishes to move it.

Tomasello's fifth claim may be questioned based on the corpus of data on the abilities of the bonobos. Further, this question was addressed by Sue Savage-Rumbaugh in her work with

the chimpanzees Sherman and Austin (Savage-Rumbaugh, 1986). Sherman and Austin successfully acquired the use of symbols, i.e., lexigrams, to coordinate events between them, such as tool-use or food sharing, with shifting roles. In 1977 (Savage-Rumbaugh, et al., 1977) a study was conducted on bonobo gestures in relation to copulatory positions. The results suggested that the individuals coordinated positions with the aid of iconic gestures resembling body movements. The study was specifically aimed at investigating two-way communication prior to symbolic competencies and the results suggest that this ability is present even in apes who are not considered language-competent. More recent, discourse and conversational analysis applied to bonobo-human discourse has indicated that these bonobos are capable of coordinating events through using their lexigrams, symbols, at appropriate junctures in the conversation, assuming the changing roles in the conversation as fitted in order to make communication happen (Benson, et al., 2002; Pedersen & Fields, 2008). The linguistic abilities of these bonobos are not merely an ability to match a symbol and an object, but are, as evidenced in the publications cited and in our data in appendices 2 and 3, an ability to use these symbols to participate in conversations. Other apes may be capable of two-way coordination even without human symbols.

Tomasello holds that these abilities must be acquired imitatively. Whether that covers how human children acquire language is beyond the scope of this paper, but it suffices to acknowledge that while Sherman and Austin were explicitly trained in using their symbols, Kanzi, Panbanisha and Nyota acquired this competence without any explicit training but through an immersion in early childhood into a culture where important figures used lexigrams and spoken English for communication. This is to say, these bonobos acquired the use of symbols as bidirectional devices in a manner that resembles how human children acquire language.



Photo 2. Kanzi and Panbanisha are taking to Sue Savage-Rumbaugh. Panbanisha points to the box of clay in SSR's hand. Seconds before, Kanzi and Panbanisha both answered CLAY on their keyboard when asked what they thought would be in the box. They are now commenting on the clay, sharing attention and excitement. Kanzi pointed to the clay right before this photo.

Our data do not directly address Tomasello's claims 3 and 4, but some general objections may be raised. It is not clear that apes do not share or cooperate. Throughout our data, the bonobos do provide information to the other interlocutors, both upon request and because it is a part of the direction the bonobo wishes the conversation to take. On a daily basis, we observe bonobos helping either their human companions or another bonobo. Food sharing has been observed among apes (Jaeggi, Van Noordwijk, & Van Schaik, 2008; Stevens & Gilby, 2004) as has cooperation among wild female bonobos (Parish, 1996), but the motivational basis of these behaviours and their frequency is still unclear. However, the motivational basis for altruistic behaviour such as sharing and cooperating is not settled for humans either, neither is how it originates ontogenetically or phylogenetically. What our data do suggest, though, is that the manifestation of such behaviours is an acquired skill that is within the reach of apes, not a uniquely human adaptation.

## **Why Apes Point**

Great apes are mainly quadrupedal while humans are bipedal. This difference is expressed already from infancy where infant apes cling to their mothers, which contrasts with the situation of human children who are carried. This means that apes most often do not have their hands free for index finger pointing. Among other behaviours that have been facilitated by upright walking, index finger pointing is perhaps the most linguistically significant and the least acknowledged. The rearing history of these bonobos may have facilitated their pointing behaviour also on a physical-motorical level. As infants, they were carried by humans as they travelled around the forests (Savage-Rumbaugh, et al., 1998). This may have freed their hands and encouraged their use of the index finger to point. By comparing these bonobos with Povinelli's and Tomasello's chimpanzees we may also get a hint of what shaped this behaviour into something that we may recognize as communication, even language. Close social bonds and use of, in this case, the pointing gesture in meaningful social activities, create the motivation. This contrasts with Tomasello's position that humans, and exclusively humans, arrive to the world with this ability ready to develop. This is more in line with the social intelligence hypothesis as proposed by Cheney and Seyfarth (2007) than Tomasello's claim of a specific capacity for social cognition, the capacity for which only evolved in the human lineage.

The bonobos use index finger pointing. This does not mean that they could not perform the same semiotic meaning-making in other ways, or that this has a priority over other ways of performing this semiotic gesture. As they grew up in a culture using index finger pointing, this form became a communicative act for them. It is further questionable whether index finger pointing can be classified as a human universal. While the motor behaviour of stretching out the index finger as described in the definition proposed by Povinelli et al. is certainly facilitated by human hand morphology, the semiotic and communicative significance is not the same across cultures, nor does it always have prevalence over other forms of pointing, e.g. lip-pointing or pointing with the whole body (Wilkins, 2003). Wilkins argues that indicating directionality with the body may be a human universal, but index finger pointing is not. The semiotic meaning of pointing and index-finger stretching can only be understood in the context of the culture and pragmatics of language use.

The previous reports on pointing among captive apes are readily dismissed by Tomasello. In line with the rest of his argument, a likely explanation would be that Tomasello regards apes, in

this case bonobos and chimpanzees, to have one static natural repertoire of behaviours and that human contact somehow induces artificial behaviour that is not appropriate for an ape. This is a questionable view, reinforcing dichotomies between culture and nature, human and animal, which we should rather investigate than presuppose. Tomasello (Tomasello & Call, 2004) does investigate the role of humans in the cognitive development of apes. However, his awareness that the issue does exist does not carry into a rethinking of the theoretical framework.

## CONCLUSION

The gesture of pointing is not a uniquely human ability. Rather, enculturated and language competent bonobos spontaneously developed the use of their index finger to point at appropriate junctures in their conversations, both to indicate directions, make requests, indicate objects and persons talked about, as well as to control the conversation by maintaining or changing topic. By “spontaneously” is meant that they developed this behaviour through immersion into a culture where pointing serves as a meaningful part of conversational interactions, not that they invented the use of the gesture. Tomasello’s argument that the absence of pointing in nonhuman apes indicates a species difference in the abilities for social cognition, summarized as *we-intentionality*, is thereby questioned on empirical grounds. If Tomasello’s first claim, that apes do not point, is incorrect, then the theory which is supported by the claim is weakened.

We began with an examination of Tomasello’s method and assumptions; in other words, why does Tomasello conclude that apes do not point? He cites test results and comparisons with human children as support for his claim. However, the human children and the apes have had very different rearing histories. Our study of enculturated apes who competently participate in linguistic exchange elucidates how easily the common primate laboratory research supports premature conclusions that a behaviour or skill is uniquely human, unreachable by other species. Our work also shows that the widespread tendency to view human test subjects in cultural categories, versus nonhuman primate test subjects in species categories only, may prevent us from reaching a more adequate understanding of genes-culture mutual interactions early in the evolution of modern humans, and more specifically, of how language came about. Relevantly reared apes are necessary to understand both the fundamentals of behaviour such as pointing in present day humans and to evaluate theories of what factors went into shaping this behaviour into the form it takes today. Further, relevantly reared apes help researchers notice when they make unwarranted conclusions and unknowingly reduce cultural differences to genetic differences.

We suspect that bonobos and other apes not enculturated into human language, both captive and free living, may point in ways that we do not recognize as pointing, such as pointing with their eyes, mouth, or something different in communicational frameworks that differ from human linguistic frameworks. It is even conceivable that index finger pointing will one day be observed in a wild ape population. How closely that behaviour would be to human index finger pointing would have to be investigated in relation to the communicative framework it is used in. Whether it is the case that such behaviours exist and are waiting for scientists to observe them, we do not yet know, but in order to merely pose the question in a

meaningful way, this discussion of the nature of pointing and the conduct of primate research had to be raised.

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## APPENDIX 1

### The Transcript Conventions Used

Capitalized words signify a word spoken by pointing to the lexigram on the keyboard, which then speaks out the word aloud. Humans often accompany this by saying the word aloud themselves. In other words, in this transcript, when a word is capitalized in the speech of SSR, she points to the lexigram, while both she and the computerised keyboard speak the word aloud. Spoken proper nouns are transcribed with first letter capitalized as ordinarily.

(...) is description of behaviour carried out by the participants, deemed significant for understanding the interchange.

For the rest, I follow standard transcription:

(.) is a short pause

? is rising intonation

. is falling intonation, as in the end of a sentence

, is continuing intonation

## APPENDIX 2

### From Film NHK 121.1

1. SSR: DO YOU WANT THE VISITORS TO BE BUNNY
2. PB: (POINTS AT BUNNYS HEAD)
3. PB: (POINTS AT VISITORS)
4. SSR: DO YOU WANT ME GIVE VISITORS BUNNY HEAD?
5. PB: (MOVES DOWN FROM THE PLATFORM SHE IS SEATED AT, PUTS ON A MONSTER MASK AND PRETENDS TO SCARE THE VISITORS THROUGH THE GLASS. TAKES THE MASK OFF)
6. PB: (POINT THROUGH THE GLASS, DIRECTION OF THE VISITORS)
7. SSR: (TAKES MASK AND HANDS IT TO ASSISTANT THROUGH A BOX IN THE WALL)
8. Assistant: (STANDS BESIDES VISITORS, HOLDS UP MASK SO PB CAN SEE IT. SSR GETS ALL VISITORS TO THE WINDOW)

9. SSR: okay who do you want to put the bunny head on?
10. PB: (POINTS TO FEMALE VISITOR)
11. SSR okay
12. Female visitor: (PUTS ON THE MASK – PRETEND TO SCARE)
13. PB (POINTS TO MALE VISITOR)
14. Male visitor: (PUTS ON MASK, PRETENDS TO SCARE, PB MOVES CLOSER)

## APPENDIX 3

### Transcriptions of Conversations

#### Conversation 1: From film NHK 276.1

Context: SSR and KZ are in a room together. KZ sits on a blanket which is normal procedure. However, at this point, SSR is attempting to move the blanket

1. SSR: sit over there (POINTING) sit over there
2. KZ (MOVES TO WHERE SSR IS POINTING)

#### Conversation 2: From film NHK 147.2

Context: SSR and KZ sitting in a room together, they went through a sentence comprehension test and are now relaxing.

1. SSR: kanzi can you find your bowl? Where's your bowl? see if you can find it, it is behind the keyboard
3. KZ: (KANJI TURNS AROUND)
4. SSR: your bowl is hiding behind the keyboard
5. KZ: (KZ GRABS THE KEYBOARD, THERE IS ANOTHER KEYBOARD BEHIND IT)
6. SSR its hiding behind the keyboard
7. SSR: that's good that's the keyboard
8. KZ: (USES A LEXIGRAM ON THE KEYBOARD, CANNOT HEAR WHICH ONE)
9. SSR: you want them to -see your bowl it is right under there (POINTING TO THE SECOND KEYBOARD)
10. KZ (GAZE FOLLOW POINT)
11. SSR: look see it see it
12. KZ: (GETS UP AND GETS THE BOWL)
13. SSR: good job, good job thank you



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*Chapter 4*

## **USING SEXUAL DIMORPHISM AND DEVELOPMENT TO RECONSTRUCT MATING SYSTEMS IN ANCIENT PRIMATES**

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### **ABSTRACT**

Male and female interactions are often reconstructed for fossil primates for a number of reasons: To argue that a particular social system is the primitive or ancestral form; to investigate the evolution of mating systems; to examine the potential for infanticide and female counterstrategies; and to study how behaviors like sexual selection and mate choice may have influenced primate speciation. Behavioral reconstruction from fossils is extremely limited. Yet, sexual dimorphism has been used since the 1980s to infer polygynous mating systems in early anthropoids like *Aegyptopithecus*. Rates of growth can be studied from fossil remains using a number of techniques. Despite extensive study, living primates show no good link between degree of dimorphism and social structure. Group composition can be analyzed for fossil primates (including humans) in a few rare cases. In addition to maturation rates in fossils and comparative soft-tissue evidence from living primates, group composition allows a rough outline of social structure to be reconstructed for a limited number of fossil primates. Much more attention has been directed to fossil humans, especially given the existence of multiple hominid species, and sympatry between some early species. The degree of sexual dimorphism in fossil hominids has been used to document hominid status itself and increasing hominization through time, and to infer behaviors such as pair-bonding.

**Keywords:** fossil primates; sexual dimorphism; maturation rates; sperm competition; mating systems; hominization

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## INTRODUCTION

Ever since the 1960s, primatologists have studied the anatomy and behavior of living taxa in order to infer the behavior and ecology of extinct primate species. Links between variables such as body size and diet and predation risk are used to reconstruct the behavioral ecology of extinct taxa. However, close examination of body size, diet, and predation risk in eight sympatric species of West African cercopithecoid monkeys shows that these links may be very loose [McGraw & Zuberbühler 2008]. Sociality, mating system, and dispersal appear to follow directly from the number of females in a group. Is it possible to infer social behavior and mating systems in extinct primate taxa? Living primates have a diversity of social systems [Figure 1], and one might argue that the variety of primate social systems rivals the range of social systems found throughout other living mammal orders. Schematic illustrations of primate social systems routinely appear in introductory textbooks of human evolution—for example, Boaz & Almquist [2002:Fig. 8-4], Boyd & Silk [2009:Fig. 5.29]. In fact, primate social systems often constitute the sole basis for most reconstructions of fossil human sociality, and early human sociality is a fundamental topic in paleoanthropology. Fossil humans, in general, are the subject of intense curiosity, but reconstructions of their behavior elicit especially passionate scrutiny. Dating and description of fossil taxa and their presumed phylogenetic relationships languish in the wake of the interest generated by behavioral reconstructions.

Virtually every introductory textbook in human evolution contains a detailed breakdown of the behavior of early hominids [e.g., Lewin & Foley 2004:Fig. 7.10]. Many authors even compare and contrast the behavior of different hominid species. An intricate breakdown may be presented of behavior within and between groups, including dominance interactions, coalition formation, competition for access to mates, long-term associations between males and females (pair-bonding), territoriality, and inter-group aggression [e.g., Binford 1987, 1992, Foley 1989:Table 3]. Theoretical frameworks may be generated for the evolution of divergent hominid social systems [e.g., Foley & Lee 1989]. It is usually assumed that hominids have always been social, residing in groups and interacting with other hominids more than for purposes of reproduction or rearing of the young. Yet, what real evidence exists for sociality in fossil hominids? I shall discuss this topic at the beginning of the paper.

In a more general sense, what can human or non-human primate paleontology actually reveal about ancient mating systems? I shall try to answer this question in the following sections. I shall begin with hominids, because they have received the bulk of theoretical attention, and then continue with non-human primates. In each section, I shall proceed in chronological order. I shall first discuss the earliest hominids whose fossil record is well known (the australopithecines), and then advance to the discussion of members of early genus *Homo* (*Homo habilis sensu latu*), *Homo erectus*, the Neanderthals, and finally anatomically modern humans, who may be chronologically ancient. I shall rely principally on the strict evidence of palaeontology. Thus, using skeletal and dental evidence from fossils, I shall report differences between body size and tooth size in adult males and females that have been associated with various mating systems in mammals. Skeletal and dental evidence has also been used to reconstruct changes in growth regimes in fossil animals. These changes have implications for parental care, food-sharing, and the degree to which the social group contributes to the rearing of the young. Skeletal evidence of body build, relative muscle mass,

and trauma contribute to speculations about aggressive interactions between group members or between neighboring groups. Finally, a limited number of sites contain a relatively rich record of contemporary hominid fossils. These sites allow one tentatively to reconstruct group size and the number of adult males and females that are present, as well as allowing one to reconstruct group composition, to a limited degree. By group composition, I mean the number of individuals in different age classes—e.g., infants, juveniles, adolescents, or adults.

Although relying principally on the evidence of human paleontology, I shall also introduce some anatomical and behavioral evidence from living humans and non-human primates. Some comparative evidence from other mammals will also be introduced in the following sections.

## THE EVIDENCE FOR SOCIALITY IN FOSSIL PRIMATES

Anthropologists and primatologists generally take the presence of sociality in the earliest fossil hominids as a given. However, because one living great ape species, the orangutan, is non-social, it is crucial to present any evidence for the existence of social groups in the australopithecines, the earliest undoubted fossil hominids. Two pieces of evidence exist: the Laetoli trackways and the fossil assemblage from AL 333.

The Laetoli trackways occur in a hardened volcanic ash deposit dating to 3.6 mya at the site of Laetoli, Tanzania. Fossils of *Australopithecus afarensis* occur elsewhere at Laetoli. Footprints of many mammal and bird species were impressed in the wet volcanic ash, which was gently laid down during a rainfall. Among these footprints are the tracks of three hominids, two made by individuals walking side-by-side, and one made by an individual trailing the others, and partly stepping into the prints made by one of the leading individuals. One of the leading hominids is larger than the other; the individual trailing behind approximates the larger of the leading hominids in size. Because the Laetoli ashfall represents a very narrow window of time, it is reasonable to interpret these trackways as being a record of three hominids simultaneously traversing the landscape. Multiple trackways of hoofed mammals, for example, are interpreted in a similar fashion.

The hominid fossil assemblage from the AL 333 locality in Hadar, Ethiopia, provides less equivocal evidence of early sociality. The locality is often referred to as “The First Family” site, and dates to just over 3.2 mya. Over 250 specimens of *Australopithecus afarensis* are preserved here, representing at least 17 individuals. A sudden mass death occurred in a dry, abandoned river channel. There are very few fossils of other species. Extensive stratigraphic analysis reveals no cause for the hominid deaths, although they were not killed by flooding, or by being mired in thick mud or boggy sediments [Behrensmeyer et al. 2003]. One of the most important features of this site is that it establishes that early hominids were, in fact, living together in a social group. However, there is no reason to believe that the 17 individuals within the assemblage represent either a median number for group size in *Australopithecus afarensis*, or a lower size limit for a social group.

I know of no catastrophic death assemblages in non-human primates. Remains of the fossil colobine monkey *Mesopithecus pentelici* are so abundant at the Miocene site of Pikermi, 21 kms east of Athens, that population-level variability can be studied [Delson 1973]. Paleoecological study of this 8.3-8.2 mya locality shows the predominance of C3 plants [Deng 2006]. Thus, the dominant ancient vegetation was forest and woodland.

*Mesopithecus* bones occur in lenses within a red clay/silt matrix, and few elements are in association. This appears to indicate that floods and fluvial processes were concentrating the remains. Their abundance therefore indicates taphonomic processes, and does not reflect sociality. Although fossil papionin cercopithecoids occur in dense concentrations within the limestone breccias of South African Plio-Pleistocene sites, these fossil monkeys accumulated through time in karstic fissure-fills, as water and gravity washed material (including bones, animal carcasses, and partial carcasses) from the ancient land surface down narrow chimneys cut into limestone bedrock [Brain 1981]. Bones and sediments then become cemented together into a rocky matrix. These concentrations of fossil monkeys therefore reflect taphonomic processes occurring over geological time, and cannot be used to infer the existence of social groups.

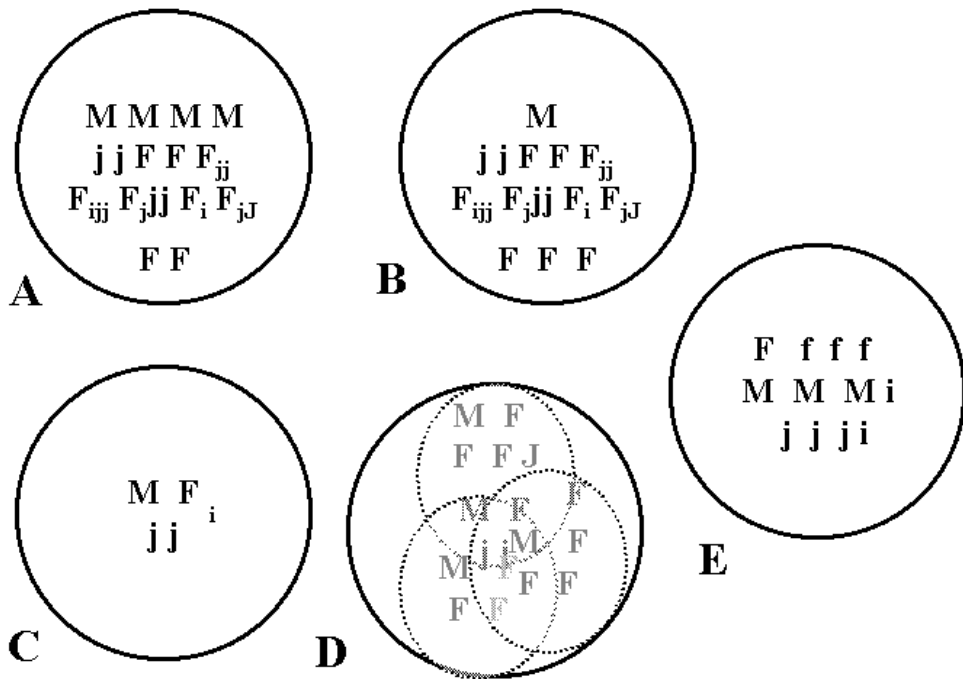


Figure 1. A representative sample of social systems found among living primates. A. Multi-male, multi-female group. Females permanently remain within their natal group, males emigrate when they reach adulthood, and may emigrate from group to group a number of times during their lives. B. One adult male with multiple adult females. The male may be replaced by another male after only a short tenure. C. An adult male and female are permanently associated. When subadults mature, they are expelled from the group by the parent of the opposite sex. This is the social monogamy of the lesser apes (gibbons and siamangs). D. Multiple "harems" (one adult male, females, and young) assemble at sleeping sites and disperse at dawn, when harems forage individually during the day. This is the social system of hamadryas baboons. E. Facultative polyandry. One adult female breeds with several males; subordinate females do not breed. Multiple adults care for the twin infants that are characteristically borne by the dominant female. This is the social system of marmoset and tamarin monkeys of the New World. Dizygotic twinning is the norm in this family of New World monkeys. Symbols: M = adult male; F = adult female; f = subordinate, non-breeding female; j = juvenile; i = infant. Subordinal letters indicate that infants and juveniles are still dependent on the mother for food, transport, and social support.

## SEXUAL DIMORPHISM

Sexual selection, involving male competition for females and female mate choice, is generally considered to be the principal cause of dimorphism in primates [Plavcan 2001], although other causes for dimorphism can be invoked (e.g., terrestriality, niche divergence, and phylogeny). I shall discuss dimorphism in primate body size and canine size in the following sections, and shall also discuss sperm competition in a later section. These topics have often been invoked in ideas about fossil hominid behavior. Pelage, skin, and soft-tissue dimorphism cannot be retrieved from the fossil record, and will therefore not be discussed in this paper.

### Body Size

In contrast to other catarrhine primates, body weight is only moderately dimorphic in modern humans, as is stature. Dimorphism in human stature varies between 4-7 percent, and body weight dimorphism averages about 11 percent [Cachel 2003, 2006]. Populations that are tall on a global scale have a higher degree of statural dimorphism. For example, the Dutch are the tallest of living humans; Efe pygmies are the smallest [Leroi 2003]. By 2012, the average height of Dutch males is predicted to be 186 cms, when Dutch females will average 172 cms. The Efe males currently average 142 cms, while the Efe females average 135 cms. The greater the stature, the greater the degree of statural dimorphism.

The reduced degree of body size dimorphism of living humans in contrast to their closest primate relatives has been used to infer mating systems in early hominids since the 1940s, after the first field observations of wild gibbons appeared to link reduced dimorphism in these animals with a monogamous mating system. In 1937, the Asiatic Primate Expedition traveled to northern Thailand (then Siam) to shoot and collect primate specimens. However, one member of the expedition, Clarence Ray Carpenter, managed simultaneously to observe the behavior and ecology of white-handed gibbons (*Hylobates lar*). Carpenter [1940] studied 21 social groups in this species, and described the social group as being composed of an adult male and female—a monogamous mated pair—and subadults and juveniles born to this pair. Males exhibit a great deal of parental care. At puberty, offspring are driven out of the group by the parent of the same sex. Solitary offspring wander away, and eventually found a new social group, once they encounter a suitable mate. Because gibbons are hominoid primates, classified in the same taxonomic category as humans (Superfamily Hominoidea), gibbon sociality was soon used to infer the ancient presence of monogamy, and, indeed, the nuclear family. For example, the Harvard physical anthropologist Earnest Hooton [1942:155] used Carpenter's work to characterize gibbon sociality as follows: "Thus it is clear that the typical gibbon family consists of a father, mother, and their young."

This early theoretical focus on pair-bonding was not accidental. The presence of pair-bonding and the nuclear family is often taken to be an important hallmark of the human condition, or even the trigger for hominization itself [Lovejoy 1981]. It is therefore ironic that its presence can only be documented with the advent of an historical record (i.e., writing or representational art). Paleontology and archaeology yield no evidence for pair-bonding and the nuclear family existing deep in the fossil or archaeological record. In fact, the most



ancient evidence for the presence of a human nuclear family dates only to 4,600 yrs B.P. Warfare during the Late Stone Age at Eulau, Germany is documented by multiple burials. Mitochondrial DNA and Y-chromosome analysis established parent-child relationships between four individuals buried in a single grave—a mother, father, and two boys [Haak et al. 2008].

The consensus opinion is that the degree of sexual size dimorphism in the earliest hominids, the australopithecines, approximates that of the great apes. Because fossil finds are fragmentary, and the association of material from different parts of the body is rare, this opinion is based to a large extent on the assumption that these hominids were strikingly pongid-like in both anatomy and behavior. Challenging the notion of extraordinary body size dimorphism in australopithecines, Reno et al. [2003] argued that sexual dimorphism in body size in *Australopithecus afarensis* was approximately 15 percent—that is, similar to that of living humans. Plavcan et al. [2005] have recently challenged this reconstruction by using multiple body parts and by using fossils from a broader geographic range. Plavcan et al. arrive at a figure of more than 50 percent body size dimorphism in this species. However, Reno et al. [2005] strongly defend their original conclusion. Reno and his colleagues rely on the fossil material from the AL 333 site in Hadar, Ethiopia, which is currently the closest approximation to a true demographic sample that exists for *A. afarensis*. This is “The First Family” site, discussed above, and all of the fossils represent contemporary individuals from the same area. Implications of monogamy and pair-bonding lie embedded in this abstract discussion of the degree of dimorphism. C. Owen Lovejoy, one of Reno’s co-authors, has long argued that pair-bonding and sexual fidelity (“monogamy”) concomitant with male provisioning of a female and her young is an ancient hominid feature. In fact, it is a keystone feature in “the origin of man” [Lovejoy 1981].

As recent as this paleoanthropological discussion is, it has already percolated into the popular press [Bower, 2005, Selim 2005], illustrating the degree of intense scrutiny that speculation about early hominid mating systems receives from the general public. Size dimorphism is not the object of interest—rather, it is the mating system. Were the australopithecines monogamous? The titles of these article are even more telling: “How Loyal was Lucy?” [Selim 2005], and “Faithful Ancestors” [Bower 2005]. Thus, not only is monogamy versus promiscuity the focus of attention, but also the degree to which the ancient hominid Lucy was faithful to her mate.

Size dimorphism is thought to decline markedly with the advent of the species *Homo erectus*. That is, size dimorphism in later members of genus *Homo* resembles that seen in modern humans. However, when a reasonable sample size of contemporary fossils is available, the degree of dimorphism in *H. erectus*, while reduced from the australopithecine condition, appears to be larger than in modern humans. A nearly complete female pelvis and last lumbar vertebra have recently been described from Gona, Ethiopia [Simpson et al. 2008]. The material is presumed to come from *Homo erectus*, although there are no associated cranio-dental fossils that would unequivocally determine this. Furthermore, the age of the material is unconstrained, because the finds date from between 1.8 mya to <0.16 mya. This female individual was 1.20-1.46 m tall. She was therefore markedly shorter than the subadult male KNM WT-15000 specimen, who might have had a stature of 1.85 m at the completion of growth. The wide trunk and bi-iliac breadth of the new female Gona fossil exceed both male and female mean widths in eight modern human populations [Simpson et al. 2008:1091]. The trunk and bi-iliac breadth of the Gona fossil are far wider than the WT-

15000 specimen, which has an exaggeratedly narrow trunk and bi-iliac breadth. If the new Gona fossil belongs to the taxon *Homo erectus*, both adult body size and shape are thus highly variable in this species. Postcranial material of *Homo erectus* from the 1.8 mya site of Dmanisi, in the Republic of Georgia, certainly shows a greater degree of dimorphism than in living modern humans [Lordkipanidze 2007]. Because cranial capacity also varies significantly in the Dmanisi sample, the possibility that this site contains multiple hominid species has been discussed. However, this is unlikely to be the case. Finally, when many postcranial traits are used to estimate sexual dimorphism in 300,000 year old Neanderthals from Sima de los Huesos, Spain, the degree of sexual size dimorphism resembles that of living humans [Lorenzo et al. 1998].

Extreme sexual size dimorphism is thought to be the primitive condition for Old World higher primates (catarrhines). This is because fossil remains of the stem catarrhine taxon *Aegyptopithecus zeuxis* from the early Oligocene of Egypt show extremely large differences in male and female body mass, cranial size, craniofacial morphology, brain size, postcanine tooth size, and canine size [Simons et al. 2007]. These data have been used to support the idea that *Aegyptopithecus zeuxis* experienced strong sexual selection with male-male competition for mates. *Aegyptopithecus zeuxis* is also thought to have possessed a polygynous social structure [Simons et al. 2007:8735]. Given the basal status of this taxon, this mating system and degree of intense male competition may have been the primitive catarrhine condition.

## Canine Size

Stereotyped displays of canine teeth are widespread among catarrhines. An animal exhibiting a canine display opens its mouth in a wide gape, and holds this position for a few seconds, as if the mouth were frozen in mid-yawn [Figure 2]. Given the widespread nature of these displays, it is generally understood that canine size is important in social communication, and is not an indicator of carnivory. Canine displays are covertly aggressive, and serve to advertise the displayer's high rank and the potential for physical dominance. A display of large canines may therefore curb or limit aggressive interactions. However, canine teeth are highly sexually dimorphic in catarrhines, and there is abundant documentation of males wounding or even killing other males as they compete for status, access to mates, or other scarce resources. Canine size is smaller in adult females, and is thought to reflect a lesser degree of female aggression and female-female competition. Nevertheless, females do compete for food, and matrilineal groups within a social group compete for food [Su 2003]. Females may bite and severely wound each other, and there is at least one report of females from an African monkey species (*Cercopithecus diana*) mobbing and killing another female of the same species [McGraw et al. 2002]. An autopsy confirmed that multiple lethal canine punctures were responsible for the death.

Canine dimorphism is common in higher primates. Maxillary canines are more dimorphic than mandibular canines. When canine dimorphism is assessed in non-human catarrhines, the degree of dimorphism usually ranges from extreme to strong [Plavcan 2001:Table 1]. Male baboons and mangabeys have canine teeth that are up to four times the length of canines in female conspecifics. Relatively large canines in female members of *Cercopithecus* species yield a dimorphism rank of moderate; the two chimpanzee species have moderate dimorphism; and gibbons have slight dimorphism. Human canine dimorphism, like that of

gibbons, is ranked as slight [Plavcan 2001:Table 1]. The first lower premolar, which hones against the upper canine, is also highly dimorphic in non-human catarrhines [Swindler 2002]. Of all the teeth in adult living humans, the canines show the greatest degree of dimorphism. The mean canine dimensions of males are 3-9 percent larger than those of females (Kieser 1990).

Marked canine reduction and a loss of a honing function in the first lower premolar is a hallmark of the hominid family. It unequivocally appears with the first well-dated and dense hominid fossil record after 4.4 mya, and hominid finds dating to 6 mya also show this feature. Reduced canine dimorphism therefore precedes the first appearance of stone tools (2.5-2.6 mya) by 3.4 million years. It is therefore unlikely that tool or weapon use was responsible for the decline in hominid canine dimorphism. Plavcan and van Schaik [1997] note that the complex of slight canine dimorphism and large body mass dimorphism is peculiar to early hominids, and has no equivalent in other primates. They therefore argue that it is unwise to use dimorphism to infer the existence of a particular mating system in fossil hominids.

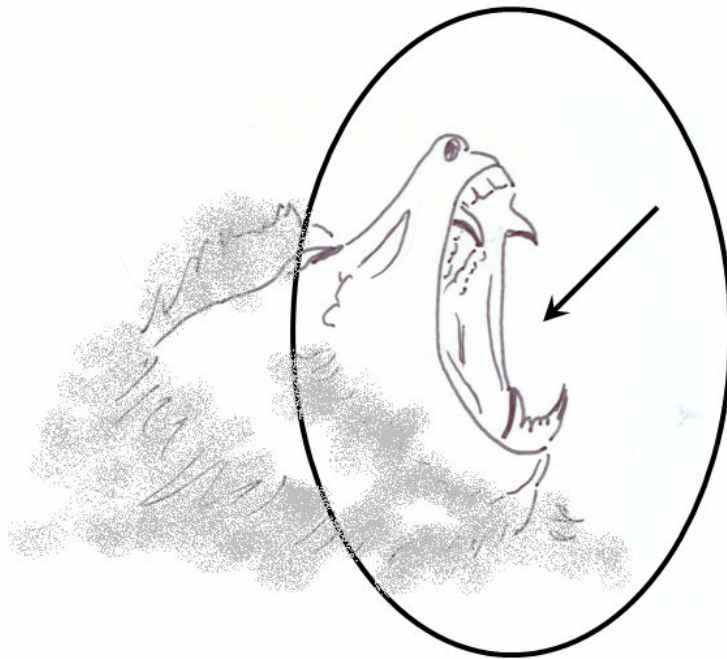


Figure 2. An adult male olive baboon exhibiting the stereotyped canine display that is widespread among living primates. The position of frozen maximum gape is shown. The arrow points to the mid-point of the gape. From cover art of Swindler (2002).

## CHANGES IN GROWTH AND DEVELOPMENT

The traditional reconstruction of early hominid social groups emphasizes that a long period of infant and juvenile maturation mandates the existence of complex communal interaction in order to rear the helpless young. Paleoanthropologists like Glynn Isaac clearly had living hunters and gatherers in mind when they reconstructed this type of sociality for

australopithecines and other early hominids [e.g., Isaac 1975, 1976:483-485, 1978]. Adult caretakers are in constant contact with the young. The young and their adult caretakers are provided with food by other members of the social group. Specifically, adult males provide meat to females with whom they are pair-bonded, and also provision the young of these females, which were presumably fathered by the provisioning male. However, this reconstruction assumes that the prolonged maturation seen in modern humans also characterizes fossil hominids. This assumption is questionable. The relatively complete male adolescent *Homo erectus* specimen from the West Turkana Basin (KNM-WT 15000), dating to 1.53 mya, is 160 cm tall [Ruff & Walker 1993]. Final, adult stature would be larger, and would depend on the existence of an adolescent growth spurt, as seen in modern humans. Growth is incomplete in this fossil, because the epiphyses of the long bones have not yet fused. Enamel growth patterns in the teeth indicate that the specimen may have been only 8 years of age [Dean et al. 2001, Gibbons 2008]. This individual was clearly large and actively mobile, and was probably not very dependent upon adult caretakers, in spite of its chronological age [Cachel 2004, 2006]. In fact, slow rates of dental maturation, equivalent to those in modern humans, appear only in Neanderthal fossils and later, anatomically modern humans. One might infer that a modern type of hominid sociality, with communal rearing of the young, appears only with the advent of the Neanderthals.

### Labile Maturation Rates in Living Species

Maturation rates accelerate in living humans who are experiencing the many changes in diet and lifestyle associated with industrialization and modernity. These changes have been termed “the secular trend,” and are the subject of intensive investigation by many physical anthropologists. Maturation rates also accelerate in captivity for common chimpanzees (*Pan troglodytes*). When detailed information that includes known ages of subjects is available about maturation in wild chimpanzees, maturation is delayed. This is true for wild chimpanzees in East Africa (Gombe, Tanzania) and West Africa (Taï Forest, Côte d’Ivoire). The Gombe habitat is relatively open woodland; the Taï habitat is lowland tropical rainforest. Because the trend for delayed maturation is observed in both sites, it is clear that chimpanzee food supplies are limited under natural conditions irrespective of the environment. Maturity in female chimpanzees is defined as the age at first parturition. Female chimpanzees at Taï mature on average at 14 years of age [Boesch & Boesch-Achermann 2000]. Captive chimpanzees mature three years earlier, at about 11 years of age [Tutin 1996].

Labile maturation rates are important, because they signal that species can respond within a generation to improvements in diet and a change in activity patterns. Hence, maturation rates are not necessarily firmly constrained by the genome.

## CONSPECIFIC AGGRESSION

The ethnographic record and mammal behavior both demonstrate that aggressive interactions can occur when adult males are competing for mates. Paleontologists can document trauma, but are generally unable to identify its source. Sometimes, however, the

pattern of trauma is characteristic of aggressive interactions. Species-specific weapons (horns, claws, enlarged canine teeth) can leave characteristic damage on bones). Hominids lack such biological weaponry, and so the existence of intraspecific aggression in fossil hominids is best established when skeletal trauma is caused by tool use. Although physical anthropologists can often identify the signatures of particular weapons (e.g., arrow, sword, ax) on skeletal remains, fossil humans lacked specialized weaponry until late in prehistoric times. Any trauma inflicted by unmodified stones or early stone tools usually cannot be differentiated from that caused by accidents. Thus, it is not until the invention of specialized stone points that conspecific aggression can be documented among fossil humans. For example, an anatomically modern fossil human specimen from the site of Skhūl in Israel dates to 110-90,000 years ago, and has a stone point deeply embedded in the pelvis. However, the circumstances that led to such intraspecific violence will remain forever unknown.

Carrier [2004] argues that body proportions *per se* in fossil hominid species can reflect the importance of aggressive interactions between individual males. The short legs, great torso, long arms, and powerful musculature of genus *Australopithecus* contrasts with the long legs, small torso, short arms, and delicate musculature of genus *Homo*. Carrier explains the disparity in hominid body shape by behavioral differences that relate to intra-specific aggression and mating system. He analyzes the dichotomous body build of two adult male dogs—a pit bull and a greyhound [Carrier 2004:Fig. 1]. These two individuals have the same body mass, but very different body proportions. One has been bred to fight, and the other has been bred to run. Similarly, australopithecines had evolved to fight, and members of genus *Homo* had evolved to run. Australopithecine body build exhibits a high degree of sexual dimorphism, very robust, long arms, short legs, and a broad pelvis. Carrier believes that fighting between bipedal adult male australopithecines selected for great arm length and robusticity in this genus. A low center of gravity and a wide pelvis conferred stability during aggressive bipedal encounters. An individual with such a body build could be thrown or wrestled to the ground only with difficulty. Furthermore, Carrier argues that the australopithecine leg was excessively muscular—muscularity cannot be explained by walking alone. This muscular leg allowed australopithecines to engage in rapid twists, turns, dodges, and short distance sprints. Carrier imagines the following behavioral scenario. Adult male australopithecines are polygynous. They exhibit a high level of sexual dimorphism, and engage in aggressive male-male encounters as they fight for status and mates. While standing erect and confronting each other, they violently strike at and wrestle with each other using their hands and arms. Although descended from an australopithecine ancestor, genus *Homo* eventually abandons bare-knuckle brawling, and begins to fight with weapons. Aggression remains undiminished. Polygynous adult males presumably continue to fight for status and mates. In addition, because *Homo* can dissipate body heat through evaporative cooling of sweat, and can engage in deep respiration because of the flexible structure of the torso, long-distance running and walking becomes possible. Genus *Homo* is thus characterized by “both greatly increased distance transport and increased lethality in a lineage that was already specialized for fighting.” [Carrier 2004:155-156]. Using Carrier’s analogy, these are the hominid greyhounds, although they retain the temperament of pit bulls.

The idea that hominids possess a natural capacity for violence and intra-specific aggression is not new: it dates back to Greco-Roman antiquity [Stoczkowski 2002]. In its modern incarnation, after the advent of natural selection theory, the idea was considerably elaborated by Raymond Dart, describer of the first australopithecine fossil [Dart 1949, 1957].

Dart envisioned the australopithecines as major predators in the Plio-Pleistocene African ecosystem. They manufactured tools and weapons from ungulate bones, teeth, and horn cores. They used weapons to subdue prey, but also used weapons in violent confrontations with each other. Dart's reconstruction of australopithecine lifestyle was celebrated by some, but denigrated by others who experienced a profound revulsion towards the notion of a human capacity for violence or even for hunting animal prey [e.g., Cartmill 1993].

Stable carbon isotope analyses of enamel from the teeth of South African australopithecines demonstrate that both *Australopithecus africanus* and *Australopithecus robustus* were not relying on fruit, leaves, sedges, or termites. They were probably eating a large quantity of animal foods [Sponheimer et al. 2005]. Their diet was very different from that of modern chimpanzees living in similar habitats. Chimpanzees living in wooded grasslands retain their frugivorous diets. Australopithecines were far different. Furthermore, early hominid diet as inferred from cut-marked bones discovered at the oldest known archaeological sites demonstrates that hominids were butchering carcasses with flesh [Dominguez-Rodrigo et al. 2005, Dominguez-Rodrigo & Barba 2006]. That is, they had early access to carcasses, and were not simply foraging among the ravaged scraps left behind by contemporary carnivores.

## SEX RATIOS AND GROUP COMPOSITION

A crucial piece of information about hominid sociality remains entirely unknown until the advent of cemeteries or ossuaries that are used through several generations, or until the beginning of historical record-keeping. This is the operational sex ratio, the relative number of breeding females available to males within the same population. This measure is the ratio of adult males to adult females weighted by the inverse number of females available to males at a given point in time. This critical figure affects the likelihood of encountering a mate, and also affects the degree of intrasexual competition for access to a mate. This figure is considered to be the most exact measure of male-male competition for mating partners [Mitani et al. 1996]. However, the operational sex ratio can never be reconstructed without good demographic evidence, and this is impossible to retrieve until the end of prehistory, or until detailed written records about births, deaths, and individuals registered on tax rolls become available. Hence, the operational sex ratio can never be retrieved from the hominid fossil record until mass deaths caused by an unpredictable sudden catastrophe occur (e.g., flood, volcanic eruption, mudslide). However, details of group composition can sometimes be inferred from the currently available paleontological record.

Of the 17 *Australopithecus afarensis* individuals present in the Hadar AL 333 assemblage ("The First Family"), 10 are adults, 2 are subadults or adolescents, and 5 are youngsters. The fragmentary nature of the fossils does not allow much of the material to be sexed. The operational sex ratio is therefore unknown. The youngest individual is represented by an unworn deciduous incisor. This demonstrates that even very small fossils have been retrieved from sediments at the site, and that the absence of remains is a legitimate datum. Subadults or adolescents appear under-represented. It is therefore possible that subadults or adolescents were spatially separated from the rest of the group, and were therefore spared when the catastrophe that felled other group members occurred. This pattern of behavior takes place in

many non-human primate groups. Youngsters begin foraging for their own food as soon as they are weaned, and they form age-graded play groups as soon as they are independently mobile.

A second fossil assemblage, far later in time, may also allow some detailed reconstructions of behavior. This is the Neanderthal assemblage from Sima de los Huesos (the Pit of the Bones), in Atapuerca, Spain [de Castro et al. 2004]. The assemblage dates to about 300,000 yrs B.P. It contains the oldest known Neanderthals, and represents the oldest and richest hominid site in Europe. About 80 percent of all known Middle Pleistocene hominid fossils come from Sima de los Huesos. The site has 28 individuals, retrieved from the bottom of a long, narrow chimney deep inside a cave complex. The remains of these individuals were apparently deliberately disposed of, because natural taphonomic processes cannot account for their accumulation at the bottom of the pit. Humans had to traverse very narrow subterranean passageways while transporting a corpse in order to reach the top of the chimney. They then hurled the corpse down the length of the shaft. It appears that some type of ritual disposal of the dead was occurring. The assemblage might therefore approximate a natural demographic sample. Patterns of dental development, and hence maturation rates, resembles that of modern humans [Cunha et al. 2004]. The age distribution of the dead is unusual. Rather than showing increased mortality among the young and elderly, the young and elderly are spared. No individuals between 6-10 years of age are present. A single milk canine tooth documents a youngster between 1-5 years of age. Nine individuals each occur within the 11-15 and 16-20 year categories in the assemblage. These 18 individuals account for over 64 percent of the hominid finds at Sima de los Huesos. Only 10.7 percent of the individuals died after 35 years of age. Figure 3 shows the age distribution at death of these fossils. Unfortunately, most of the fossils are too incomplete to estimate sex. The operational sex ratio and differential mortality between males and females cannot be gleaned from the evidence. The peculiar age distribution is not catastrophic; neither is it attritional. It is possible that frail skeletons of youngsters did not survive a variety of taphonomic alterations. However, examination of enamel hypoplasias (defects in enamel deposition that occur during formation of the tooth crowns) reveals a low frequency of these defects [Cunha et al. 2004]. Because these defects are non-specific indicators of stress, low levels of physiological or systemic stress occurred during development of the Sima teeth. Young individuals, whose teeth were developing enamel crowns, were spared from disease or starvation. If one therefore takes the Sima mortality distribution at face value, one might infer something about Neanderthal social organization at this site. Adolescents suffer the burden of mortality. The young are particularly spared, but adults also suffer low mortality up until the advent of old age (35 + years in this sample). This might imply the existence of special caretaking mechanisms to ensure the survival of the young. Adults are spared from mortal risk. Is it possible that adults were valued because they were repositories of crucial information? Adolescents participate in dangerous activities. Is it possible that adolescents suffered the major burden of difficult foraging or hunting tasks? A major factor affecting life history is the age at which females first reproduce. If one estimates this age to coincide with the eruption of the third permanent molar, the onset of Neanderthal female reproduction was similar to that observed among living human hunter-gatherers, occurring between 15-18 years of age. However, growth of the larger Neanderthal brain may have required a slightly more extended childhood than in modern humans [Gibbons 2008].

### The Sima de los Huesos Assemblage



Figure 3. Age distribution of the hominid fossils from the Sima de los Huesos assemblage, Atapuerca, Spain, 300,000 years B.P. The fossils accumulated as the result of a mortuary ritual, and therefore have a good probability of approximating a sample of a real population. Note the paucity of young and old individuals, but the mortality peak among adolescents. Most individuals are sexually unidentifiable, and so the sex ratio at different ages cannot be reconstructed. The sexual identification of some individuals reveals no dimorphic mortality pattern. Modified from de Castro et al. (2004:Box 1).

### SOFT-TISSUE ANATOMY AND OTHER EVIDENCE

Another line of evidence about ancestral mating systems derives from the theory of sperm competition. This is a body of theory that examines sexual selection not at the level of the whole organism but, rather, at the level of the gametes. Soft-tissue evidence from living organisms yields a way of assessing the degree of male-male competition for mates, or diverging male and female reproductive strategies. Thus, when the living hominoids (great apes, lesser apes, and humans) are arrayed to compare testicle size relative to body weight, the two chimpanzee species are found to possess the largest testicles, orangutans and gorillas are intermediate, and the lesser apes have the smallest testicles [Harcourt et al. 1981]. The mating systems of these species are correlated to relative testicle size. Chimpanzee females mate promiscuously with multiple males when in estrus. They receive sperm from multiple males, and sperm from different males compete together to fertilize a female's egg. Hence, sexual selection occurs within the female reproductive tract. The lesser apes have social monogamy—mated pairs exist in a territory along with adolescent offspring. Although modern humans vary in testis size, depending on the major population group that is sampled [Harcourt 1997], male humans as a species resemble the orangutan in relative testis size. The



relative testicle size in humans is above that of the lesser apes, larger than that of the gorilla, but far below that of the two chimpanzee species. Hence, it is argued that the ancestral human mating system was very divergent from that of the two living chimpanzee species or from that of the gorilla. It was not social monogamy, promiscuous mating in a multi-male, multi-female group, or mating within a harem system. Based on the soft-tissue evidence, the ancestral human mating system may have been a limited form of polygamy.

Jolly [1999] believes that the ancestral human society contained multiple males and females, and that some limited degree of male-male competition occurred for mates. She bases this reconstruction not only on the relative testicular size of hominids, but also on ethnographic evidence. Normal human mating occurs in relative secrecy in all surveyed human societies, and Jolly conjectures [1999:79, 186-187] that mating in private reduces the potential for male-male confrontations. She notes a parallel among common chimpanzees in East Africa, where a male and female surreptitiously leave the group for several days, in order to mate in private. Boesch and Boesch-Achermann [2000] also note that common chimpanzees of the Taï Forest in West Africa tend to mate away from other members of the group. They may form consort pairs, and stay together for several days in complete isolation from the group. Like Jolly, Boesch and Boesch-Achermann believe that this is a mechanism for reducing social stress and the potential for violence.

Finally, a comparison of the human and common chimpanzee genomes reveals that there are marked differences in the Y chromosome of these two species [The Chimpanzee Sequencing and Analysis Consortium 2005]. It is assumed that the chimpanzee genome reflects the human ancestral state, and differences between the two species thus reveal derived human genetic traits. If this is the case, then the clearly divergent Y chromosome implies that strong selection pressure for male reproductive function has occurred in humans. The human Y chromosome has many active regions, in comparison to the chimpanzee Y chromosome, where many functional genes have been lost. In addition, the human genome exhibits strong positive selection pressure relating to spermatogenesis and fertilization. Why do these genomic differences between human and chimpanzee occur? Chimpanzees have a promiscuous mating system, in which receptive females mate with multiple male partners. Chimpanzee males compete intensely with each other for access for mates, and sperm from multiple male partners compete within the female reproductive tract to fertilize an egg. Human genomic differences, including Y chromosome differences, imply that hominids evolved another type of mating system since separation from the ancestral species. Presumably, the intense male-male competition for mates and concomitant sperm competition observed in living chimpanzees was reduced in hominids. Thus, comparative genomics might reveal something about the evolution of human mating systems.

## **RECONSTRUCTING ANCIENT MATING SYSTEMS**

Male-female interactions are a frequent item of conjecture by paleoanthropologists. Such interactions can be brief episodes of copulation or long-term associations. Long-term associations between males and females include courtship and mating behaviors, but also comprise non-reproductive interactions. The entire suite of these behaviors falls under the

rubric of “pair-bonding.” Reconstructing the evolution of pair-bonding is a major palaeoanthropological endeavor.

### **What is the Meaning of Reduced Body Size Dimorphism and Reduced Canine Size?**

All hominids since the time of an abundant australopithecine fossil record about 4.4 mya are characterized by a reduction in canine size and canine size dimorphism. Hence, in spite of the plethora of authors reconstructing early hominids as exhibiting strong, baboon-like polygyny, it is very possible that a lessened degree of male-male competition for mates appeared very early in human evolution. Body size in adult australopithecines remains dimorphic, and has led some researchers to infer that male-male competition for mate access may have remained substantial [e.g., Carrier 2004]. A reduction in body size dimorphism appears with the advent of genus *Homo*. It is possible that this reduction was not associated with declining sexual selection in *Homo*. There are substantial differences in adult stature and adult body weight between living populations of modern humans. These differences are not explained by sexual selection or mate choice. Rather, it appears that long-term population responses to nutritional differences in diet and energy expenditure may explain much of the variation in stature and weight observed among living humans. For example, Stini [1982:Table 14.1] is able to list both high and low values of statural dimorphism even within the circumscribed limits of Europe. There is a 3 percent difference between the two European populations that have the highest value (Macedonians and Swedes) versus the two European populations that have the lowest value (Highland Bernois and Poles). It is likely that long-term population response to nutritional differences (e.g., protein calorie differences) explain this type of pattern.

## **CONCLUSION**

Primate paleontologists have long used sexual dimorphism to infer the mating systems of extinct species, and so the earliest evidence of primate sexual dimorphism becomes theoretically important [Krishtalka et al. 1990]. Yet, the degree of sexual dimorphism in extinct species only allows for faint indications about sociality in the species. At best, extreme dimorphism in the body size or canine size of an extinct species can really only be used to infer polygyny, without any detailed reconstruction of precise mating system [Plavcan 2000]. However, extreme dimorphism in fossil material may also be used to signal the presence of two species, rather than a dimorphic single species. Taxonomic controversy ensues.

Far more information is available from modern humans than for any fossil human species or archaeological collection of modern humans. Is there a link between the degree of sexual dimorphism and a particular mating system in living humans? No. A cross-cultural investigation of the number of polygynous marriages in a society and the level of male parental investment found no link between these variables and the degree of sexual dimorphism, using stature as the indicator of dimorphism [Wolfe & Gray 1982]. Hence, researchers may be too eager to associate morphological differences between the sexes and

complex societal variables in fossil humans, given the lack of correlation between sexual size dimorphism and mating systems in living humans. Nevertheless, it is likely that paleoanthropologists will continue to generate intricate societal reconstructions for fossil human species. Future reconstructions will undoubtedly use new methodologies to infer sexual differences. Such methodologies would include sexual differences in bone or enamel chemistry that would indicate differences in diet and ranging behavior between males and females, or study of cortical bone differences in the limb bones that would indicate different activity patterns between males and females.

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*Chapter 5*

## **HOW LATENT SOLUTION EXPERIMENTS CAN HELP TO STUDY DIFFERENCES BETWEEN HUMAN CULTURE AND PRIMATE TRADITIONS**

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*“If you have a talking chimp you have a talking chimp”* Brian Hare

### **ABSTRACT**

Population specific behaviors shown by primates are often regarded as simple forms of culture. In some cases it has been suggested that that the learning processes underlying these primate traditions may be the same as for human culture, namely, process copying (sensu imitation). For example, Mountain gorillas (*Gorilla beringei beringei*) in Karisoke, Rwanda, feed on a diverse range of defended plants by means of complex processing skills. Claims have been made that the required skills are (and must be) learned socially from each other via some form of process copying. However, in general it is often very difficult or even impossible to directly test for underlying transmission processes – especially under field conditions. In this chapter we focus on a straightforward and simple, yet powerful experimental methodology to determine the most likely acquisition modes responsible for such primate “cultural” patterns. The underlying idea behind this methodological approach is not a new one: if a population specific behavior represents culture then it should not occur spontaneously in naïve individuals exposed to comparable environmental affordances / constraints. Even rare instances of the same behaviour appearing in only a few naïve individuals (or even in individuals of a related species) should be taken as strong evidence against the cultural hypothesis. In this chapter we discuss selected publications as well as previously unpublished data of our own that has applied this methodology. We conclude that in general it is premature to put any population specific behavioral patterns in primates into the cultural category. Instead these behaviors seem bound and restricted by “zones of



latent solutions”, i.e. the solution space set by the general physical cognitive abilities of a given species.

## INTRODUCTION

Humans produce culture as an inherently social enterprise; no single human could do so alone (Tomasello, 1999; van Schaik & Pradhan, 2003). Take for example language. It has been posited several times in the not too distant past that humans are capable of developing language even when raised in complete isolation. Acting on such beliefs, it is said that rulers like Psammetichos, Frederick II and James V of Scotland infamously caused children to be raised in conditions of complete isolation (now-called “language deprivation experiments”). The question was: which language would these children begin to speak – and thus which language is the “natural” language? Today we know that there is no such thing as a genetically fixed language. Children come pre-prepared by evolution to learn a language, but there is no other possible way to learn language other than by copying each others utterances or by being taught (Tomasello, 1999).

Language develops and is perpetuated as a meta-phenomenon in a process of conventionalization and standardization by humans interacting with each other – a process that works over generations. Language then can best be seen as “improbable design” because in the course of this social and evolutionary process language reaches a point of complexity that would have been impossible to reach within one individual’s lifetime and which would not have been exactly replicated were the process to have been started anew (if restarted, the resulting language would then look different, see Richerson & Boyd (2005) for a similar argument on technology). This is the very reason why there exist so many mutually non-compatible languages: their histories have separated them from each other resulting in different trajectories and (current) end-points. It is not just the precise design features but also the general complexity of a modern language that would be impossible to develop within one generation’s lifetime - say if the language production process were to be started with a language-naïve population and measured over one generation. Some more evidence for this view can be found in a recent study on deaf Nicaraguan children, who developed a kind of proto sign-language together, which then spread and subsequently developed into a more elaborate sign-language (see Senghas, Kita, & Özyürek, 2004). Nevertheless, no single human would invent any language if raised in complete isolation (and the data of Senghas et al. is also consistent with this view).

The same logic that applies for language can be applied to human technological culture: humans selectively learn from each other inventions, and thus accumulate technology over time. The resulting techniques tend to be more efficient over time because better ones are selected over apparently worse ones (“ratchet effect”, Tomasello 1999). This cultural evolution is a complex and interactive process, and it ultimately led to massive changes in human life<sup>1</sup>. It is intuitively the case that instrumental culture also needs time (in generations) to accumulate beyond the possible inventive abilities of individuals: the very paper or monitor that you are looking at now could not have been invented in a single lifetime if its inventor

<sup>1</sup> We have no room in this chapter to elaborate further on this topic (see Laland, Odling-Smee, & Feldman, 2000, Richerson & Boyd 2005, Tennie et al. 2009, for more information).

had been raised in a technologically-naïve group. Instead, just as in the case of language, such a “feral” group’s culture would then have merely resulted in a minimal technological culture and only over time would it have turned into a full-blown, “cumulative culture” (i.e. the cultural state we humans are living in right now, see Tomasello 1999). In the following we will argue that great apes, in contrast, seem stuck in a minimal and non-cumulative culture.

What are the reasons for believing that ape culture is different from human culture? The main reason is simply that one does not find clear evidence for cumulative culture in apes. This is true both if one analyses what types of material culture apes exhibit (see all examples in Whiten et al., 1999), as well as if one compares what apes do now with what they did four thousand years ago (Mercader et al., 2007). The only available evidence for cumulative culture in apes is of an anecdotal kind (see Matsuzawa 1994) - and so one finds no proof for accumulation in ape traditions. In other words, apes do not hunt with bows and arrows, and we need to explain why.

Despite the general absence of clear evidence, the general possibility remains that apes can and do sustain some cumulative cultures. This might lead to comparisons between human and ape culture, which raises the potential issue that one may not compare like with like. Maybe there is no absolute cumulative culture, i.e. what counts as an example of cumulative culture in one species may not be an example in another species: nutcracking may or may not be a type of cumulative culture in chimpanzees (And the fact that nutcracking has by now been found in *several separated* populations of chimpanzees (Morgan & Abwe 2006) suggests that it is not), but nutcracking would perhaps *more* likely be an example of cumulative culture if seen performed by a community of, say, sloths. Likewise, clock-making is clearly a case of cumulative culture in humans (Richerson & Boyd 2005). But, theoretically, clock-making might come naturally to a feral alien baby from outer space, and thus clock-making would not be a type of cumulative culture for these aliens. In other words, even though a particular behaviour might not look like cumulative culture to the human eye, it might actually be cumulative culture for the ape species that performs it – it all seems to depend on the general inventiveness of the individual of a species. Thus, if there is no clear evidence for apes having cumulative culture as judged by human eyes, is there perhaps some indirect evidence for it?

One can try to answer this question in at least two ways: 1) one can determine and compare which social learning processes are used spontaneously by apes and humans. In the event that apes learn socially in a different way from humans, one can then speculate about the likely consequences this would have on the types of cultures they are able to produce and sustain. As we will argue, most social learning processes do not facilitate the evolution of cumulative culture, and these are predominantly the ones that apes tend to use. 2) It is possible to run ethically sound studies, even when following the general logic (but not the cruel procedure) of the aforementioned language deprivation experiments. In other words, to study whether the proposed types of ape material cultures appear in captive individuals that happen to be naïve to the task (‘deprivation’ would not be a fitting label here, since such subjects were not intentionally deprived of anything). In this instance, it would suffice to show that subjects can learn to solve the problem on their own, even if they were raised without demonstrations or prior knowledge for this particular task, i.e. remained naïve prior to testing to the relevant technology, problem situation, and materials. If so, then cumulative culture is not a pre-requisite for this behaviour and the transmission process of the behaviour most likely results from baser social learning mechanisms than process copying, since

apparently the general inventiveness of the species can account for the production of the behaviour.

## **CULTURE: A COMPARISON OF HUMANS AND APES**

### **1. Learning Mechanisms Seem to Differ between Humans and Apes**

Over the last one hundred years the everyday word ‘imitation’ has become a complicated concept (Tomasello & Call, 1997; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). Imitation is no longer described as a solitary mechanism, but has been split into a myriad of different sub-divisions, some of which seem to barely reflect anymore what the layperson might regard as imitation (for an overview of these sub-divisions, see Whiten et al., 2004; Zentall, 2006). Nevertheless, there is much sense in this hair-splitting approach, since, as has transpired, there are indeed multiple mechanisms that can lead subject A to behave like subject B, after subject A has seen subject B behaving in a certain way. For example, subject A might simply become more interested in either the type of stimulus that B has acted upon (stimulus enhancement: Spence, 1937), or in the general location where B has acted (local enhancement: Thorpe, 1963). Later, only as a result of individual (and not social) learning, A might derive at the same behaviour as B – thus, A did not really copy any of B’s behaviour. Furthermore, A might not have learnt from B the precise bodily actions, but instead might copy the resulting changes in the environment – with all “action information” lost by A (there are in fact several distinct forms of this learning process, subsumed under the umbrella term “emulation” (Tomasello, 1990; see also Huang & Charman, 2005, for an overview of current subdivisions)).

Thus, there are many forms of social learning, but for the current purposes it should suffice to draw one general division between them so that they fall into two categories: those social learning mechanisms fuelled by the power of individual learning (“product copying”: e.g. stimulus enhancement, local enhancement, emulation) and those fuelled by the power of process copying (mostly “action copying”, reflecting more the everyday connotation of imitation, see also Tennie, Call, & Tomasello, 2006). Action copying, or process copying in general, effectively leaves the problem of individual learning to be solved by others. Once a solution is found, it is then ‘simply’ copied as a complete process. If individuals then bias their process learning towards copying only the better solutions then better solutions may spread amongst others<sup>2</sup>, enabling cumulative culture (see Laland, 2004, for an overview of such differentiating processes). And thus, determining the ability for action copying becomes of importance as a proxy to determine whether a given species has or lacks the minimal potential for something deserving the term cumulative culture. What is the evidence for such copying in great apes?

Evidence for spontaneous action copying in great apes is scarce. This is not to say that apes cannot copy actions per se: they can - if extensively trained (e.g., Custance, Whiten, &

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<sup>2</sup> However, the species must also have some minimal level of cognitive inventiveness as well before culture can potentially develop along this route – as in the human case – because without inventions fuelled by this cognition, no solution would be worth copying (for other important factors see Richerson & Boyd 2005, as well as Tennie et al., 2009).

Bard, 1995; but see Byrne & Tanner, 2006, for a case study of one less well-trained human-raised gorilla). However, when tested in controlled experiments for spontaneous (i.e. untrained) action copying, they fail (see e.g. Tennie et al. 2006; but see Hopper, Lambeth, Schapiro, & Whiten, 2008; Hopper et al., 2007, for a different view). On the other hand apes do show ample evidence for results copying (emulation); that is, social learning powered mainly by individual learning capabilities, and which does not give rise to cumulative culture (see Tennie et al., 2009).

All in all, it is possible that action copying is absent in the spontaneous social learning of apes, which might in turn explain the apparent lack of cumulative culture in ape traditions. This statement seems at first glance to be in stark contrast to some recent findings that apes can be influenced by demonstrations of solutions, in so-called “2-action tasks” (i.e. studies in which two groups of subjects are each shown one out of two particular solutions to a given problem; for a recent review of such studies see Whiten & Mesoudi, 2008). In the case of positive findings, the authors of these studies have hypothesized, in general, that imitation (via action copying) was the underlying learning mechanism (in which case apes may have the minimal requirement to produce cumulative culture). However instead of such action copying, the apes in these studies might simply have learned something about how their environment works, and thus they might have “filled in” the required actions themselves and without having copied them (see Hopper et al. 2008 for some evidence on this, but see also Hopper et al. 2007). Thus, results copying, via the copying of the apparatus’ movements (“object movement re-enactment”: Custance, Whiten, & Fredman, 1999) is a potentially confounding factor in such studies. Such results learning, however, is probably not enough to sustain cumulative culture – since, after all, the copied changes in the environment are of a very basic kind and are easily capable of being invented by the individuals themselves (see also Tennie et al., 2009). Furthermore, even if learning in 2-action tasks really revolved around actions, then another potential confound arises: the demonstrated actions are typically not strictly novel to the observers – thus, these types of demonstrations might simply trigger some pre-learned actions within the observers, and therefore nothing novel is really learned – or, in other words, nothing improbable in the sense of cumulative culture could be learned (see also Byrne & Russon, 1998; Hoppitt, Blackburn, & Laland, 2007).

In accordance with this view Tomasello and Call (1997) concluded, in a review of all primate social learning studies that existed then, that each ape must “re-invent the wheel” at every step of transmission – which would suffocate cumulative culture. This high motivation and ability in apes to perform such re-inventions has recently led to the “zones of latent solutions” (ZLS<sup>3</sup>) hypothesis: that is, that ape traditions may be forever stuck inside a zone determined by the maximal technological complexity achievable for each (sub-)species’, as determined by their underlying cognitive skills (Tennie et al. 2009). The ZLS hypothesis assumes that product copying, not process copying, is the basis of great ape cultures, and that each ape uses his/her physical problem solving skills at each step of transmission (‘latent solution’; latent, because each ape can potentially invent the solution on his/her own – which means that the solution was simply dormant prior to the demonstration). In other words, apes re-invent observed products (product copying) rather than copying the precise techniques or processes that were modeled. Thus, the ZLS, by way of the underlying power of the physical

<sup>3</sup> The ZLS encompasses the sum of potential solutions, acquired by individual learning and constrained by the learners’ problem solving skills.

problem solving capacities of the individual, both predicts and restricts the kinds of traditions a given ape species harbors (and for different (sub-)species the size/reach of their ZLS might differ). In short, good problem solvers like apes are also good emulators (product copiers) and they are not inclined to copy another's actions because they can easily re-invent the solutions themselves. In general, it appears that the better a species is at individual learning (or problem solving in general), the higher its ZLS, and the further away the "threshold" for true cumulative culture. Outside this threshold lie difficult solutions that no single individual could invent on his/her own and that therefore must be transmitted via process copying – and which would represent cases of cumulative culture. Thus, an important next step is to test the reach of the ZLS of a given species: tasks shown to be inside the species' ZLS cease to be good candidates for cumulative culture and also largely cease to be good candidates for process copying. It is those tasks that are outside the species' ZLS (either by their difficulty or by their improbable design) that would, if they can be shown to spread, constitute cases of cumulative culture and which would then provide indirect evidence for process copying abilities in the tested species.

Current 2-action tests are not able to solve the question of whether apes have such a cumulative cultural potential since these studies typically just "move" the apes along one of two particular trajectories of learning – both within the species ZLS. Each of the two demonstrated solutions could have been invented individually by the apes (the typical 2-action task involves two relatively trivial solutions, such as, e.g. an object moving forwards or backwards, or left or right). Thus, current 2-action task studies can be re-interpreted as studying "founder effects"<sup>4</sup> on different latent solutions (the latent solutions that are demonstrated first may simply determine which latent solution trajectory a group of animals takes; see also Tennie et al., 2009). Due to the relative simplicity of their solution space current 2-action studies do not touch on the question of whether the apes could learn anything that they themselves could not have invented themselves (i.e. tasks outside their ZLS). To test the latter question (which gets at the ability for cumulative culture since it requires process copying skills) one would need to study the copying of very difficult solutions to a wholly different set of tasks. As of yet, there is only one study that has tested this ability directly, i.e. using a task whose solution was not capable of being invented by the apes (as determined by baseline performance). In this study, the apes failed to show cultural learning of the necessary solution, even though they had no other alternative strategy available to them - while children had no problem following social demonstrations (Tennie et al., 2009). Apes also failed in a further two studies related to this question: these studies could not find evidence for even a simple switch from an inefficient technique to a more efficient one once the apes (chimpanzees in this case) had already learnt another technique first (crucially, here both techniques were within the species' ZLS, see Hrubesch, Preuschoft, & van Schaik, 2008; Marshall-Pescini & Whiten, 2008). All in all, then, there is no convincing direct evidence to date that apes a) learn a piece of cumulated culture (i.e. a task outside their ZLS) and b) learn spontaneously via process copying.

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<sup>4</sup> Not to be mistaken with the same term used in population genetics to describe a different and unrelated mechanism.

## 2. Latent Solution Experiments can Evaluate “Culture” Candidates

Since (currently) we cannot identify features of ape culture or behavior that provide direct and clear evidence for cumulative cultural evolution (which would count as indirect evidence for process copying) and since there is no direct evidence for process copying in apes, one is practically left with only one (indirect) method of determining whether cumulative culture (and indirectly: process copying) is a feature of ape cultures: “cultural naivety experiments”. Such experiments take on the general logic of the infamous language deprivation experiments described above (but unlike these, they need not be unethical). Here the experimenter takes advantage of the fact that captive populations exist which have never had contact with the culture in question, i.e. they are naïve to the task. Ideally, the subjects have never seen a model, and have never had contact with the material needed to solve the task (e.g. hammer stones) and/or indeed the problem itself (e.g. closed Coula nuts). In our nutcracking example, this would take the following form: provide such naïve captive chimpanzees with all the necessary material (i.e. closed nuts, hammers & anvils) and make also sure they like the nut kernels (“motivation check”). Will they start nutcracking without having seen demonstrations of this behavior? If some of these naïve subjects start to nutcrack and if they do so in a style *like their wild cousins*, this would be tantamount to “children spontaneously developing speech”, and thus nutcracking may not be a case of cumulative culture anymore – for it would have become highly unlikely that process copying is responsible/necessary for its spread. As a general rule of thumb, if any behaviour is shown by this method to be within a species’ ZLS<sup>5</sup>, then it is an unlikely candidate for cumulative culture, and to a large degree, it is also an unlikely candidate for process copying.

We prefer to call these types of experiments “latent solution experiments” since really what is tested is whether a certain behaviour falls under the zone of latent solutions; i.e. if it is capable of being invented by naïve individuals and thus is not a candidate for cumulative culture. In addition, we prefer this term over “deprivation experiments” since deprivation is not really happening in any meaningful sense, and using this term would mislead one into thinking that the experiment involves unethical treatment of the test subjects (which is not the case). As we will see, such tests are relatively easy to do, and surprisingly, few of such studies have been performed on primates until now.

## EXAMPLES OF LATENT SOLUTION EXPERIMENTS

### 1. A Natural Latent Solution Experiment: Grooming Hand Clasp

Latent solution experiments in primatology owe much to a descriptive data set on grooming in chimpanzees. Such observations found that the so-called “grooming hand-clasp” (McGrew & Tutin, 1978), a behaviour thought to be a socially transmitted via process copying, has multiple independent origins in several populations, including one in captivity (de Waal & Seres, 1997). Thus, there is no need to invoke process copying or cumulative

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<sup>5</sup> Importantly, even a single individual performing the target behaviour under such circumstances would be enough to fulfill this criterion (see also the quote at the start of our chapter: if target behaviour shown by a single tested individual in well-controlled study is of sufficient complexity, it is unlikely to be a mere chance event).

culture as an explanation for the occurrence of this behaviour. Instead, hand-clasp grooming develops spontaneously, i.e. is within the chimpanzees' ZLS.

## 2. Latent Solutions in Captivity I: Leaf Swallowing

The first experimental study to directly apply the latent solution experimental method to primates<sup>6</sup> focused on "leaf swallowing" behaviour in chimpanzees. Wild chimpanzees, bonobos and gorillas (Huffman 2001) swallow certain hispid leaves *unchewed* in a rather particular way (possibly in order to physically rid themselves of intestinal parasites). To determine the acquisition mechanisms for this peculiar behaviour, Huffman & Hirata (2004) provided some naïve, captive-born chimpanzees with very similar leaves. Two of the completely naïve chimpanzees that they tested performed the original leaf swallowing behaviour spontaneously, and in their first trial. Other chimpanzees seemed initially afraid, and possibly upon observing leaf swallowing in others, started to swallow the leaves themselves (and a few remaining chimpanzees never swallowed the leaves). In this case, the act of naïve chimpanzees swallowing leaves in this particular style is similar to language-deprived children talking fluently. The chimpanzees performed the target behaviour perfectly, and did so from the very beginning of the experiment<sup>7</sup>.

In conclusion, chimpanzees seem to be genetically predisposed to conduct the complex behaviour that occurs in leaf swallowing: it seems neither socially learned nor environmentally shaped (even though it could be environmentally triggered). Whether or not this behaviour materialises depends on internal and external motivational factors (e.g. possibly also on some form of social contagion (Thorpe, 1963)). Leaf swallowing thus seems a clear example of a latent solution: it likely does not involve a cumulative culture component and process copying is likewise not necessary to explain its occurrence.

## 3. Latent Solutions in Captivity II: Gorilla Nettle Feeding

The second study to use the latent solution method directly on primates was done with all four species of great apes (Tennie, Hedwig, Call, & Tomasello, 2008), but the target behaviour was one that was originally observed in gorillas. In the last few years, it has been argued by several authors that Mountain gorillas (*Gorilla beringei beringei*) at Karisoke, Rwanda show food processing skills of such an elaborate and complex nature that they must have been copied by process copying (i.e. by so-called "program level imitation", Byrne & Russon 1998, see also below). Tennie et al. set out to directly test this hypothesis by running a latent solution experiment.

Mountain gorillas live in an environment low in fruits, feeding mainly on various herbs (Watts, 1984). Many of these herbs possess defences such as thorns, spines, and irritant hairs that individuals have to neutralize prior to ingestion. Mountain gorillas tackle these plants by

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<sup>6</sup> Note that the general logic of such studies in social learning experiments is considerably older and has been used with great success to detect the apparent lack of precise process copying underlying some bird behaviour (i.e. Sherry & Galef 1984; see also Kenward et al. 2005 and Tebbich et al. 2001).

using complex manipulative sequences that apparently render the plants' defences ineffective. One of the staple foods of Virunga Mountain gorillas is the African stinging nettle *L. alatifipes* (Watts 1984). This African nettle has developed stinging hairs, which upon contact with skin produce a painful reaction. Apparently as a consequence, Mountain gorillas feed on this nettle by means of a hierarchically organized processing program: (Byrne & Byrne, 1993; Byrne & Russon 1998; Byrne, Corp, & Byrne, 2001b). When all non-socially transmitted features are left out (e.g. lateralization) this particular nettle eating process reaches a standardization level of 88 % in the Mountain gorillas (Byrne & Byrne 1993). Byrne and Byrne (1993), and also Byrne & Russon (1998) claimed that such high levels of correspondence are most parsimoniously explained by process copying (which they called "program level imitation" in this case).

According to Byrne (2005) program level imitation is "copying the structural organization of a complex process by observation of another's behaviour, regardless of how the exact details of actions are acquired". For our purposes, therefore, we can treat program level imitation as a special form of process copying (i.e. where program = process). Byrne and colleagues argue that process copying best accounts for Mountain gorilla's complex feeding techniques due to this program's "improbable complexity" (Byrne, 2005). Byrne bases his argument upon the "improbability" of technique convergence due to "the improbability of this happening, reliably for every Mountain gorilla, in the 3 year period of skill development, and especially with plants (like nettles and thistle) that discourage playful exploration by the pain they induce". The general argument is that if one observes complex skills with high reliability and standardization of form, then process copying should be considered responsible. Thus, the distilled argument in favour of social learning at the heart of Mountain gorilla's complex feeding technique appears to be one based on its improbability and complexity.

Several authors have offered alternative explanations for the acquisition of food processing skills in Mountain gorillas, but lacked the necessary data to support their case. They have proposed that the combination of trial-and-error learning, plant affordances, genetic predispositions and motivational factors may be sufficient to produce the observed feeding pattern (Bauer, 1998; de Waal, 1998; Matheson & Frigaszy, 1998; Tomasello, 1998; Vereijken & Whiting, 1998). Thus, the existence of hierarchical organization in itself may not be ultimate proof of social learning (Bauer, 1998; Midford, 1998; Miklósi, 1998; Tomasello, 1998). Several authors have proposed that the case for program level imitation would be much stronger if another population of Mountain gorillas living in the same environment, eating the same plants, had developed a group-technique which is different from the one described – that is, if alternative techniques existed (Bauer, 1998; de Waal, 1998; Tomasello, 1998; Vereijken & Whiting, 1998). Of course, one can also turn this argument around; i.e. the case for program level imitation would be much weaker if another population of nettle-eating gorillas had developed a group-technique the same as the one described.

Tennie et al. (2008) examined the various alternatives that have been postulated to explain the acquisition of nettle processing by performing a latent solution experiment. To them, the combination of observational and experimental approaches was key to determining the mechanisms that may explain the acquisition of a particular behaviour (Tomasello, 1998).

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<sup>7</sup> It does not matter that a few chimpanzees did not swallow the leaves at all: after all, one talking feral child would have been enough to prove an "original language".



In a manner like Byrne and Byrne (1993), Tennie et al. collapsed single actions into functional categories to create a program. The following four categories were thus distinguished: (1) procurement (2) gathering a whorl of leaf blades, (3) processing the whorl, and (4) insertion into mouth (see Fig. 1). These are the same categories (in the same order) used by Byrne and Russon (1998) to describe nettle feeding of Mountain gorillas, except that two processing parts of Byrne and Russon were collapsed into one category by Tennie et al. since both served for one and the same function (“3”, i.e. to process the whorl of leaves in order to ease ingestion).

## Experimental Studies of Nettle Feeding in Captive Gorillas and Other Ape Species

The main goal of Tennie et al. (2008) was to find out whether captive gorillas would or would not show any consistency in the sequential organisation of nettle feeding actions compared to Mountain gorillas and compared with each other (program-level)<sup>8</sup>. If they did, this would provide evidence to support the view that nettle feeding is a latent solution, and would have the afore-mentioned consequences for the social learning hypotheses with regards to this behaviour. To this end, they provided nettles (European Nettle *Urtica dioica*) to 12 captive western gorillas (from here on: captive gorillas) from three different zoos in Europe. Importantly, they also provided this nettle to one nettle-naïve captive gorilla at a zoo in Stuttgart, Germany. Additionally they also provided gorillas with a different plant (willow *Salix sp.*) which is very similar to the nettle in its overall structure but lacks any defensive mechanisms, such as stings. This enabled them to test to what degree the affordances of the plants (Tomasello, 1998) influenced the way the gorillas processed them. Finally, they were also interested in whether or not the three other species of great apes would show the same feeding behaviour, and thus they were also provided with both types of plants.

Ten of 12 tested captive gorillas of the three groups fed on nettles, including the naïve gorilla, and they all showed a large overlap in their sequential ordering of nettle feeding actions – both when compared with each other as well as compared to Mountain gorillas. Thus, all gorillas (including the naïve subject) sorted their actions into sequences (i.e. programs) in highly similar ways. Also, and importantly, the nettle-naïve gorilla performed the Mountain gorilla sequence as well, even though she did so less frequently as compared to the experienced gorillas due to her occasionally leaving out the final “processing” (i.e. sting neutralization) step (see Fig. 1).

Previously unpublished data on nettle processing in one other group of captive gorillas in Apenheul Primate Park, Apeldoorn (Netherlands) by the same authors is also in accordance with Tennie et al.’s findings. In this study, which was done in 2006, ten of the fourteen tested captive gorillas that were nettle-experienced also fed on *U. dioica*. Furthermore, in doing so,

<sup>8</sup> Tennie et al. (2008) also analyzed nettle feeding at a more magnified level; i.e. they tested whether there was any evidence for copying of small-scale actions during nettle feeding. Action copying was not found in the original case of MGs (Byrne & Byrne 1993), and Tennie et al.’s data also largely points to this conclusion (e.g. seven out of the eleven actions used by mountain gorillas were also performed by captive gorillas). Here we are concentrating on the program level, since it is this level that was reported to be transmitted via process copying (Byrne & Russon 1998). Thus, the entire program for nettle feeding was the target behaviour that was tested in Tennie et al.’s latent solution experiment.

these subjects showed a substantial overlap with the behavioural repertoire of the above captive gorilla study (i.e. Tennie et al. 2008) as well as with the Mountain gorillas. Four of the five individuals in Apeldoorn, for whom more than one feeding sequence was available, most frequently performed the original Mountain gorilla sequence, and apparently ubiquitous gorilla sequence: (“procure- gather- process- insert”, see Fig. 1).

To summarise, many captive gorilla groups (including, importantly, one nettle-naïve gorilla) applied the same overall technique as wild Mountain gorillas. When pooling the actions constituting the modal technique for nettle feeding in Mountain gorillas according to the functional categories applied in this study, no differences remained between the sequential organization of nettle feeding of Mountain gorillas and captive gorillas (Fig. 1). Thus, nettle feeding is a latent solution in gorillas, just like leaf swallowing is a latent solution in chimpanzees. But would gorillas use this technique automatically and inflexibly when presented with plants of a general nettle structure? The answer is no: Compared to the nettle technique, captive gorillas performed only sub-parts of the nettle technique when feeding on willow leaves (and four out of the five gorillas tested by Tennie et al. (2008) fed on willow), but never processed willow leaves (presumably since these do not need processing due to their lack of stings) and sometimes even gathered willow leaves for ingestion *directly* from the stem with their mouth (Fig. 1). Thus, gorillas adjust their feeding style flexibly towards the details of the plants they feed on.

In stark contrast to the captive gorilla findings, none of the non-gorilla apes (Five chimpanzees, five bonobos and five orangutans), except one orangutan, ate nettles regularly despite the fact that nettles were available in all outdoor enclosures<sup>9</sup>. However, unlike the gorillas, this particular orangutan never performed the processing step when feeding on the nettles. In contrast to the unpleasant nettles, seven out of the 15 non-gorilla great apes consumed the undefended plant, i.e. willows. When doing so, they employed an alternative technique to the gorilla willow method: whilst gorillas used the highly efficient action “strip-up” to gather whole bundles of leaves at once, the other apes always ate single willow leaves directly from the stem. This comparison suggests several things: gorillas are naturally more inclined than other ape species to eat plants defended like nettles, and they do so using a highly efficient program that can best be described as a latent solution (see fig 1). The findings also suggest that gorillas (and only gorillas) use another, more basic, latent solution (“strip-up”) for undefended plants of the same general overall structure as defended nettle plants.

The exact ordering of the steps that make up a certain program is key for Byrne and Russon’s (1998) program level imitation argument. Tennie et al.’s 2008 study, as well as our presented study, found that *U. dioica*-experienced and naïve captive gorillas showed the same overall nettle tackling program as is found in Mountain gorillas feeding on *L. alatisipes* (Byrne and Byrne 1993). This evidence is most consistent with an individual learning (and/or genetic predisposition) hypothesis.

One might still argue that wild-born captive gorillas may have learned the technique by process copying in the wild and that they (and their offspring) transmitted the technique when they were brought into zoos. Thus, the technique could still have spread through the captive population by program level imitation. One major problem with this explanation (besides the

<sup>9</sup> Nettles were also available in the captive gorilla outdoor enclosures, which is why Tennie et al. (2008) only considered one subject in a different Zoo (where no nettles were even available) fully naïve to nettles.

apt performance of the naïve gorilla in Tennie et al. (2008)) is that captive gorillas belong to the western lowland gorilla species which are not known to eat nettles in the wild (Rogers et al., 2004). Therefore, it is unlikely that captive gorillas imported the technique from the wild and consequently the technique must have been invented in captivity – much like the case of the naïve gorilla in Tennie et al. (2008). The existence of multiple inventions shows that the nettle feeding steps in fact cannot be easily combined in multiple ways to form functioning nettle feeding patterns, which is hard to reconcile with the view of Byrne (2005) that it is improbable the technique was learnt by a mechanism other than program level imitation.

Reinventing the same program in order to feed on nettles could have arisen from individual learning constrained by the affordances of the nettles. This is supported by Tennie et al. (2008) whose data show that willow leaves, whose overall structure is similar to nettles, are not eaten according to the same program as nettle leaves by nettle experienced captive gorillas. Thus it is the fierceness of nettle stings that induces the method of tackling them, and it is the stings' distributions together with the structure of the plant that determines the overall tackling technique.

Second, the program used by the naïve gorilla tested by Tennie et al. (2008) was the same as that used by the nettle-experienced captive gorillas and Mountain gorillas, even though social learning of any kind could be fully excluded in this case. Finally, the very rare attempts to eat nettles by non-gorilla species were very different to the gorillas' techniques. Taken together, these findings support the view that gorilla nettle feeding develops naturally in gorillas. In fact, we agree fully with Bauer (1998) who has even questioned “whether the target behaviour [i.e. nettle feeding in the style of Mountain gorillas] is inevitable, given the organism, its goals, its environment and the constraints imposed thereby”. The gorilla nettle feeding program seems inherently constrained, both by the nettle's features, as well as by “gorillas' features”. The organizational steps, so it seems, could not be re-shuffled; in other words, the situational and motivational constraints do not allow for any degree of freedom. These constraints instead reliably result in the observed sequence and are the reason for its apparent ubiquity. Thus, and using the logic of latent solution experiments outlined above, our data, as well as Tennie et al. (2008), suggest that program level imitation is unlikely to be responsible for the acquisition and spread of the nettle processing technique. This may not be totally surprising, as gorillas have not yet been proven to be capable of process copying in controlled experiments (Stoinski, Wrate, Ure, & Whiten, 2001, but see Byrne & Tanner 2006). The non-cultural verdict likely reaches beyond just the case of nettles because the same reasoning may apply to the programs that Mountain gorilla's use to tackle other defensive plants (thistles: Byrne, Corp, & Byrne, 2001a; bedstraw: Byrne & Byrne 1993) or to plant tackling observed in other primate species (e.g. in chimpanzees: Corp & Byrne, 2002). Instead our data support the notion that individual learning, channelized by plant affordances and possibly paired with genetic predispositions and/or social enhancement effects (Spence, 1937; gorillas: Watts, 1985) is responsible for the acquisition of the nettle processing program. Nettle feeding in gorillas, just like chimpanzee leaf swallowing, is a behaviour subsumed under their respective zone of latent solutions. As such, nettle feeding is unlike human culture in that it is not cumulative and in that it does not require process copying in order for it to spread.

## SUMMARY AND OUTLOOK

Human culture looks different from ape ‘culture’, and this seems not to be a mere matter of point of view. While there seems to be no direct examples of ape cumulative culture that would strike the human eye as unequivocal evidence, it has also proven hard to establish indirect evidence supporting such an ape culture view. This is true both if one compares social learning mechanisms spontaneously used by apes (likely restricted to product copying) as well if one determines whether process copying is strictly needed in order for certain ape behaviors to appear (i.e., in latent solution experiments).

Concerning latent solutions, we have argued that despite “cultural (& material) naivety”, chimpanzees perform leaf swallowing (Huffman & Hirata 2004) and invent hand-clasp grooming (de Waal & Seres, 1997) – both of which are behaviors that were once strongly believed to have been transmitted via process copying. We have also presented evidence that the Mountain gorilla nettle eating technique, despite its apparent complexity, develops spontaneously and with apparent ease in gorillas (but it does not develop in other ape species or in captive gorillas tackling plants which lack such defenses). Nettle eating, once thought to be transmitted via process copying, instead develops under “cultural naivety” conditions in latent solution experiments, thus leaving the former claims in a very weak position (i.e. Tennie et al. 2008, as well as data presented here). In general, and in contrast to the claims made by Byrne (2005), social learning cannot be accurately inferred from observations of complexity alone (see also Bauer 1998). Environmental pressures can be sufficient to induce the behaviour in question (individual learning), and the species’ genetic makeup can also matter – indeed inherited action patterns can sometimes play a large role in the development of quite complex behaviours (see Kenward, Weir, Rutz, & Kacelnik, 2005; Tebbich, Taborsky, Fessl, & Blomqvist, 2001). In general, spontaneous solutions, be they due to internal and/or external factors, are all subsumed under the umbrella of the ZLS – and can then be compared with truly cultural behaviors.

As for other primates, or other candidates for animal cultures in general, we have no doubt that many of these will eventually appear spontaneously in “latent solution experiments” like the ones described above. For example, nutcracking may appear in naïve chimpanzees in such a test, given enough motivation, enough trials and free access to all necessary materials – while in contrast no “feral” human would ever invent a hovercraft even if given all of the necessary tools and enough motivation. And so, if behaviors that are thought to be candidates for culture appear in latent solution experiments, they will largely cease to be good candidates to prove cumulative culture and process copying skills.

Thus, a difference remains between ape and human cultures: ape traditions are individually re-invented again and again – and thus only products (if anything) are being copied by apes, hindering accumulation. In humans, culture works differently: human culture is dependent on its own history, since culture accumulates to eventually produce improbable design – and this is brought about by a different, a social process involving process copying (see also Richerson & Boyd 2005, Tennie et al. submitted). Re-inventions of human cultures done in a cultural and social vacuum are thus bound to look different to their originals (at least at some point), unlike the case for ape’s “cultural” items, whose re-inventions basically remain the same and are thus not cumulative in nature.

We believe it is high time to start a major project to individually test the invention rates of a diverse set of primate behaviors currently regarded as cultures (see, e.g. Whiten et al.

1999, van Schaik et al., 2003) using latent solution experiments like the ones described above. Should a tested behaviour occur under such conditions, then they would lose their cultural “label” – at least until clear evidence surfaces to corroborate some of the proposed process copying and/or accumulated components involved. Instead, such cases might better referred to as ‘traditions’, since in all likelihood they are based on lower level learning mechanisms than are understood to be at work in process copying.

Although process copying and accumulation cannot ever be completely ruled out, this is rather due to the fact that one cannot in principle demonstrate that something is *not* the case. But for all practical considerations one can – in special circumstances - assume that it is not the case - and latent solutions provide such a case: if it is spontaneously inventable, neither cumulative culture nor process copying are strictly needed, and the most parsimonious explanation is that they are indeed not responsible. Therefore we believe that the burden of proof rests with those who maintain that the trait is an imitated and/or cultural trait – and these proponents need to re-establish that process copying does noticeably change the pattern of the behaviour (i.e. by adding some style factor that could not be explained by the given internal and external constraints). Until such proof is clearly established we would then assume that the given trait is non-cultural.

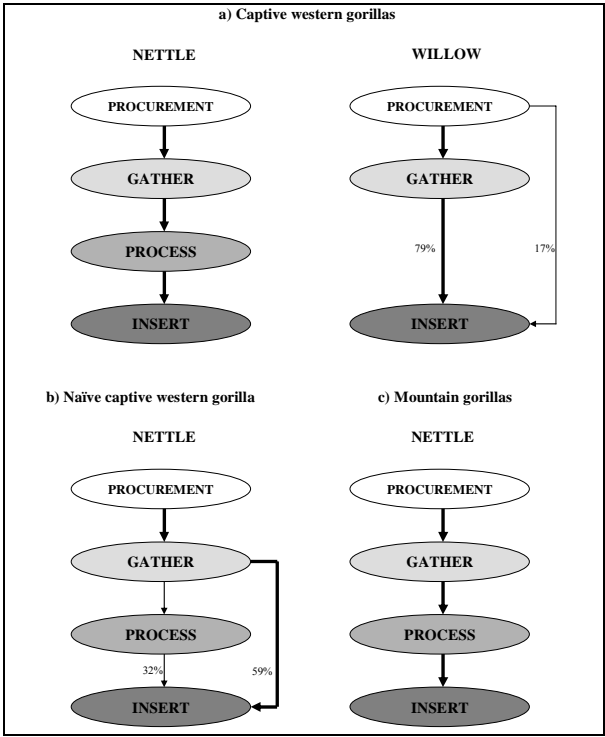


Figure 1. Leaf feeding programs of captive western lowland gorillas and Mountain gorillas. Thick arrows indicate behavioural sequences most frequently performed. Thin arrows indicate divergences from these. a) Nettle (*Urtica dioica*) and willow (*Salix spec.*) feeding programs of nettle experienced captive western lowland gorillas. b) Nettle feeding program of the naïve captive western lowland gorilla c) Nettle (*Laportea alatiipes*) feeding program of wild Mountain gorillas.

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## *Chapter 6*

# **THE TENDENCY TO MAKE MAN AN EXCEPTION**

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## **1. INTRODUCTION**

We are all familiar with the old saws we hear in the press of how special man is, he is the only animal to build houses, change the landscape, have agriculture, make war. These have all long been shown false, in his delightful 1974 book von Frisch demonstrates the vast number and variety of structures animals of all kinds build and Vander Wall (1990) shows the diversity of food preparation and storage in animals, while E.O. Wilson (1975) and Chavin (1968) describe insect agriculture and warfare. Nevertheless, I am often surprised by the propensity of journalists to magnify any discovered difference between *Homo sapiens* and some other animal as a universal example of man's special place in nature. Even more disappointing is when other scientists display the same tendency. This essay will address a number of areas of *Homo sapiens*' biology and behavior in regards to distinctions with all other animals, the "special place" idea. First I will discuss ideas put forward concerning man's special biology that were argued to place us in a separate taxonomic relation. Secondly I will cover arguments that our biochemistry and molecular chemistry set us off from all other species and finally I will address the areas of behavior and sociality.

## **2. THE BIOLOGY OF MAN AND PRIMATES IN GENERAL**

Adolph H. Schultz published an article in 1949, "The physical distinctions of man," where he states, "Generally speaking, the list of man's physical distinctions has been lengthened, whereas the significance of the single specific characters has diminished with advance in our understanding of man's true nature." He goes on to point out that most investigators of man's physical distinctions had limited themselves to the study of the adult and to the use of only European averages, thus producing a distortion of what it is to be

human. Even these “averages” were often idealized as when a skull from Central Asia (Caucasian) was used to typify the “European” populations.

This emphasis was a reversal of an earlier trend begun by the early Greeks and Romans, specifically in references to Galen in the first century of our era all the way to people like Tyson in 1699 up to the middle of the 19<sup>th</sup> century, of the remarkable similarity of apes and humans to these investigators. Here the focus was how human apes appeared. It was the effects of the opposite emphasis of Darwin, Huxley and Haeckel to concentrate attention on the ape-like qualities of man. Certainly to Haeckel, the lens of the developmental process was one means to study evolution. One might say that with Linnaeus the tradition of including man in a comprehensive analysis of the vertebrate world began, as he placed man in the Order Primates among animals he considered having hands on the anterior extremities. Others soon disputed this inclusion, like Schreber (1775) who removed man and placed him in a separate unit of those animals with only two hands, all other Primates considered to have four. This was followed by Blumenback in 1791. This continued, as Schultz points out in another publication (1950), this separation was utilized by Cuvier (1805) and retained by most taxonomists until the end of the last century.

The contrast in the form and function of the feet and hands of humans and other non-human Primates seemed so distinct that the genetic distance was assumed to be substantial. As more anatomical information and an understanding of the variation in hands and feet in the Primates became available in the last hundred years this distance appeared to fall away. Napier (1962) even argues, that, it seems surprising the human hand “...should constitute, in a structural sense, one of the most primitive and generalized parts of the human body.”

To Schultz (1950) much of the information to undermine the distinction came from studies of development and his Figure 1 showing the early stage of limb growth in humans and a macaque is persuasive. Variation in populations came to show significant differences within species, as with the Mountain gorilla, where the “feet” are shown to be very poor “hands.” In many specimens. The failure of many students of man in the last century to familiarize themselves with collections of Primates allowed some to produce statements entirely contrary to the facts, as when Wood Jones as late as 1948 could state that the incorporation of the big toe in the general mass of the foot differed from the Apes where it was free. This later condition is only found in the Hylobatidae. Or where individual traits, like the peroneus tertius muscle, as Schultz (1936) tells us, was once regarded as peculiar to man as it was found in 91% of Europeans, but then was found in a number of gorillas, and a baboon. This kind of myopic separation of traits has led to efforts to given distinct species status to Neandertals on the basis of partial DNA coding from ancient samples compared to millions of contemporary modern humans (Caldararo & Gabow, 2000; Caldararo, 2003). Similar distinctions were used in the past to deny specific status to some peoples (Montagu, 1967) so we should be careful how we apply categories today.

The means of hominid locomotion was used by some taxonomists (e.g., Illiger, 1811) as a primary distinction to separate man into a distinct taxon, but many Primates are partially bipedal, as is the Sifaka and Spider monkey, the African apes, the gibbon and siamang (Schultz, 1950). Schultz (1950) also demonstrates considerable overlap in lower limb length between man and several Primates. The same kinds of difficulties in identifying specific characters in the fossil record to distinguish phylogenetic relationships among both fossil apes and early hominids has been emphasized by Schwartz (1997; 2006).

However, the fields of anthropology and human biology largely abandoned comparative anatomy by the end of the Second World War and many students of human evolution lacked substantial backgrounds in the physiology of other vertebrates, were concerned with embryology or the variability of human populations. Essentially this has been part of an ever more specialized science and has paralleled specialization in other fields as the complexity of technique and the mass of literature make generalists rare or impossible.

### 3. SOME EXAMPLES

Some popular texts from researchers in other fields have entered the public mind with the idea of the special nature of man. The most significant in the 1960s was Desmond Morris' *The Naked Ape*. Morris, a zoologist claimed that the nature of man's naked skin set our species apart from all others. This so astounded Ashley Montagu that he titled his critique, "The naked Englishman". What struck Montagu as strange was that Morris was a respected zoologist who seemed to think that all there was to talk about regarding human body hair could be found on the streets and heath of that generally foggy nation. Of course, Montagu had written an article a few years before where he claimed that, "Man is the only hairless primate,..." (1964). Thus Montagu had lent himself a degree of license by the title, however, which used the words, "near hairlessness." Nevertheless, it is only the sensational headlines of such claims that reach the popular press, the corrections seldom do.

That Montagu took exception to the idea of "naked" but not "hairless" is significant as I show in my discussion of hair and human evolution (Caldararo, 2005). While Montagu pointed out that Morris's definition of "naked" was unscientific because he did not apply his analysis to the whole human population, Montagu also succumbed to the feeling that we are different, and so much so that a distinction was necessary even though it was unscientific. Montagu's charity in this case was misplaced, and conflicted, and we are flooded yearly with not only scientists making claims of man's uniqueness in this or that trait, but a herd of journalist publications. This is true of exaggerations by the press of solid research, as in the case of blushing, but this is not true of exaggeration by some scientists like the assumptions concerning "whites of eyes" (the sclera, see Anthony, 1959) being a "uniquely" human trait (e.g., Tomasello, 2007). As one can see from the illustration of a macaque in figure 1, "white" sclera are not unique to humans. That all humans have such sclera may have other reasons and that is interesting, but not unique. The points he made were, nevertheless solid regarding how researchers have to be not only thorough about all life if they are going to say a species is the only one to possess some trait, but they should understand and have a comprehensive knowledge of human variation, at least of the trait they are championing.

Now and then books and articles appear that treat certain features of humans as special, distinct from any other animal. Freakish is almost implied as if human existence was an abnormality on the planet. One such book was Jared Diamond's *Why Sex is Fun* which labored to demonstrate that human sex was so different from all other sex among animals that it was almost outrageous. This could only be accomplished by the tortured stereotyping of human sexuality, mainly stereotyped ideas of middle class European sex. Diamond's many books have largely focused on the field of anthropology though he is trained as a physiologist

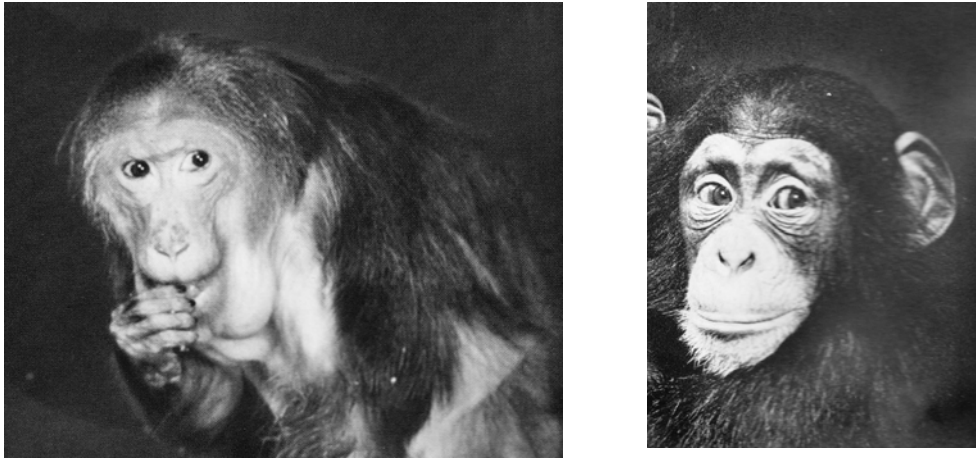


Figure 1: Macaque on left and Chimpanzee on right, both with white scleras

of the human body but practices in ornithology. In his book, *Why Sex is Fun*, Diamond argues that humans are the only species that have sex in private. This is what the public takes away from the book, and I know since I have had hundreds of students read the book and put that statement in their reports. What does Diamond say though, “Marriage partners usually have sex in private, rather than being indifferent to the presence of other humans.” What does he base this on? Nothing, no citation, no data. Among other claims that appear to overreach as to why human sex differs from other animals, here one wonders where Diamond got this idea, except that his population of study seems to have been quite restricted. The idea of “private” space or privacy is at the core of this claim and a reading of the wide variation in concepts of sex, and sexual behavior contained in a text like that by Unwin (1934) leave little veracity to the argument. Even if limited to the modern west, however, ignoring the wide range of locations and group settings for sex among many peoples, one finds that many Europeans, even recently given one room homes or homes with only one room for sleeping, provided only opportunities for sex in “public”. That is, where they could be watched. It is also rather apparent in recent years, if not for at least 2,000 years of complex society in the west, that pornography, group sex, and sex in public are pursued by many people of European backgrounds. Though this behavior is often sanctioned with arrest and fines in recent years, the sheer number of yearly arrests is contradictory to his argument, and though arrests have gone down in recent years (Anglen, 2007), some reports indicate sex in public is increasing (Em & Lo, 2007). This makes it certain that something is seriously wrong with Diamond’s theory.

Other comments on the special nature of human sex have appeared in recent years. Sara Hrdy produced a book setting human gender in a biological context and then made statements in lectures and to the press that set man apart. On November 6 of 1986 the *San Francisco Chronicle* published a statement arguing that, “Unlike female chimpanzees or baboons, which have very brief periods of sexual availability, they (humans) do not advertise for sex with prominent swelling around their sex organs. The pattern is seen in other primates, too.” This was, of course, before “availability” for sex among bonobos was better understood (de Waal,

2005). Here we have to question also the nature of the term “availability” and its presumed association with estrus as well as the distribution of “swelling”. This I will comment on later.

In another example, a textbook by John Langdon (2005) presents a list of “Human characteristics” (Table 2.8) beginning with “Relatively and absolutely large brain size.” He adds that it is the most remarkable feature of our species. No qualification appears to this to indicate that other animals, for example, dolphins (H of P, Chanis & Morino, 2005) have large brain sizes compared to their body size or that their brains are highly convoluted like ours or that their neural cell density is high. While we do have large neurons, in some cases, compared to other vertebrates, the nature of brain size to plasticity of behavior or survival is never attempted. The significance that dolphins have had large brain sizes for over 15 million years compared to our mere 2 million, as John Lilly noted (1962) is ignored. Langdon mentions whales and dolphins but only in reference to a theory of the role of DHA in brain development. This neglect is curious and leads one to wonder if what is left out is intentional in an effort to enhance human exceptionalism and not a lack of knowledge. Like many books on human evolution that refer to the evolution of the brain Langdon also mistakes the evolution of the mammalian brain structure for the basis of the bird brain and states that “birds have also added an area of cortex, but it is relatively simple and not homologous to the mammalian neocortex.” Here at the end he is partly correct, the bird brain segment that is homologous to the neocortex in mammals is the wulst (Stettner & Matyniak, 1968), so why not say so instead of making their brains sound, well, small and rudimentary?

In 2004 Neufeld and Conroy published an article in the journal *Evolutionary Anthropology* arguing that human head hair was not “fur” and that human hair grows at a continuous rate unique among animals. The problem with this assertion is that human hair is not unique and that it does not grow continuously at the same rate in all humans but is varied, most likely by environmental selection and sexual selection. Also, as I pointed out in a 2005 article in the same journal, other animals have continuously growing hair on parts of their bodies, mainly animals domesticated by man, like the horse and sheep.

In his book *Thumbs, Toes and Tears*, Chip Walter we hear that humans are alone in possessing big toes, opposable thumbs, laughter, tears, kissing and speech. Certainly human variation in the size and shape of big toes is significant as is that among other Primates as Schultz (1936;1950) has shown, other variations among the great apes also show considerable overlap in traits (Grehan, 2006) while Gould (1980) has demonstrated the variations in “thumbs” and opposability.

In his book, *The Growth of Humanity*, Barry Bogin, addresses issues related to the evolution of human development and ontogeny and the biocultural consequences of the increase in density in human populations. Comparisons of the evolution of human society and demographic structures have been made in other fields (Cipolla, 1962;1970). Nevertheless, this is a valuable and compelling work not only for its achievements in elucidating aspects of demography with the context of human development, but because it is written from an anthropological perspective. As one of his main theories, however, Bogin proceeds to demonstrate that during human evolution of the last 2 million years hominids added a childhood stageto the life cycle and that in the past 100,000 years *Homo sapiens* added a “distinct adolescent stage”.

The explanation of the growth of humans in the context of other mammals and primates is comprehensive and clear as is the demonstrationof socio-economic status (SES) in human growth and development. However, the author makes a clear distinction about the features of

stages of human growth in his initial definitions but then uses the terms childhood, juvenile, adolescence, early adulthood in varying ways which tends to undermine the clarity of his definitions. The transitions from infancy to childhood and the role of childhood and adolescence are often unclear or contradictory. The conclusive establishment of the idea of a stage of human development as “childhood” and “juvenile” is lacking as it was in his earlier book (Bogin 1999). It would be instructive for the author to provide data on other vertebrates to support this concept in a precise fashion. In fact, the presentation of data concerning the release of FSH, LH and GnRH in *Macaca* seems to contradict the author’s theory, as does data for other primates (Plant, 1994). Parallel patterns of adrenal steroids related to adrenarche are noted in dogs and rabbits (Cutler, et al., 1978). Comparisons with other vertebrates show a considerable variation in growth rates, survival of young, size, etc. (Case, 1978) but building separate stages out of this is questionable. Bogin attempts to support his thesis by stating 1.) That in humans there is a long period between puberty and adulthood as opposed to monkeys and apes which is less than three years and 2.) That there is a human adolescent growth spurt. However, even in the author’s 1999 publication to which we are referred, there is no data to support this idea as a median event or distinct from other mammals or vertebrates. Grehan (2006) shows that this is a difficult proposition to uphold from the Primate data. Is this related to life history, longevity, population structure, etc.? Do we know enough about the life histories of other long lived vertebrates to make such a broad statement, dolphins, whales, turtles, birds?

This problem makes the author’s position more difficult due to the introduction of definitions which are meant to establish support but are not always logical. For example, “fertility does not indicate reproductive maturity” page 95 and that neither does viable sperm and ova. The problem here is that the author is setting cultural proficiency as a category which we cannot apply to other animals and which ignores the fact that many humans have children without achieving his supposed “reproductive maturity”.

What is a very interesting sideline to the discussion is Bogin’s remark that while growth and development have evolved under selection, aging and death in human society are recent by-products of cultural development for which no predictable pattern has been established by evolution. Perhaps what Steven Jay Gould might call an exaptation, this needs to be compared with other animal life histories on a more precise scale, however. Bogin explains life history theory and proposes 5 stages to explain human evolution from apes and the different biological events which punctuate stages including some biosocial examples like care and feeding which certainly vary by SES, culture, technology and economic history. Fabrega (1997) considers some aspects of care which impinge on sickness to be pathological and nearly parasitic, so we have to be, again, careful in how widely we make our assertions.

Bogin stumbles into the debate over neoteny and hypermorphosis in another attempt to separate humans from the animal world. This constant theme seems strange. Why make such an effort to draw such distinct lines when natural science has made such profound strides since the days of Cuvier to demonstrate how well man fits into the natural world? Do chimps and humans differ concerning adrenarche? Generally most zoologists call the cyclic activity of females, the estrus cycle, some extension of a specific “rut” season is referred to as “...seasonally polyestrous and some wild, temperate climate species run cycles all year long (permanently polyestrous)...” (Etkin, 1964). But we often read that humans do not have an estrus cycle. Human females do not display cyclic physiology?

But what of learning? Does the data indicate a “childhood” for chimps? The “learning hypothesis” to support the evolutionary need for childhood in hominids is confounded by a constant shuffling of the terminology of stages: infancy, juvenile, adolescence, young adulthood, adult, with references to work by Pereira & Fairbanks (1993) who provide a tripartite plan: infancy 0 to end of lactation, juvenile feeding independence to sexual maturity, adulthood sexual maturity to death. Then we are not given a cultural or biosocial definition of childhood and there are no cross-cultural comparisons. The chimp is argued to have M1 erupt at 3.1 years (a mean again) but is still dependent after 5 years to learn foods necessary for survival for at least another year. This seems to argue for childhood in chimps, but Bogin goes off without detailing means of clarifying this but does return to the issue on pages 207 and 215 in discussing qualities of childhood to adolescence with changes of a developmental nature associated with social-cultural conditions, density of population and food supply regularity. But this model is presented without data to convince us that this is unique to humans and applies to all human societies and is not just an artifact of some. His statement that *Homo habilis* had the first childhood requires skepticism. The assumption being that this is man with tools and thus more food, while many paleoanthropologists would argue that human life at 2.2 mya was likely to be rather less sunny than he supposes. This idea of tools equal bigger brains is no longer generally accepted just as the idea that big brains led to bipedalism is out of favor. As Harvey and Bennett argued in 1983, “... some mammals, notably the Primates lie above the typical mammalian line (scale of brain size to metabolic needs) and thus have larger brains for their metabolic needs than most other mammals.” Plus simple arrangements of brain size without reference to patterns of brain growth do not reflect accurately evolutionary patterns as noted by Kaas and Collins (2001). We can compare this problem with Langdon’s comments on brain size above.

Why the feeding of *Homo habilis* infants and children should be different in learning food types from chimps is unclear and several definitions of childhood do not help. The learning of lid technique in birds to get at contents (Weir, et al., 2002) denotes “plasticity” (especially with social learning, Fritz & Kotrschal, 1999) or among macaques learning to wash potatoes (Kawai, 1965; de Waal, 2003), or dolphins and nose sponges (Krutzen, et al., 2005; Mann, et al., 2008) or tandem-running in ants (Franks & Richardson, 2006), but does this mean their young have a stage we can call childhood? Again, a special quality is placed on human or hominid behavior as opposed to other animals for no reason, as in the emphasis Bogin places on *Homo erectus* being able to leave Africa. This exaggeration of the biocultural edifice is unnecessary since there is evidence (though contested) that there was a hominoid exodus from Africa too (Cote, 2004), once the environmental conditions provided an opportunity in the Miocene though movement of animals over land bridges is not unusual (Simpson, 1965; Kurten, 1969 for two views). I see no difference between the hominoid success and the hominid one, especially since the fossil record tells us that other fauna moved in and out of Africa over land bridges in many periods in the past (Simpson, 1965). Further, the ideal of the tool being so advantageous in survival is questionable, as an adaptation we can assume that scavenging was promoted, but toolmaking might not have been any more significant than bird’s nest construction or beaver dam and lodge building. What has always bothered me about the toolusing and making hypothesis is that it should provide us with a dramatic increase of evidence for human success no matter how we define it. Where is this evidence? We certainly see evidence of tool making and using after 2.5 million years ago, but no significant evidence of more hominids, no dramatic evidence of hunting success or a



decrease of predators of hominids or their supposed prey. In fact, we can only suggest that the tools possibly made scavenging more effective as Blumenshien (1988) has argued, Though this model is under discussion presently (Dominguez-Rodrigo & Barba, 2007). Nevertheless, can we assign special success to hominids after the invention of tools over what Kurten (1969) has shown to be the great diversification of mammals (and birds) in the last 65 million years over that of reptiles in the previous 200 million? Our present numerical and environmental success can only be argued to be at most 10,000 years old. Can this expansion challenge that of the insects and will it be as enduring? This is especially important as ants have been found to not only control the behavior of aphids but to engage in selection (partial predation, see Molnar, et al., 2000; Billick, et al., 2007) both activities central to domestication.

I think a more uniformitarian view is necessary to understand the evolution of *Homo sapiens*, one which always compares man's physiology and behavior to that of other animals. This view is based on the fact that the more we have learned about other animals' physiology and behavior the more of a continuum we see rather than uniqueness. For instance, we need to keep in mind that humans are not the only animals that make tools. Certainly the uniformity of Achelean tools brings into question a unique cognition different from a generality of ability which is necessary for the construction of a bird's nest or tools Caledonian crows make (Weir, et al, 2002). This is especially so when one considers the manipulative limitations of claws.

To again return to Bogin (2001), mainly because he expresses so many of the uniqueness ideas, one might believe that Bogin was expressing anthropocentric views as when he gushes over human parenting but ignores widespread and complex parenting and alloparenting in other mammals and birds. This gets extreme is his reproduction of Alley's experiment which involved no actually parenting but only attitudes and was not cross-culturally challenged, but in light of Harlow and Harlow's experiments in the 1950s (Harlow, 1958), and Beach's work in the 30s and 50s (Beach, 1937; Beach & Jaynes, 1956) which argued for the interaction of instinctual and developmental processes and experience, I must be skeptical of Bogin's proposal of a genetic component to parenting. I am sure this would hardly explain current levels of child abuse or abandonment. This essentialism goes on to page 126 where we are asked to believe that nonhumanprimate infants will die if their mothers leave them. He later describes how during industrialization in Europe children were left to die on the streets as their parents could not feed them. As one student of childhood has stated, "The history of childhood is a nightmare from which we have only recently begun to awaken. The further back in history one goes, the lower the level of child care, and the more likely children are to be killed, abandoned, beaten, terrorized and sexually abused." (deMause, 1974). Is there a contradiction here? The argument returns with an attack by behavioral scientists on the cultural construction of childhood at the beginning of chapter 6 and a restatement that human children cannot fend for themselves when evidence supplied on page 161 from the Hadza demonstrates their ability to collect food. Bogin also cites evidence from the Industrial Revolution of children working long hours and being quite adaptable for jobs, so much so that businesses preferred to hire children. Recent research by Douglas and Rebecca Bliege Bird (e.g. 2000) shows just how competent children are in collecting food. That human children are able to endure terrors, torture, abuse, starvation and still survive is a fact that Bogin might have chosen to use as a distinction where nonhuman primate young would die.

Bogin argues on page 108 that special diets are required by young humans which demands special adult care. I am left wondering “what diet”? Bogin obviously recognizes the developmental problems of the Guatemalan children who are underfed, but he continually idealizes humanity in contrast to other animals. The idea that our hominid ancestors were successful in the Pliocene over apes and monkeys because they could provide their young with a unique diet necessary for hominid children to survive when the diet of a perfectly “successful” child of 6 or 8 living on the streets of Rio is essentially garbage produces a rather absurd feeling. G.A. Harrison warned of such “fishing expeditions” in his 1982 article on “Life-styles, well-being and stress”. This tendency of Bogin and others is compounded by a continual reference to means, “brain complete at 7 years”, “first molar at...”, is too typical. Here we often see averages replacing means or medians. Why this stereotyped presentation of humanity?

Recently Frans de Waal stated in *New Scientist* this January, 28<sup>th</sup>, that scientists cannot understand why blushing evolved. Arguing that we are the only Primate that blushes, he speculates on the evolutionary role of this feature. Aside from the fact that the feature of blush cannot be recognized visually due to skin pigmentation in many humans today, as far as I know there is no evidence that all people respond to the same emotional situations with “blush” or that all people blush.

The idea that blush was part of an evolutionary pressure driving the appearance of color vision in Primates has been proposed (Changizi, et al., 2006). We should consider this idea in the context of studying the architecture of the skull and the nature of the combination of features described by LeGros Clark in the context of Primate evolution as derived from the forest environment. There are a few problems with this theory.

1. To have "blush" function as a means of sexual selection as proposed, it must be visible to members of the opposite sex. This might require a few biological features to be present in addition to vascular changes in the epidermis. First, one would assume there must be naked skin or at least less hair and more exposed skin for the "blushing" to be visible. In their analysis of the amount of skin visible in different primate species and the function of the biochemistry of color in the eyes and brain, Changizi, et al., (2006) center their discussion on the trichromats and the optimization of the M and L cone sensitivities given factors like skin reflectance. This gives a Primate-wide format for analysis from face to rump.
2. This requires that increased blood flow in the surface of the skin in capillaries is visible. This is not an original idea. Desmond Morris proposed this relationship in his book *The Naked Ape*, (1967:70-1). In heavily pigmented skin this affect is not visible, but Morris simply states this ability has been sacrificed, a subtle cue that he believed darker skin was a later evolutionary development.
3. Does Primate color vision differ from other mammals, that is, what is color vision? In Bourliere's book, *The Natural History of Mammals* (1964) he identifies a number of mammalian candidates that have color vision.
4. The authors have not defined color vision so that it leaves only Primates with the particular kind of color distinctions necessary. Many mammals have cones and rods in their eyes but experiments have not unequivocally proven they can "see" colors. The presence of opsin genes in the genome likewise may not be accepted as proof of

color vision. See Lythgoe, *The Ecology of Vision*, 1979 and Jacobs, *Comparative Color Vision*, 1981.

What is more interesting that all the variations in attempts to establish some trait in which humans are unique, is the desire to find one. Why is this so important, and why do these ideas grab the headlines while those which find that, well, we are like other animals, do not? The principle point I would like to make in this article is that humans are no more unique than other animals and that we fit in to a series of variation in the animal world (both living and dead) that becomes apparent the more one knows about comparative physiology and behavior. We need to keep in mind that our current social and technological complexity is very new and may be very brief as was the case of some of the now extinct experiments in complex insect life (Danforth, 2002).

In recent years many of the old distinctions that seemed to separate humans from other animals have either fallen away or been severely limited by new research. Humans are no longer regarded as the only tool-users, many primates use tools routinely, capuchins with great dexterity. Nor is man the only toolmaker, chimpanzees, ravens and crows are known to produce tools. This complicates discussions of the changes in cognition and physiology which seemed to characterize human evolutionary success. Beavers make houses, dams and change the environment. We find complex societies in ants that also have agriculture and we now know they apply fertilizer (Moore, 1996). Ants fight wars and take prisoners making them slaves. Even language seems undeniably present by most definitions in dolphins and certainly in bees (Chavin, 1968).

The more we learn about the natural world, the less “freakish” *Homo sapiens* appears. The big brain is not that big compared to the dolphin in brain to body ratio and when we exercise the scale of brain size we find that there is a relationship in the animal world between increasing brain size, larger neurons and lower density (Jerison, 1973; Shariff, 1953). Thus the “big brain” seems even smaller than ever today as we become aware of many of its complexities (Mazziotta, 1995). Therefore, it was a surprise for me to recently read in the paper that some scientists had found that human hair was quite, well, unusual. While Aristotle had noted that humans were featherless bipeds (he did not know of penguins) one imagines that contemporary sages would be more informed about the diversity of traits in the animal kingdom.

The article by Arthur Neufeld and Glenn Conroy shocked me as I was familiar with Professor Conroy’s work as a biological anthropologist. Neufeld and Conroy (2004) claim that human head hair is not fur. They separate the idea that humans lost their body hair from this discussion sparing themselves the embarrassment of Morris. Explanations of body hair reduction in humans are numerous as Neufeld and Conroy note, and research by Alan Rogers that one of the genes affecting skin color is involved in hair reduction would seem to support the thermoregulation theory. Hair holds in moisture producing an insulating affect which also reduces moisture lost. This is ok as long as one is not running or very active in the middle of the day in a hot and dry environment as East Africa was about a million years ago. Claims that hair reduction occurred in response to parasites belies the fact that humans are still plagued with them nonetheless and does not explain the density of head hair in most people. “Most” is the important word here for, as in the case of Morris, not all people have the kind of hair nor the rate of growth asserted by Neufeld and Conroy. Thierry’s (2005) and Jolly’s (2005) championing of head hair as a communicative device is of interest and reflects some

of Darwin's musings (1871) though others (Synnott, 1987; Leach, 1958 & Hallpike, 1978) have produced comprehensive analyses of the subject.

Neufeld and Conroy believe that human head hair is characterized by long hair which grows continuously throughout life. Thick head hair would seem to argue against it being a thermoregulating device. This would be especially true for dark hair, but then we know that hair on the head is infused with moisture from the scalp during activity or in hot temperatures and forms an insulation layer reducing the effects of heat gain. The rest of the body gives off heat by evaporation also reducing heat buildup.

The clearest problem with Neufeld and Conroy's theory is that most of humanity does not have one uniform hair type. Second, many hair types do not grow in straight, continuous fibers like the terminal hair of Europeans and many Asians. There are generally 4 types of hair, lanugo or infant hair, primary terminal (children's hair), secondary terminal (adult hair) and vellus hair. Hair fiber length and shape is governed by a number of factors (Ryder, 1958) including diet which affects both the sebaceous glands and nature of hair production as well as the hormones which also vary by sex and population as well as activity. Most humans with straight hair produce a head hair growth of about 16cm per year to a maximum of 3 feet. However, hair growth in the mid to late twenties undergoes hormonal changes which slow growth for head hair which begin to grow shorter and finer (Robbins, 1994). Neufeld & Conroy refer to recent experiments showing that terminal hairs transplanted to the legs grow at a slower rate than on the head. This confirms knowledge that terminal hairs are found naturally on the legs (Robbins, 1994) and that proliferative tissue behaves differently depending on its location and influence of local hormonal and other effects. This was reported by Garn in 1948. It has been known for more than 50 years from skin grafts that they produce hair shafts characteristic of the donor site (Garn, 1948).

There are unusual examples of continuously growing hair to unusual lengths which is the result of peculiar conditions of diet and lifestyle (sedentism) and hormonal abnormality as in the examples shown in the illustration. If we were only to focus our attention on humans, however, we would be doing a disservice to the study of hair. Like any proliferating tissue, hair has a relationship to development, diet and maturation (Price, 1958; Bradfield, et al., 1967). Hair pigmentation differs between individuals and groups (Hausman, 1925 and 1928). A study by Myers & Hamilton (1951) found a significant difference in hair growth in males and females, with hair growth faster in males. Seasonal growth rates have been quantified (Randall & Ebling, 1991). But the nature of continuously growing hair is found in some other animals, namely a few that have been selected by humans for this trait. Thus hair growth is partly a product of domestication. We find in sheep continuous growth of hair (Ryder, 1958) in domesticated varieties and this growth varies from other members of the same genus. This is especially true with the Merino sheep which has developed persistently growing hair follicles (Norback, 1951). Horse mane and tail also seems to grow continuously (Roser, 2005). This is to be expected since we know that hair growth varies significantly among different human populations (Hamilton, 1958; Saitoh, et al., 1967) as well as within human groups. The factors, developmental and genetic, affecting the ontology of hair growth are not clearly understood.



Figure 2: Panda neonatals, more helpless than humans?"

#### 4. CONCLUSION

The problem I have discussed is, in my opinion, related to the nature of our curriculum, where few students receive a comprehensive education in biology today. It is also a problem of curriculum materials where books are written by committees of people whose own narrow education leads to mistakes of omission. This was made clear in 1995 when Burks et al. demonstrated that the human sperm enters the ovum, where previously it had been believed that the head of the sperm did not enter, nor the mitochondria (Ankel-Simons & Cummins, 1996). As Ankel-Simons & Cummins, (1996) argue, many students of human reproduction had been taught that the head did not enter, but it was known and published in numerous textbooks at the beginning of the 20<sup>th</sup> century. Another example can be seen in neurology where a recent article (Oberheim, et al., 2009) argues that hominid astrocytes are unique, but the authors cannot know this is true since we have no non-Homo sapiens astrocytes of other hominids to compare to prove such a claim. The authors also trumpet the finding that human astrocytes are “2.6-fold larger in diameter than rodent counterparts.” This certainly cannot stand as sufficient evidence that no other organism’s astrocytes are as large as they provide no comprehensive data. On the other hand, we know that Shariff published findings in 1953 from cell counts of most Primates to show that, with regard to size, there is a “three-fold increase as we go from Tarsius to Man, more than has been recorded for any other type of cell.” Thus while there may be differences in vertebrates in sizes of astrocytes, we cannot use Oberheim, et al.’s data to support this until more comparisons are made. Shariff (1953), did not identify in this paper the neurons he was counting as larger, but it is implied in the paper these are of the gray/cell population, or glia. Unfortunately, Oberheim, et al. do not quote or cite Shariff (1953) so one is left with the feeling they were unaware of his work.

Essentially, one is left with the feeling that ideas of human exceptionalism while based on a lack of knowledge and the result of an educational strategy that produces narrowly focused scientists, also has affected the curious nature of scientists. We should always fear that we do not know everything and that we need to make sure we have covered the field before we make global statements.

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*Chapter 7*

## **STUDYING SOCIAL DEVELOPMENT AND COGNITIVE ABILITIES IN GIBBONS (*HYLOBATES* SPP): METHODS AND APPLICATIONS**

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### **ABSTRACT**

Social development and cognitive abilities in wild gibbons has received very little attention due to the difficulties of habituating enough animals for a large-scale study. Data from gibbons in captive situations (zoos, sanctuaries and rescue centers) can provide insight into the development of both social skills between individuals, and the development of cognitive abilities within the individual. Gibbon behavior in captivity has correlates to gibbon behavior in the wild and can be used to infer why certain aspects of social or cognitive behavior are seen in the more demanding and complex wild environment. I will present data collected from gibbons in a sanctuary (UK), a rehabilitation centre (Indonesia) and the wild (Indonesia) highlighting the development of social skills and cognitive abilities. Data were collected in a variety of ways and I will discuss the methods and their applicability under different conditions. Data will be presented on object manipulation and tool use and will challenge the assumptions that gibbons are inadequate tool users among the apes. I will also challenge the notion that gibbons have poor social interactions in the wild. The study of social development at all ages can shed light on how gibbon groups maintain their cohesion, not only when traveling but also how the pair bond between the adults is formed and sustained. By using both direct tool manipulation tests and non-invasive behavioral observations by studying gibbons in a variety of captive and wild situations, we can begin to answer more questions about the development of social behavior and its function as well as gaining insight into the problem solving and cognitive abilities of the smallest ape. With increased understanding of the development and presentation of cognitive abilities, we are in a better position to aid gibbons in rehabilitation and reintroduction programmes and to understand more about these apes in the wild.

## INTRODUCTION

In response to the growing concern for gibbon conservation and the lack fact that the smaller apes are frequently overshadowed by the larger apes, the primatologists present at the Workshop on Gibbon Diversity and Conservation held at the 19<sup>th</sup> Congress of the International Primatological Society in Beijing (August 2002) composed the following resolution to address these concerns:

### Resolution

The ape closest to extinction, with less than 50 individuals, is a black crested gibbon hanging on in tiny forest fragments in Vietnam and China. This exemplifies the crisis facing the most diverse and endangered of the apes. The unique songs of these spectacular acrobats are fast fading from Asia's disappearing forests. Considering that the gibbons include the most critically endangered primates in the world, we, the gibbon specialists within the International Primatological Society at its 19<sup>th</sup> congress at Beijing, China, resolve that:

- Top priority be given to preventing the first ape extinctions of the 21<sup>st</sup> century;
- Immediate action is taken to protect remaining gibbon populations and their habitats.

Of the 17 gibbon species comprising at least 29 taxa we have identified the following as the 10 most endangered:

1. Cao-vit black crested gibbon *Nomascus nasutus* – critically endangered
2. Hainan black crested gibbon *Nomascus hainanus* – critically endangered
3. Northern white-cheeked gibbon *Nomascus leucogenys* – critically endangered
4. Western black crested gibbon *Nomascus concolor* – critically endangered
5. Silvery gibbon *Hylobates moloch* –endangered
6. Kloss's gibbon *Hylobates klossi* –endangered
7. Southern white-cheeked gibbon *Nomascus siki* –endangered
8. Yellow-cheeked gibbon *Nomascus gabriellae* –endangered
9. Pileated gibbon *Hylobates pileatus* –endangered
10. Western hoolock *Hoolock hoolock* – endangered

Workshop participants recommended the following priority actions:

1. Promote gibbons as flagship species at local, national and international levels.
2. Conduct a conservation status review, including population census and monitoring.
3. Create community support for conservation at local level.
4. Provide training and support for protected area management and law enforcement.
5. Create private public partnerships for developing sustainable funding initiatives.

6. Increase support for research on conservation biology, systematics, demography and behavioural ecology.

Of 16 (as recognised by the 2008 IUCN Red List (IUCN, 2008)) species of gibbon, one is listed as vulnerable, 11 are listed as endangered four as critically endangered due to habitat destruction for logging, habitat conversion to plantations, fire and exploitation for medicines and the illegal pet trade.

The scientific name for the gibbon family group is Hylobatidae meaning ‘dweller in the trees’ (Nowak, 1999). Gibbons are small, arboreal apes that live in the canopy of the rain-forests of south-east Asia: they are widely distributed from Assam and Bangladesh in the north-west through Southern China, Vietnam, across the Malay Peninsula, Thailand, Sumatra (including the Mentawai Islands) and into Java and Borneo. The long arms and legs of the gibbons make them excellent climbers and they can swing, pendulum-like, through the canopy at great speed without losing their rhythm. The genus comprises 16 species found only across Southeast Asia (see Table 1).

**Table 1: Gibbon species recized by IUCN Red List 2008.**

Subgenus	Species	Common Name
Symphalangus	<i>H. syndactylus</i>	Siamang
<i>Nomascus</i>	<i>N. concolor</i>	Black-crested
	<i>N. gabriellae</i>	Yellow-cheeked
	<i>N. leucogenys</i>	Northern white-cheeked
	<i>N. siki</i>	Southern white-cheeked
	<i>N. nasutus</i>	Cao-Vit crested
	<i>N. hainanus</i>	Hainan black-crested
<i>Hoolock</i>	<i>H. hoolock</i>	Western Hoolock
	<i>H. leuconedys</i>	Eastern Hoolock
<i>Hylobates</i>	<i>H. agilis</i>	Agile/black-handed
	<i>H. albibarbis</i>	Bornean southern
	<i>H. lar</i>	Lar/ white-handed
	<i>H. moloch</i>	Javan/ Silvery
	<i>H. muelleri</i>	Grey/ Bornean
	<i>H. pileatus</i>	Pileated/ capped
	<i>H. klossii</i>	Kloss/ Mentawai

The organization of gibbons into family groups of an adult male and female plus any combination of a sub-adult, juvenile and infant has been well known since Carpenter’s (Carpenter, 1940) pioneering study. The social structure of gibbons is a point of much current debate, as some exceptions have been found to the view that gibbons are strictly monogamous. The generally accepted view is that gibbon grouping; mating and breeding systems are probably far more plastic than was previously thought, especially in fragmented and isolated forests, though the debate still rages as to the degree of plasticity and how flexible the social system truly is within and between groups.

Gibbons are also unique among the apes because they sing complicated songs made up of duets between bonded adults and/or complicated solo songs. The resident adults are divocal i.e. males and females have their own vocal repertoire (Geissmann, 1984). The most

recognized of gibbon songs consist of a spectacular duet between the mated adults with the young occasionally joining in. The Kloss gibbon and the Javan or silvery gibbons (both endemic to Indonesia) are the only gibbon species not to duet. Carpenter (1940) noted nine different types of call in the lar gibbon alone. The largest of the gibbon species, the siamang, has been shown to have the most complex song of any animal apart from humans (Geissmann, 2000a) and is unique in producing booms during the call which resonate from the throat pouch of both males and females. Bonded adult gibbons will defend their territory in the forest by singing a duet to warn other gibbons that they are bonded and to stay away.

## Threats and solutions

Gibbons are rapidly disappearing. All gibbon species are listed on CITES under Appendix I highlighting the pressing need for active conservation before these species become extinct. Every year thousands of gibbons lose their lives as their forest home is destroyed (Photos A-D) and many more die in the illegal pet trade before they even reach the marketplace (Photos E and F).

Infant gibbons spend the first two years of their lives being carried by their mothers. Without exception, the young are captured by killing the mother (usually by shooting her: see photo E), and taking the infant when the mother's body falls to the ground. This is very stressful and upsetting for the infant gibbon. The young gibbon is then transported in a tiny cage, often with inadequate air or water and frequently with several other young animals packed into the small space like sardines. Many infant gibbons (and other animals) die before they even reach the market. Infant gibbons are very cute and make adorable pets until they reach sexual maturity (age 5-7 years). When they become adults, they can become aggressive, as their natural instinct is to find a mate and establish their own territory.

This is an unacceptable waste of life, especially if there is the possibility that these gibbons could be rescued and reintroduced to areas where they have become locally extinct and where they can be protected. While this is an admirable goal, history is replete with failed and/or mismanaged primate reintroduction attempts caused by a combination of a lack of adequate planning, insufficient knowledge about the primates' behaviour and ecology in the wild leading to inadequate or inappropriate training in the rehabilitation centre, and a serious lack of pre- and post-release monitoring of the primates.

Though the trade in gibbons still continues, the conservation and disease message is being disseminated and people are beginning to understand that gibbons do not make suitable pets and belong in the forest. This results in a growing number of gibbons finding their way into rescue centres and sanctuaries. Some of the problems associated with gibbons that have been raised in captivity are (Cheyne, 2004; Cheyne et al., 2008):

- Developmentally-stunted social skills due to living with humans e.g. lack of auto-grooming, fearful of conspecifics and often socially attached to humans.
- Often show signs of stereotypic behaviour associated with confinement in inappropriate cages e.g. self harm, repetitive rocking/swinging
- May be malnourished and/or unable to brachiate properly

- Under-developed cognitive abilities e.g. poor limb coordination, inability to forage and manipulate food items
- Maybe unable to produce appropriate calls e.g. the great call and coda
- 

Many of these gibbons are candidates for return to the forest, **if** they are provided with adequate rehabilitation and if this rehabilitation is carried out under scientifically proven guidelines.



A



B



C



D



E



F

Threats to gibbons: A: deforestation in the Bukit Baka Bukit Raya National Park, B: forest fires, C: oil palm plantations, D: smoke and pollution from fires, E and F: pet trade © Susan M. Cheyne

## Stages of rehabilitation

The main purpose of rehabilitation is to remove orphaned animals from the illegal pet trade and provide them with an environment, where they are (1) encouraged to become more self-sufficient through being placed in suitable groups or pairs (age dependant) and (2) provide them with the opportunity to live as they should in the wild. This must include improving cognitive development which will be essential if the gibbons are to learn about fruiting patterns in the wild, learn to manipulate food items and master the complex skills needed to move through the canopy.

1. Receive gibbons and carry out strict quarantine and medical checks especially for Hepatitis A, B and C, TBC and *Herpes simplex* as well as skin and faecal parasites (Mootnick et al., 1998).
2. House the gibbon in a pair or group (depending on age and availability of suitable companions). Great care must be taken to ensure that the gibbons are compatible and that there is a minimum of aggression between the individuals. This process re-socialises the gibbons to a feral lifestyle and breaks their ties with humans (Cheyne et al., 2008).
3. Compatible sub-adult or adult pairs are monitored to observe their behavioural and social adaptation to a more feral lifestyle. Once the gibbons form a pair bond (demonstrated by copulating, duetting, allo-grooming and frequent, non-aggressive interactions), the pair can be considered for the third stage of rehabilitation: release into an area free of conspecifics. Juvenile gibbons in the socialization cages are monitored for developing bonds and suitable pairs are separated to observe the development of the pair bond. Continuous monitoring of the gibbons ensures that potential problems are spotted quickly and appropriate actions can be taken (Cheyne, 2007; Cheyne et al., 2008).
4. Pairs are reintroduced into a protected forest where there are no wild gibbons. Here they must be monitored but not provisioned. On the island, behavioural and social monitoring is continuing as well as a more detailed ecological study to assess the gibbons' ability to locate food, maintain the pair bond, establish and defend a territory and avoid predators. Again, continuous monitoring of the gibbons will allow any problems to be identified immediately (Cheyne, 2004; Cheyne et al., 2006; Cheyne et al., 2008).

## History of cognitive studies on gibbons

Much of the original work involving cognitive development (tool use and/or food puzzles) was carried out using laboratory primates who often spent their entire lives housed singly (Abordo, 1976). The first experiments to explore the intellectual behaviour of gibbons were carried out by a French zoologist (Boutan, 1913, 1914). This work involved the observation of one female gibbon manipulating puzzle boxes and concluded that the gibbon easily generalized the solution to complex puzzle boxes after learning on more simple ones. Following this, (Drescher and Trendelenburg, 1927) used a simple problem box where the gibbon had observed food placed. The gibbon required a number of trials, spread over three

days to open the box. (Thompson et al., 1965) used shock avoidance techniques to train baboons, gibbons and chimpanzees in a variety of tasks involving stimulus response. They concluded that their study revealed little about the conditionability of gibbons to aversive stimuli. Full reviews are given in (Yerkes and Yerkes, 1929) and (Abordo, 1976) but all authors agree that the performance levels of the gibbons may have been affected by poor motivation to complete the tasks, suggesting the fault may lie with the design of the experiments, not with the cognitive abilities of the gibbons *per se*.

Previous studies which have focused on gibbons have all noted that they are as responsive as other apes but that studies on gibbon cognition are difficult due to their timidity or idiosyncrasies with regard to motivation (Berkson, 1962; Bernstein and Schusterman, 1964; Bernstein et al., 1963; Cunningham and Anderson, 2004; Cunningham et al., 2006; Glickman and Scroges, 1966; Menzel and Draper, 1965; Ujhelyi et al., 2000). For these reasons, and the relatively few studies conducted on gibbons compared to other apes, it is unreasonable to conclude that gibbons are intellectually or cognitively deficient and there is scope for developing these studies, and their applications further.

## **Learning and problem solving: importance for captive gibbons**

For gibbons that have been confiscated from life in the animal trade, encouraging them to be active and adopt more natural behaviour is an essential part of the rehabilitation process. Providing an environment where the gibbons are encouraged to express their natural behaviour, to be curious about their surroundings and to explore novel food items as they would in the wild, will aid in observations of their behaviour and allow researchers to accurately monitor their progress in the rehabilitation centre. The design of the puzzles should “encourage the expression of skills and the fundamental psychological processes that reflect both capacity and potential for adaptation to problems in the real world” (Abordo, 1976). Understanding the impact of puzzles on gibbon cognition can help inform about the benefits of using puzzles and other environmental enrichment in a rehabilitation programme, where adequate training (behavioural, social and cognitive) will make the difference between death or survival for the gibbons once they are released.

Food puzzles that are used in a rehabilitation centre will have specific uses on top of the main use of encouraging natural foraging and providing mental stimulation during the feeding exercise. The puzzles should attempt to teach the gibbons how to look for and reach food in the wild (i.e. at the top of trees). If the food is located at the top of the cage, it should discourage the gibbon from coming down to the floor of the enclosure, a behaviour that would be disastrous in the wild. Some of the main issues to be addressed by the food puzzles are to:

- Encourage activity and prevent boredom (sitting about)
- Provide mental and physical stimulation
- Encourage the gibbons to look for food at the top of the enclosure (the way they would in the wild)
- Encourage the gibbons to spend more time at the top of the enclosure



Researchers introducing food puzzles to gibbons must answer one basic question: “Are the gibbons diligent enough to work at a puzzle long enough to obtain food from a visible source?” Providing gibbons with food puzzles may contribute to the rehabilitation process but would definitely provide some insight into the capacity of the Hylobatids to use complex puzzles. The larger apes can manipulate tools and have been shown to demonstrate Mirror Self-Recognition (indicating an awareness of self (Ujhelyi et al., 2000)). The degree to which gibbons have this and the mental faculties to use tools and benefit from complex food puzzles requires study.

The presence of objects and companions in the enclosure is closely associated with the activity of primates in captivity. Novel approaches to food provisioning and timing are essential if the primate is to spend an adequate amount of time foraging and feeding, as would happen in the wild. Captive houses must always aim to provide a sufficiently natural environment so that the animals can be maintained as normal individuals, upon whom reliable observations can be made (Cheyne, 2007). The potential for the use of food puzzles in zoo and sanctuary settings is only limited by the imagination of the primate keepers, though any food puzzle must be introduced with the species-specific behaviour in mind and with an aim to encouraging the primate to express its natural repertoire of behaviour.

Chimpanzees, orang-utans, gorillas and many monkey species have been studied to observe their response to various food puzzles (Table 2). Despite the clearly recognised need for food puzzle provision in captive primates, gibbons have so far been largely overlooked in the research, a fact that was noticed back in 1976 (Abordo, 1976). (Markowitz, 1982) developed a device that would deliver food to gibbons if they operated a mechanical device consisting of two widely spaced levers. It has been argued that this is more like classical conditioning rather than encouraging natural foraging behaviour. The only other record of enrichment designed specifically for gibbons was used at London Zoo where wild lar gibbon calls were played to the captive family resulting in increased brachiation and duetting (Shepherdson, 1988).

Because of the scarcity of data on food puzzles for gibbons, any attempt to use them will require careful monitoring if their benefit is to be reliably determined: i.e. how much will they use them and will they benefit i.e. by spending less time sitting, or will it mean that they eat less of the food type in the puzzles?

The following sections will explore the need for food puzzles in enriching the environment of captive gibbons and offering some possible designs for food puzzles. Important considerations for puzzle design are discussed as well as possible designs of a cage to be used in the rehabilitation of ex-captive gibbons.

## **Possible designs for puzzles**

Figure 1 shows a puzzle that can be designed to encourage tool use and manipulation but can also be built narrower so that the gibbon can reach the food with their fingers instead of a stick.

The dimensions of the box can be varied but should be at least 60x30cm. The puzzle is commercially available from Primate Products, Florida, USA for \$236 (<http://www.primateproducts.com>). Figure 2 shows three simple designs for dispensing food in a novel way.



Figure 1. Possible design for tool use puzzle box designed by Primate Products Inc.

**Cheap and simple puzzle dispensers.**

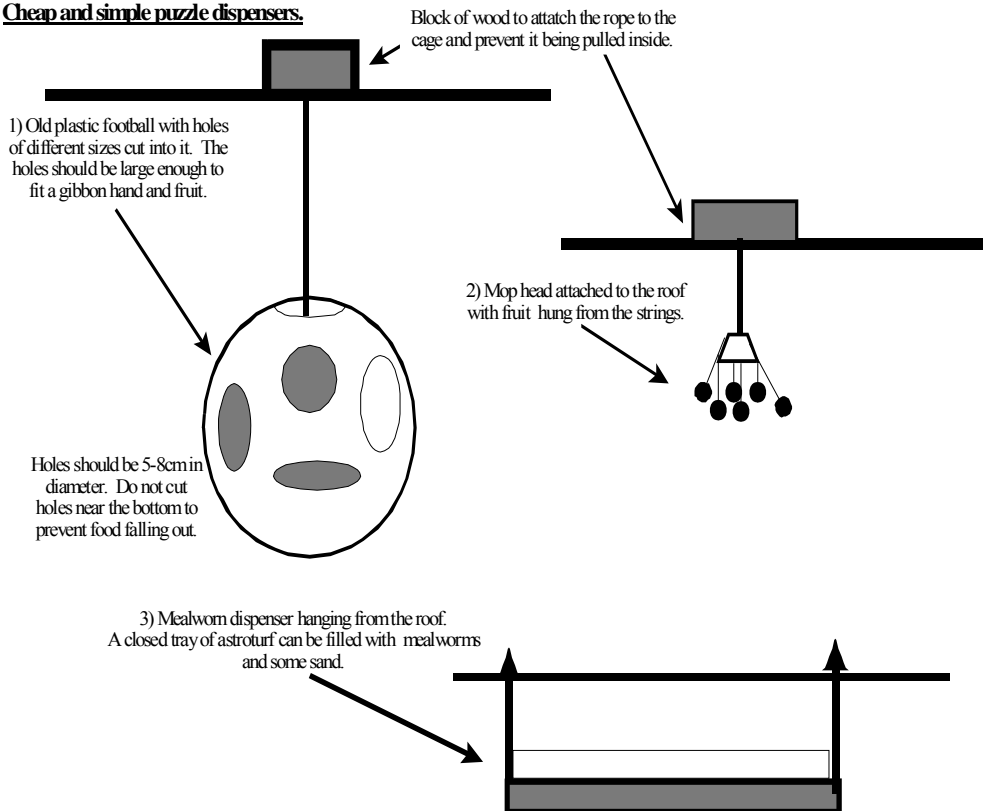


Figure 2. Novel ways of dispensing food/encouraging foraging.

The puzzles will have to be designed with the following criteria in mind, especially if they are to be used in *in situ* rehabilitation centres:

- Easy to clean so as to meet health and safety standards especially in quarantine areas
- Easy to fill and empty so as to reduce the amount of time that keepers have to spend on them
- Durable e.g. treated wood, plastic, metal
- Inexpensive

- Made from easily acquired material
- Not overly challenging for the gibbon i.e. the gibbon will remain at the puzzle until it retrieves the food and not give up after a few minutes
- Where would the puzzle go and can it be easily moved? This is important to allow keepers to easily move the puzzle to a new location to prevent the gibbon becoming bored with it.
- How would it be attached to the cage? The puzzle must be securely attached so that the gibbon cannot move it, but can be easily removed and taken to a new location.
- The puzzle would have to be monitored closely to ensure that the gibbon(s) manage to remove enough of the food to maintain their daily diet. Behavioural monitoring should be carried out before and after introduction of the puzzle comparing food intake, percentage of time spent sitting and percentage of time spend using the puzzle. This data can be used to assess the benefit of the puzzle in aiding the gibbon to use its species-specific behaviour. Only one puzzle should be introduced at a time so as to keep the behavioural data for each one independent.

**Table 2 A selection of some species of primates that have been studied with feeding enrichment (this list is not exhaustive).**

Origin of species	Species	Researcher(s)
Old World	<i>Cercopithecus diana</i>	(Markowitz, 1982)
	<i>Macaca fascicularis</i>	(Bryant et al., 1988)
	<i>M. mulatta</i>	(Reinhardt, 1992)
	<i>M. arctoides</i>	(Reinhardt, 1992)
	<i>M. fuscata</i>	(Reinhardt, 1992)
	<i>Papio</i> spp.	(Pyle et al., 1996)
	<i>Pan troglodytes</i>	(Bloomstrand et al., 1986)
	<i>Pongo pygmaeus</i>	(Gilloux et al., 1992)
	<i>Gorilla gorilla</i>	(Gilloux et al., 1992)
New World	<i>Callithrix jacchus</i>	(McGrew et al., 1986)
	<i>Leontopithecus rosalia</i>	(Kleiman et al., 1991)
	<i>Saimiri sciureus</i>	(Boinski et al., 1994)
	<i>Cebus apella</i>	(Reinhardt and Roberts, 1997)

## Design of the cages

Special consideration should be given to cages that are to be used for rehabilitation i.e. concrete underneath and mesh floor so that any dropped food falls out of reach of the gibbon and discourages them from coming down to the ground. If the gibbons are to be released, it may be an idea to have a remote watering system and a remote feeding system. This may encourage the gibbons to dissociate food and water with humans. If they come to associate

nourishment with humans too much, they may be tempted down to the ground by poachers and be taken back to a life of captivity. Obviously the level of association cannot be accurately measured and ex-pet gibbons will probably always have some association between humans and food. Food puzzles will be important in encouraging the gibbons to forage and not expect a 'hand-out' from humans. Water troughs attached to the sides of the cage can be filled with hosepipes attached to a mains pump and refilled remotely. The troughs encourage the gibbons to adopt the 'dip and drip' drinking method.

If the cages are in close proximity to each other, this may have an adverse effect on the pairs, as they would not normally be in visual contact in the wild. One way to avoid this is to hang synthetic material from the mesh of the enclosures to obscure the gibbons' view. This has the added advantage of removing any visual contact with the human keepers and researchers and will help reduce the gibbons' dependence on humans. Figure 3 shows a possible design for a rehabilitation cage accounting for cleanliness and changing the environmental enrichment with minimum disturbance to the gibbon(s) inside: large cage 4x4x4m; small cage 2x2x2m and the corridor 1x1x2m.

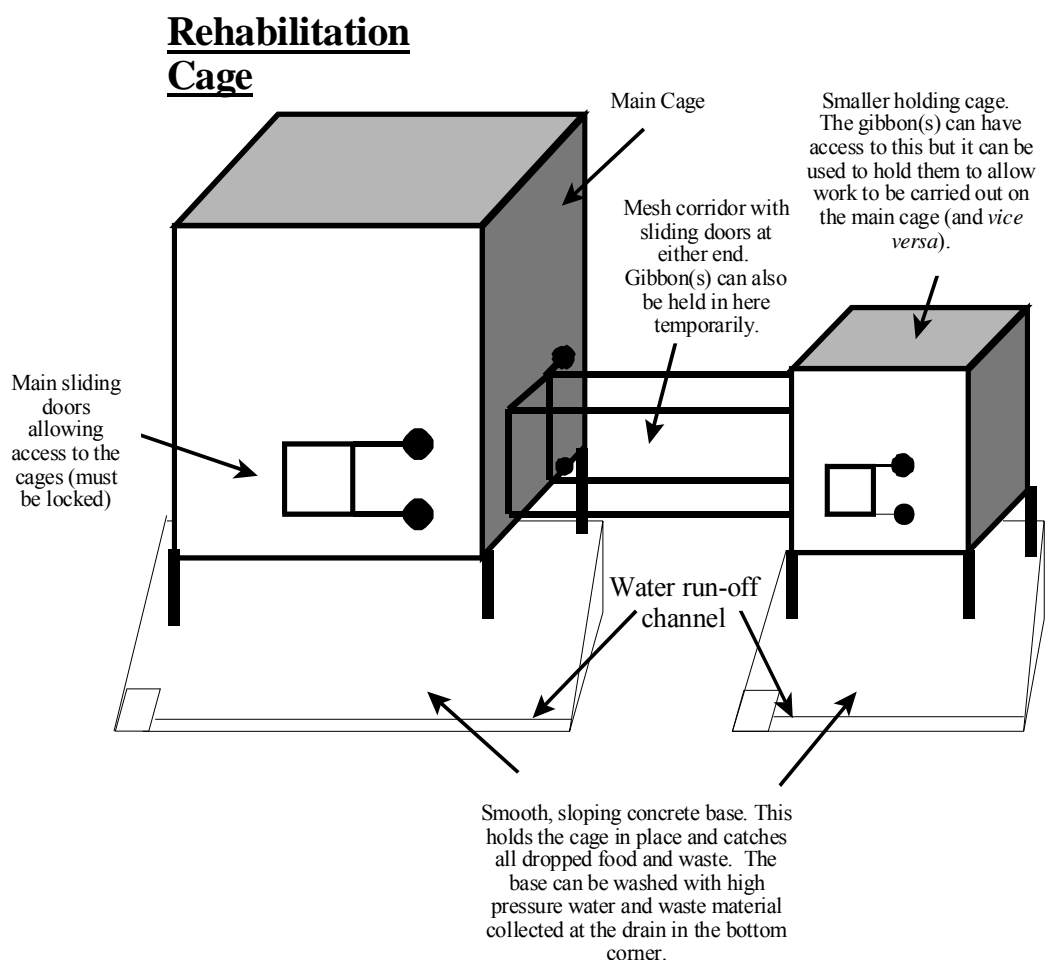


Figure 3 – suggested design for housing gibbons (especially good for rehabilitation projects).

## **CASE STUDY - GIBBON RESPONSES TO A NOVEL FOOD ACQUISITION TASK**

A complex food puzzle was introduced to twelve captive gibbons housed at Monkey World Ape Rescue Centre, England. All twelve gibbons came from the illegal pet trade and were housed in pairs. All the gibbons approached and attempted to manipulate the puzzle, though not all of them engaged the puzzle long enough to obtain food. The pair association levels when the puzzle was present showed that the puzzle caused half of the pairs to increase the time they spend away from their cage mate as one gibbon would manipulate the puzzle while the other was in another enclosure, though there was no evidence of any aggression caused by the introduction of the puzzle. The results indicate that gibbons may have a greater capacity for complex thought than previously believed and that further research should be conducted. Monkeys and great apes have attracted a great deal of attention due to efforts to improve their quality of life in captivity through environmental enrichment, particularly the use of food puzzles designed to encourage the primate to forage and manipulate the device to obtain the food item ((Bloomstrand et al., 1986; Reinhardt, 1992, 1993, 1997; Reinhardt and Roberts, 1997; Reinhardt and Smith, 1988; Seymour and Shepherdson, 1991; Shepherdson, 1998; Shepherdson et al., 1991; Vick et al., 2000). Gibbons are no less in need of suitable environmental enrichment, but very little research has been concentrated on them. Gibbon use of food puzzles has been under-represented in the literature, both from a behavioural and environmental enrichment stance, as most of the work has focused on the great apes and monkeys. The author conducted an extensive search of the literature and found only one exception where gibbons were the focus of a paper on environmental enrichment (Shepherdson et al., 1991) and three where gibbons were the subjects of mirror self-recognition experiments (Fedor et al., 2004; Hyatt, 1998; Lethmate and Ducker, 1973). The most recent published study on object permanence by (Fedor et al., 2004) proposes that the average performance of the gibbons was above the performance of monkeys and comparable to that of the large apes. The authors do note that the subject gibbons ( $n=10$ ) varied greatly in their personal performances, attributed to the taxa, sexual differences, previous and present life quality and social relationships with conspecifics and keepers. Thus, the data from this study do not shed much light on the issue of gibbon cognitive abilities. (Cunningham and Anderson, 2004; Cunningham et al., 2006) propose that the gibbon's inability to manipulate tools can be interpreted as a diminished investigatory predilection rather than gibbons possessing more limited cognitive abilities than the large apes. These few exceptions state that gibbons do not possess the same abilities as the great apes to manipulate complex food puzzles or to think through a problem to obtain a food reward. One clear result from all the studies is that gibbon cognitive abilities are poorly understood and require much more detailed study.

Food puzzles have been extensively employed to enrich the enclosures of captive primates (Byrne and Suomi, 1991; Crocket et al., 2001; Fornasieri et al., 1990; Murchison and Nolte, 1992; Seymour and Shepherdson, 1991; Shepherdson et al., 1991; Visalberghi and Fragaszy, 1995; Visalberghi et al., 1995; Vitale and Queyras, 1997). Puzzles provide a challenge to the primate, forcing them to think about how to obtain their food, rather than simply picking it out of a basket. Animals in the wild invest substantial time in foraging but are often deprived of foraging opportunities in captivity, depending upon the method of food

presentation. Puzzles have been shown to significantly increase time spent foraging (Cunningham and Anderson, 2004; Fitch-Snyder and Carter, 2000; Lethmate, 1982; Visalberghi et al., 1995) and have demonstrated the abilities of many primate species to successfully manipulate complex apparatus to obtain their food and many primates including macaques and chimpanzees have been shown to forage for food even when there is other food freely available, suggesting that the primates 'value' the opportunity to forage (Shepherdson, 1988).

This brief study involved introducing a complex food puzzle to twelve gibbons housed at Monkey World Ape Rescue Centre, Dorset England (hereafter referred to as MW), to observe their responses and ability to extract the food. All twelve gibbons some form the illegal pet trade and have been paired up at MW as part of the process to rehabilitate them and encourage them to learn and adopt more species-typical behaviour. The gibbons are being studied as part of an on-going process of cataloguing the changes in their behavioural and psychological rehabilitation. As part of the environmental enrichment at MW, the gibbons are given treats hidden in boxes, piping, plastic balls and scattered throughout the indoor enclosures to encourage the gibbons to forage. The purpose of the tube feeder was to observe the gibbons' response to a complex food puzzle, which involved them manipulating the food through a fixed maze puzzle, in order to obtain the food.

## MATERIALS AND METHODS

### *Food Puzzle*

The puzzle was made of three clear plastic tubes: 3mm thick, 2.5cm diameter and 35.5cm long. Into each tube, 10 holes were cut of roughly 1cm diameter and equally spaced along the length of the tube. The tubes were fixed together, one on top of the other in a row, by 2 metal screw bolt bars at either end (13cm long) and held in place by 4 holding bolts. The feeder tube was metal: 21cm long and 2cm in diameter. This was welded onto the top of the first tube at an angle 45 degrees. The puzzle was attached to the 2-inch standard cage mesh using 4 L-shaped hooks and 4 holding bolts. The puzzle was placed in the upper third of the indoor enclosure. The gibbons were able to sit in the metal frame of the cage for balance and comfort, and manipulate the food through the mesh. The puzzle was placed so that the holes were aligned with the gaps in the mesh of the cage. The puzzle was bolted to the cage to prevent the gibbons from obtaining grapes through shaking the puzzle. Grapes could only be obtained through careful manipulation (Photo G).

The puzzle was already filed with 3 grapes in Tube 1 (T1) and with one grape at the end of the puzzle (FIN) to show the gibbons that there was food in the puzzle and to encourage them to manipulate the puzzle to obtain more grapes (which they could see and smell). Red, seedless grapes were used. Though grapes are a part of the gibbons' daily diet, they are a particularly prized food item (Photo H).

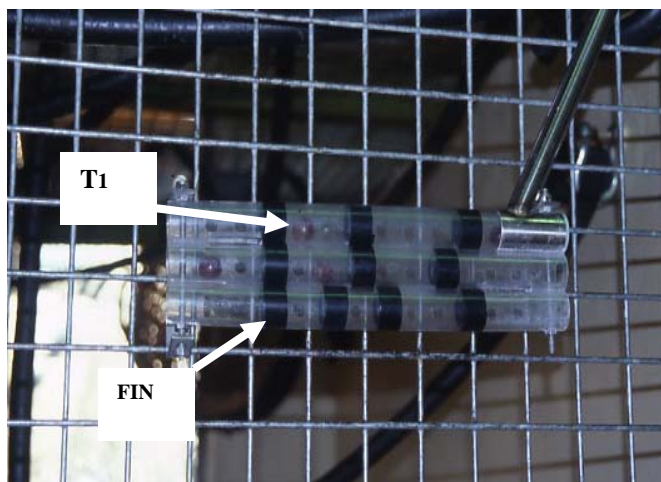


Photo G Food puzzle with grapes inside © Susan M. Cheyne



Photo H Sub-adult male and food puzzle © Susan M. Cheyne.

## Methods

- Baseline observations were collected from 20<sup>th</sup> November 2001 to 7<sup>th</sup> December 2001 (3 days/pair)
- The puzzle was attached to the indoor enclosures of each pair for half a day without any grapes to acclimatise the gibbons to the presence of the puzzle. Observations of each pairs' reaction to the unbaited puzzle were carried out 24 hours prior to filling the puzzle.
- Once filled, the puzzle was left in place for 24 hours. Continuous observations were carried out in two sessions: for 3 hours in the morning directly after the gibbons were given access to the puzzle (this depended on when the cleaning of

the indoor enclosure was completed) and for 2 hours in the afternoon from 1400h to 1600h. The status of the grapes was noted after lunch (1400h) and when the gibbon house was entered the following morning (08:30h) to look for any sign of the puzzle having been manipulated when there were no humans present. The gibbons are fed three times/day so food is available to the gibbons 24hrs/day, independent of the puzzle.

- After the puzzle was removed from each cage, additional baseline observations were made.
- The entire study lasted for 4 weeks from 20<sup>th</sup> November to 20<sup>th</sup> December 2001.

Prior to the introduction of the puzzle, baseline observations were obtained using 10-min scan sampling in the following categories:

- Position in the enclosure. The enclosure is 3m tall and is divided into four areas: floor, bottom, middle and top third.
- Posture at the time: walking on ground; walking on branch; climbing; stationary swinging; sitting; rolling; hanging.
- Substrate use at the time: bough; branch; twigs; pipe; vine; mesh; shelf; floor; partition; window; wall; basket; roof.
- Activity at the time: feeding; foraging; allogrooming; self-grooming; sexual exploration; nursing; infant carrying; copulation; play; singing alone; duetting; drinking; chasing; travelling; sexual presentation; other calling; inactive and not in view.
- Food type (if applicable)
- Interactions (if applicable): groomer/groomee; chaser/chasee. This was used in conjunction with nearest-neighbour data from the juvenile socialisation cages to determine possible pairs.
- Pair association: single; passive association (i.e. together but no contact or interaction); positive association (together with contact or interaction); 1-5m away; 5-30m away.
- Stereotyped behaviour: none, rocking, twitching, self-biting, teeth champing and bouncing.
- Aggression towards cage mate (yes/no)

When the puzzle was introduced without food, the following additional data were collected:

- Time interaction commenced (i.e. when the puzzle was approached to within contact distance) and time interaction ceased (i.e. when the gibbon moved beyond contact distance with the puzzle). This period indicates one interaction bout.
- If the interaction was through visual exploration, olfactory exploration or tactile exploration and the number of times the gibbon interacted with the puzzle in a single bout.



Once the puzzle was introduced with food, the following additional data were collected:

- Number of times the grapes were manipulated in one bout
- Number of times food was extracted in one bout and which part of the puzzle it came from.

## Results

### *Food Puzzle*

The puzzle was attached to the outside of the indoor enclosures while the gibbons were shut outside for morning cleaning. Table 3 shows the length of time that elapsed before each gibbon approached the puzzle after they were allowed access to the indoor enclosure where the puzzle was mounted. 11 out of the 12 gibbons approached the puzzle within 15mins of being granted access.

**Table 3 Time each gibbon took to approach the puzzle. 0 mins indicates that the gibbon moved straight to the puzzle once allowed access to the enclosure where the puzzle was located. Gibbons are grouped in resident pairs.**

Gibbon	Sex	Species	Age class	Time to first approach the puzzle (mins.)
Adidas	M	<i>H. muelleri</i>	Adult	14
Dalumie	F	<i>H. muelleri</i>	Adult	1
Fox	M	<i>H. muelleri</i>	Sub-adult	348
Nini	M	<i>H. muelleri</i>	Sub-adult	1
Paul	M	<i>H. agilis unko</i>	Sub-adult	0
Puma	F	<i>H. agilis unko</i>	Sub-adult	2
Alex	F	<i>H. gabriellae</i>	Adult	9
Pung-yo	M	<i>H. gabriellae</i>	Infant	0
Zoey	F	<i>H. gabriellae</i>	Adult	0
Peanut	F	<i>H. gabriellae</i>	Juvenile	0
Kitty	F	<i>H. lar</i>	Juvenile	0
Nike	M	<i>H. lar</i>	Adult	1

All the gibbons approached and manipulated the puzzle at least once though Fox and Alex only approached and interacted with the puzzle once during the observation periods (both in the morning period). Two adults (Alex and Nike), one sub-adult (Fox) and the infant Pung-Yo manipulated the puzzle but made no attempt to manipulate the grapes. Kitty and Zoey were the only gibbons to have prolonged interaction with the puzzle and to manipulate the food without extracting anything. Only 6 of the 12 gibbons managed to extract any grapes: Adidas, Dalumie, Nini, Paul, Puma and Peanut (Table 4).

The only observed changes in the status of the grapes over the lunch period or overnight were for Zoey and Peanut who had manipulated the three grapes down to T2 during the lunch period, though this could have been Peanut alone. None of the other gibbon pairs showed any change in position of the grapes after periods of being alone with no humans in the gibbon house.

**Table 4: Number of grapes presented to each pair and the number of grapes each individual removed and ate. Highlighted gibbons successfully extracted grapes from the puzzle.**

Gibbon	Sex	Age class	Number of grapes presented	Number of grapes removed and eaten
Adidas	M	Adult	4	2
Dalumie	F	Adult	4	2
Fox	M	Sub-adult	4	0
Nini	M	Sub-adult	4	2
Paul	M	Sub-adult	4	1
Puma	F	Sub-adult	4	2
Alex	F	Adult	4	0
Pung-yo	M	Infant	4	0
Zoey	F	Adult	4	0
Peanut	F	Juvenile	4	4
Kitty	F	Juvenile	4	0
Nike	M	Adult	4	0

## Behaviour and puzzle

There were no instances of aggression resulting from the introduction of the puzzle. Only one of the gibbons who manipulated the grapes showed any stereotypic behaviour prior to the introduction of the puzzle (Adidas, adult male). More data are needed to determine if the puzzle produced a significant change in expression of stereotypic behaviour. All six gibbons who extracted grapes showed clear interest in the puzzle by exploring it visually (directed gaze at the puzzle), smelling or touching it (Figure 4).

## Digit Use

The gibbons demonstrated different approaches to manipulating the grapes. It is interesting to note that all the gibbons had a preferred digit for manipulating the grapes except Puma (Table 5). Nini was seen to use a twig to manipulate the grapes and Peanut employed a runner bean from her food basket, though neither made use of these tools for long and reverted back to using their fingers.

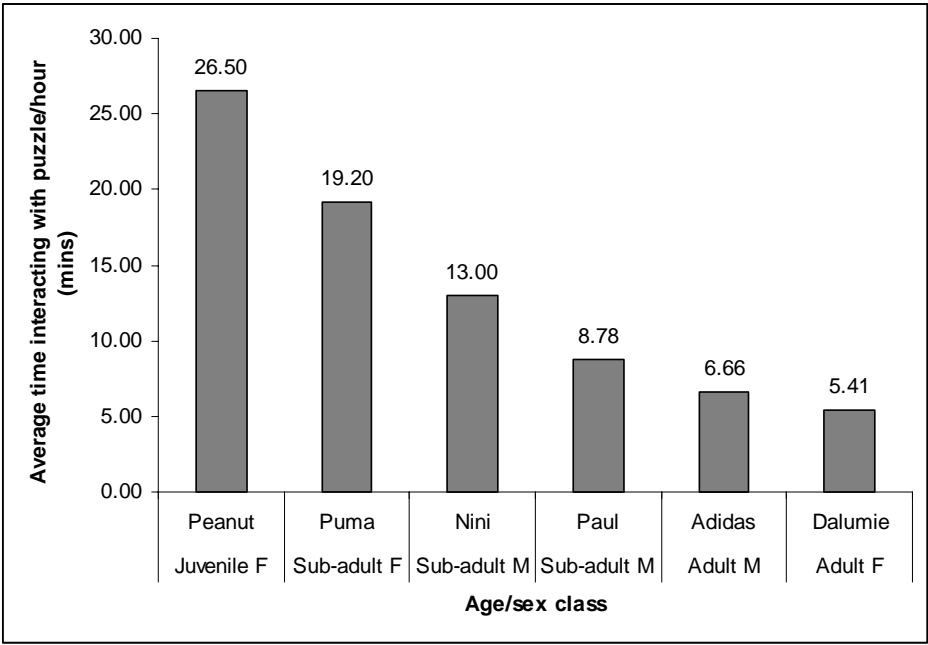


Figure 4 Time spent interacting with puzzle for all gibbons who removed grapes (mins/hour averaged over three days of study).

**Table 5 shows the different approaches the gibbons took for manipulating the grapes.**

Gibbon and sex	Digit used	Number of attempted manipulations	Frequency of manipulations with preferred digit %
Peanut (F)	Thumb	63	86
Zoey (F)	Thumb	42	67
Puma (F)	Thumb	39	56
Puma (F)	Index Finger		44
Dalumie (F)	Index Finger	34	66
Kitty (F)	Index Finger	24	71
Nini (M)	Index Finger	58	68
Paul (M)	Index Finger	45	83
Adidas (M)	Index Finger	52	70

CONCLUSIONS

Behaviour and puzzle

The results suggest that gibbons are capable of manipulating a complex food puzzle to obtain food rewards, though the puzzle has to remain in place for some time to allow the gibbons to acclimatise to its presence. Gibbons are naturally wary of new items in their enclosures (pers. obs.) and must be allowed an acclimatisation period before they can be expected to interact with the new item. Gibbons are naturally curious and given time will

explore new items in their enclosure. The preliminary results also suggest that the age of the gibbon is important in determining how much the gibbon will interact with the puzzle. Young gibbons in the wild would be accumulating information about their environment from their mother, with a steep learning curve. Thus, it would make sense that it will be young gibbons, the ones most in need of cognitive development, who would benefit most from access to puzzles.

## Digit Preference

Each of the gibbons that attempted to manipulate the grapes demonstrated a digit preference, either the index finger or the thumb, except the agile female who used her thumb and index finger with almost equal frequency. The puzzle was placed in roughly the same place on each enclosure and at the same height. It is interesting that three of the gibbons showed a preference for using their thumb, despite this being the shortest digit, and all the males showed a preference for the index finger. Both Nini and Peanut (again younger gibbons) were seen to use external objects to manipulate the grapes: Nini broke off a small twig from some branches which had been placed in the enclosure for environmental enrichment and Peanut used a runner bean from her food basket though neither gibbon made extensive use of these 'tools'. Both gibbons achieved success with their respective tools but later resorted to using their fingers. It is likely that the design of the puzzle meant that a dexterous finger was more effective at removing the grapes. There are few reports of tool use among gibbons, either in the wild or in captivity. The results suggest that gibbon may have a greater capacity for tool use than previously thought.

## DATA FROM WILD GIBBONS

Previous studies of wild gibbons have noted the paucity of social behaviour within the group (Gittins, 1982; Kappeler, 1981; Whitten, 1980) or have reported low levels of social interactions between the adults (<5%, (Ahsan, 2001; Chivers, 1975; Sheeran et al., 1998). Only two studies have reported levels of social interactions greater than 5% (Cheyne, 2004; Cheyne et al., 2008; Srikosamatara, 1984) and only one has focused on the non-adults in the group as focal animals (Moise, 2009).

Data from a recent long-term study in Indonesian Borneo on wild *H. albibarbis* is revealing that gibbons do have social interactions, but that these are difficult to observe and infrequent, perhaps explaining why other shorter studies have not recorded social behaviour. (Cheyne, in prep) found that 3% of time was spent in social activities (Figure 5).

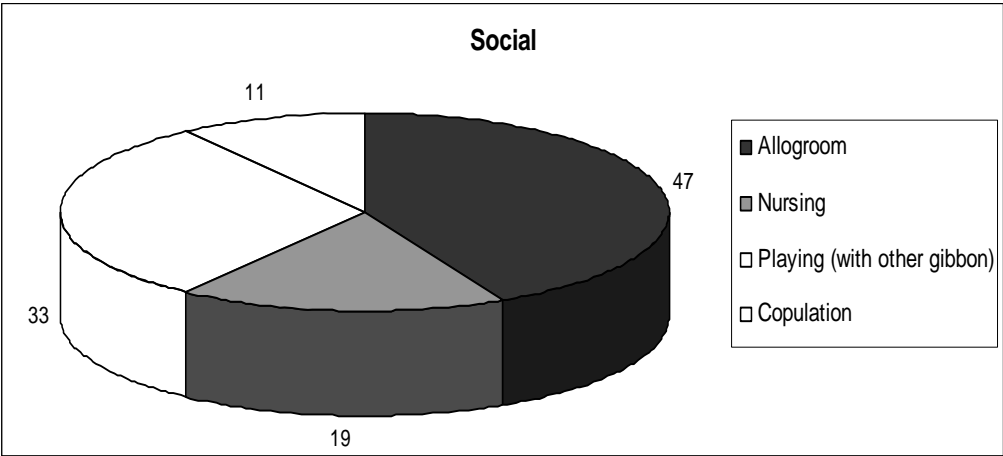


Figure 5 Breakdown of social activities (% of total social observations).

Table 6 Comparison of available social data for gibbons.

Species	Geographical area	Level of observed social interactions (%)	Number of study groups	Length of study	Reference
<i>H. hoolock</i>	India	4	15	1998-1990 (2 yrs)	(Ahsan, 2001)
<i>H. concolor jingdongensis</i>	China	4	4	1990-1997 (7yrs not continuous)	(Sheeran et al., 1998)
<i>H. pileatus</i>	Thailand	7	1	1978-1979 (1 yr)	(Srikosamatara, 1984)
<i>H. syndactylus</i>	Malaysia	2	3	1968-1970 (2 yrs)	(Chivers, 1975)
<i>H. agilis</i>	Malaysia	0	1	1975-1976 (1 yr)	(Gittins, 1982)
<i>H. klossii</i>	Indonesia	0	1	1976-1978 (2yrs)	(Whitten, 1980)
<i>H. moloch</i>	Indonesia	0	1	1975-1976 (1yr)	(Kappeler, 1981)
<i>H. albibarbis</i>	Indonesia	10	1	2002-03 (2 yrs)	(Cheyne, 2004; Cheyne et al., 2008)
<i>H. albibarbis</i>	Indonesia	4	8	2005-08 (4 yrs and ongoing)	(Cheyne, in review)

The lack of detailed studies on gibbon social behaviour and interactions has hindered a complete understanding of cognitive abilities and has perhaps biased the level of interest in studying gibbon cognitive abilities in captivity or social interactions in the wild. It is worth noting that there may be a geographical pattern in levels of observed social behaviour, though this requires much more work as the number of study groups, length of study and degree of habituation of the gibbons varies greatly (Table 6).

## **CONCLUSIONS AND THE IMPORTANCE OF STUDYING SOCIAL DEVELOPMENT AND COGNITIVE ABILITIES IN GIBBONS**

The relative paucity of data on gibbon cognition, cognitive development and social interactions in the wild is a barrier to full understanding of this complex topic. Despite this, there is a great deal still to be learned about the small apes and I hope researchers will continue to choose to study this species and develop appropriate tests to gain insight into gibbon cognition. Preliminary results suggest that there is a learning window for young gibbons where they are more motivated to try novel tasks, suggesting this could be applicable in rehabilitation and reintroduction centres, where young gibbons do not have the benefit of parental teaching. The results presented here provide strong support for including complex food puzzles as a standard environmental enrichment for captive gibbons.

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*Chapter 8*

## **COMPARING METHODS FOR ASSESSING LEARNING AND COGNITION IN PRIMATES**

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### **ABSTRACT**

One of the dominant research areas in behavioral primatology pertains to assessments of the cognitive capacities of various nonhuman primate species. Experiments in this area have shown that primates have many skills that approximate those found in humans. These tests include both manual and computerized assessments, and often the format in which tests are presented can impact the learning and behavioral responding that are produced by subjects. In this chapter, we outline two case studies that compare different methodologies and how those methodologies might contribute to differential learning and cognitive performance. In the first, rhesus monkeys responded during a learning task using either joysticks or touch-screens. The task assessed whether the monkeys responded according to stimulus-response associative processes or by using more relational rules about the task. Performance was similar using both input methods and suggested a more associative response pattern. In the second case, chimpanzees and monkeys learned to sequence stimuli using either a computerized task or through selection of three-dimensional stimuli presented in a manual test. Here, the manual test produced faster acquisition and better performance than the computer task, indicating that in some contexts a hands-on, real world format may produce improved cognitive performance.

### **INTRODUCTION**

In the past few decades, the resurgence of interest in cognitive processes (the so-called Cognitive Revolution within psychology) has crossed the species boundary to include tests with various nonhuman animal species (e.g., Tomasello & Call, 1997; Wasserman & Zentall, 2006). No group of animals has been more widely studied in this domain than the nonhuman primates (e.g., Maestripieri, 2003). Tests with these species include prosimians, New World

monkeys, Old World monkeys, and apes, and they include investigations into processes including perception (e.g., Beran, 2006; Dufour, Pascalis, & Petit, 2006; Fujita, & Giersch, 2005; Hopkins & Washburn, 2002; Morris & Hopkins, 1993; Tomonaga, 1998; Zivotofsky, Goldberg, & Powell, 2005), categorization (e.g., Bovet & Washburn, 2003; Santos, Hauser, & Spelke, 2001; Tanaka, 2001; Smith, Minda, & Washburn, 2004; Vonk & MacDonald, 2004), long-term memory (e.g., Beran, 2004; Beran, Pate, Richardson, & Rumbaugh, 1999); episodic memory (e.g., Hampton, Hampstead, & Murray, 2005; Menzel, 1999; Schwartz, Hoffman, & Evans, 2005), numerical processing (e.g., Beran, 2001; Beran & Rumbaugh, 2001; Brannon & Terrace, 2000; Cantlon & Brannon, 2007; Jordan, MacLean, & Brannon, 2008; Nieder & Merten, 2007; Tomonaga, 2007), planning (e.g., Beran, Pate, Washburn, & Rumbaugh, 2004; Biro & Matsuzawa, 1999; Osvath & Osvath, 2008), and metacognition (Beran, Smith, Redford, & Washburn, 2006; Call & Carpenter, 2001; Hampton & Hampstead, 2006; Mulcahy & Call, 2006; Smith, Beran, Redford, & Washburn, 2006; Smith, Shields, & Washburn, 2003; Suda-King, 2007). A wide variety of test paradigms have been developed, including many that rely on computer-based apparatus and software.

Much of the early psychological testing of captive nonhuman primates and other animals primarily relied on manual devices such as the Puzzle Box (Thorndike, 1898) and the WGTA (Harlow & Bromer, 1938). Occasional electronic devices were used for such tests (e.g., Ferster, 1964), but the widespread use of computerized testing of nonhuman primates has occurred only in the past 20 years. Computerized testing received a boost as more efficient and user-friendly data collection software emerged (e.g., Cohen, MacWhinney, Flatt, & Provost, 1993; Stahl, 2006; Washburn, 1990). These advances decreased the time it took to complete experiments by allowing faster creation, implementation, and data collection in comparison to the use of manual devices (Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990; Washburn & Rumbaugh, 1992). However, there remains little research directly comparing performance on computerized versus manual tests of the same cognitive and learning processes. In addition, even with the adoption of the computer as a testing method with nonhuman primates, there remain questions about the best response input methods and the potential differences in performance that can occur as a function of that input method.

## COMPARING MANUAL AND COMPUTERIZED TEST PARADIGMS

Perhaps the most famous apparatus in behavioral primatology is Harlow's Wisconsin General Test Apparatus (WGTA). This apparatus (and the many variations of it used since its introduction) allows an experimenter to present stimuli to an animal and record its responses without the possibility of providing inadvertent cues. Harlow (1949) and others have used this apparatus to present monkeys with 2-choice discrimination problems. Despite its innovation, however, the WGTA required an experimenter to manually present stimuli to subjects and record data. It was labor intensive, and data collection was slow. The introduction of computerized testing changed that situation. Today, many laboratories present nonhuman primates with visual tasks on computer monitors, in which individuals are rewarded, via automated feeders, for making joystick or touch-screen responses to task stimuli. The computerized method has several advantages over alternatives such as the WGTA. These include:

- The experimenter can gain complete control over the testing environment by producing stimuli and contingencies that are consistent between trials/sessions.
- Response accuracy and latency can be recorded by computer software with greater precision, leaving little room for human error.
- The experimenter does not have to be present for testing, further removing any potential cue-giving and requiring less time (on the experimenter's part) to acquire data. This is particularly important during the training of new animals, during which the computer software can adjust itself to the competence level of each subject and modify the difficulty of the training tasks.
- Given the speed with which new trials can be prepared and presented (which can be almost immediately), the data set that results is also usually much greater in size, per unit time.
- The computerized method can be easily adapted for use with different primate species, as well as some non-primate animal models.
- The task parameters can be automatically adjusted by the software to accommodate the proficiency of subject being tested.

Computerized tests of nonhuman primate cognition have offered much data in support of high level performance. In some cases, the use of computerized tests produced radically different behavioral outcomes compared to tests given with manual or other types of non-computerized tests. For example, Washburn and Rumbaugh (1991b) found that monkeys, when tested with a large number of computerized reversal learning problems, exhibited a more cognitive learning style than when tested previously with a small number of manually presented problems (Essock-Vitale, 1978). McGonigle, Chalmers, and Dickinson (2003) also reported that capuchin monkeys performed better on tests of seriation and classification when those tests were computerized compared to manual tests.

However, in other cases manual tests have produced stronger evidence of cognitive competence. Mandrell and Sackett (2008), for example, tested infant macaque monkeys on a variety of computerized tests and then compared performance to a substantial database of previous similar tests given in a standard manual format (WGTA). They found that for some tasks, performance was comparable between computerized and manual tests. However, in a rule learning task (learning set), the animals tested on the computer version performed more poorly compared to animals tested with the WGTA. These results stand in contrast to those of Washburn, Hopkins, and Rumbaugh (1989) who reported better performance on computer versions of the learning set task compared to manual tests (although those were adult macaque monkeys, and they used joysticks rather than touch-screens, as were used with the infants). It is important to note that this type of discrepancy is not unique to tests with nonhuman primates, as human children sometimes show differences in certain tests when presented in a computer or manual format whereas in other cases, and for the same task, they show no such differences (e.g. Feldstein et al., 1999; Carlson, Moses, & Claxton, 2004; Luciana & Nelson, 2002).

## COMPARING JOYSTICK AND TOUCH-SCREEN INPUT ON COMPUTERIZED TASKS

Despite the advantages offered by computerized testing, once a research team decides to use a computerized task, they must still determine the appropriate input device. Typically, primates respond using either a joystick or a touch-screen. In labs in which animals are provided with a joystick, they can manipulate the joystick with their hand to control the movement of a cursor on the screen or they can simply deflect (or hold) the joystick to make different kinds of behavioral responses. In labs in which primates are provided with touch-screen monitors, they contact visual stimuli directly with their hands.

Other important factors should be considered when choosing between touch-screens and joysticks. Each input works considerably well with different primate species, but they differ in expense, additional equipment needed, and the type of software needed for testing (most of these favoring the joystick). Also, each device can produce unique methodological issues that need to be considered when designing or interpreting an experiment (see Evans et al., 2008). One of these issues is stimulus contact accuracy. When using a touch-screen, it is easier for animals to make direct responses to stimuli, and touch-screens require less fine motor coordination to select stimuli. With joysticks, more psychomotor control is needed to select stimuli, and so this should be considered in relation to the task parameters themselves (e.g., the number, size, and spatial proximity of the stimuli presented on the screen). Another difference between input devices is their ability to accurately represent and record animal response time and decision time. Touch-screens can be more accurate in this respect because of the ease with which animals can select stimuli. When joysticks are used, one must consider the possibility that response times may vary because of less-than efficient cursor control, in addition to time required to make a decision.

An important difference between these two input devices is the level of spatial contiguity between the response location and the stimulus location. The touch-screen provides perfect spatial contiguity, while the joystick does not. Some researchers have argued that differences in the level of spatial contiguity between stimuli and response loci can result in differences in performance on psychological assessments. For example, rhesus macaques (*Macaca mulatta*) often had difficulty in learning two-choice discrimination tasks when there was stimulus-response (S-R) spatial discontiguity using a manual apparatus like the WGTA (McClearn & Harlow, 1954; Meyer, Treichler, & Meyer, 1965; Murphy & Miller, 1955, 1958). Meyer, Polidora, and McConnell (1961) reported that performance of monkeys was poorer when responding to stimuli discontiguous with an activating panel in a computerized apparatus than when the response loci were contiguous with the cue stimuli.

However, rhesus monkeys have overcome spatial discontiguity when testing involved joystick-based computerized tests (Richardson et al., 1990; Rumbaugh, Richardson, Washburn, Savage-Rumbaugh, & Hopkins, 1989; Washburn et al., 1989). Beran, Rumbaugh, and Washburn (2007) reported that rhesus monkeys even overcame second-order S-R spatial discontiguity when presented with Harlow's (1949) learning set task. The monkeys used a joystick to move a cursor so as to contact computer graphic "levers" (which differed in location across experimental phases) in order to select an associated test stimulus. The levers were spatially discontiguous with the response stimuli themselves (i.e., the S+ and S- stimuli to be discriminated). Therefore, the task produced both first-order (joystick and lever) and

second-order (lever and stimuli) spatial discontiguity. These performances showed that rhesus macaques do not attend simply to the region around the cursor in these computerized tests. They also attend to relevant stimulus loci even when these are discontiguous with response and reward areas, and they do so when tested using joystick methodology.

In summary, computerized testing methods offer several advantages over traditional manual apparatus methods, but this does not mean that computer tests always afford the greatest likelihood of finding positive results or the clearest evidence of some form of learning or cognition. The benefits of computer testing must be weighed against the possibility that such tests might fail to tap into important subject variables. Despite some evidence that computer tests have helped overcome previous failures of learning, it is possible that other kinds of behavioral and cognitive phenomena might not manifest as well in computerized paradigms. For example, whereas computerized tests sometimes show enhanced cognitive performance in children (e.g., Olsen, 2008), in other cases the use of computer tasks shows less cognitive sophistication in the resulting performance of children (Luciana & Nelson, 2002).

In this paper, we outline two research projects designed to assess differences in performance as a function of methodology used with primates. In the first, we directly compared performance on the same computerized learning task when presented as either a touch-screen task or a joystick task. This task, the mediational paradigm, illustrates the extent to which participants can flexibly learn discrimination rules and then modify those rules with experience in responding to pairs of stimuli. In the second project, we compared performance in an ordinal learning task (the sequencing of arbitrary stimuli on the basis of the quantitative relations to each other) when it was presented in a computerized format versus a more naturalistic, manual format. These projects will help illustrate the differences in cognitive and learning performances as a function of the methodology that is used.

## **Project 1. Mediational Paradigm Performance with Joysticks and Touch-Screens**

Rumbaugh (1971) devised the mediational paradigm specifically for differentiating associative and rule-based interpretations for reversal learning in nonhuman animals. Performance on this task would indicate whether animals responded through stimulus-response (S-R) associative learning processes such as those posited for more general learning phenomena (Hull, 1943; Spence, 1937) or whether they learned about relations between stimuli by discovering the logical task structuring. The mediational task was based on the well-established phenomenon of learning set (Harlow, 1949), and it has been used with a variety of species (e.g., Beran et al., 2008a; Rumbaugh & Pate, 1984a, 1984b).

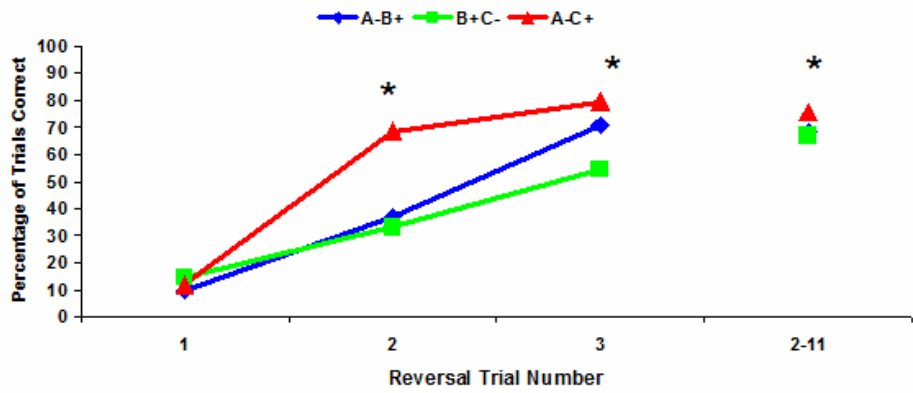
Here, we assessed performance in four rhesus monkeys (Obi – age 2 years, Han, age 3 years, Chewie, age 6 years, and Luke, age 6 years). Prior to testing, each animal received training with each input device (touch-screen and joystick). These training procedures have been extensively outlined elsewhere (e.g., Evans et al., 2008; Richardson et al., 1990). We will cover the basic details only. It is important to note that all monkeys were trained on both input forms before this study, so their experiences when entering this task were identical, and performance differences on the mediational paradigm could not differ as a result of different experiences with computer tasks.

When monkeys were trained to use the joystick, they progressed through a seven step procedure. First, they were shaped to simply touch, and then displace, the joystick. These steps usually occurred automatically and required little or no active training. Monkeys then were trained across several steps to move the cursor to smaller and smaller portions of the screen area. They then were trained to contact a moving target with the cursor. Finally, they learned to select stimuli in a matching-to-sample paradigm in which a visual sample was presented mid-screen and an identical stimulus had to be selected from the perimeter of the screen. A similar set of steps were taken to train touch-screen use. Monkeys first were rewarded to touch any part of the computer screen, and then were rewarded to touch sections of the screen that were successively smaller in size as training criteria were reached. They then were trained to touch a moving target, and then to touch stimuli in the matching-to-sample paradigm.

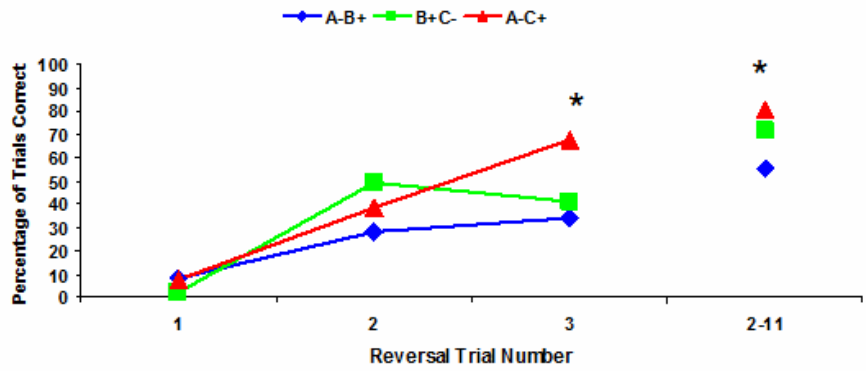
At the end of training on the input modalities, two monkeys (Luke and Obi) were presented with the mediational paradigm and responded using the touch-screen. The other two monkeys (Chewie and Han) responded using a joystick. Monkeys were housed individually, and had 24-hour access to the task, so they could work whenever they chose. For two weeks the mediational paradigm was presented continuously, and the monkeys completed thousands of trials using either the joystick or touch-screen. The task was identical as presented to the two groups except that the joystick monkeys moved a cursor on the screen into contact with choice stimuli whereas the touch-screen monkeys physically touched those choice stimuli with their fingers or hands. Correct responses provided the monkeys with a food pellet reward whereas incorrect responses led to a time-out period during which the screen was blank and no responses could be made. The mediational paradigm itself consisted of a number of unique, discrete “problems” that involved the repeated presentation of pairs of stimuli. Each problem consisted of three steps:

1. In the training step, a monkey was provided with a pair of stimuli: an S+ that, when selected, would result in a food reward, and an S- that, when selected, would result in a time-out penalty during which the screen was blank. These stimuli were denoted A+ and B-. Training trials were presented until the subject reached a 90% criterion over the last 10 trials.
2. After reaching this criterion, a single trial (called the reversal trial) was presented in which the response contingencies for stimuli A and B were reversed, making A the new S- and B the new S+.
3. After the single reversal trial, stimuli were presented in 10 test trials in one of three possible conditions. In the first condition, A and B continued to be tested with reversed response contingencies (as S- and S+, respectively). In the second and third conditions, a novel stimulus, C, replaced either A or B as new S- or the New S+, respectively. At the end of these 10 test trials, a new problem was presented (with two new stimuli, arbitrarily assigned as S+ and S-), and the training phase began again.

A comparison of performance in the three conditions provides evidence for the type of learning that occurs. If an animal has learned only to approach the A stimulus during training (A+B-), the B+C- condition should produce the best performance levels because there is no need to extinguish approach responses to stimulus A because it is no longer present. If an animal has learned only to avoid the B stimulus, the A-C+ condition should produce the best performance levels because there is no need to overcome inhibition of responding to stimulus



Luke - Touchscreen

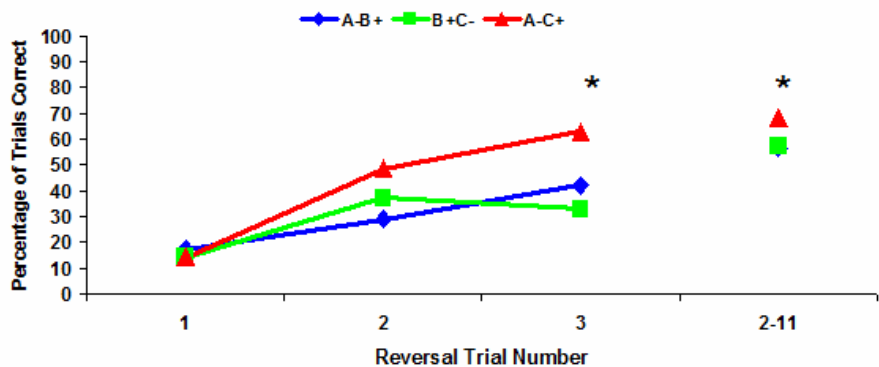


Obi - Touchscreen

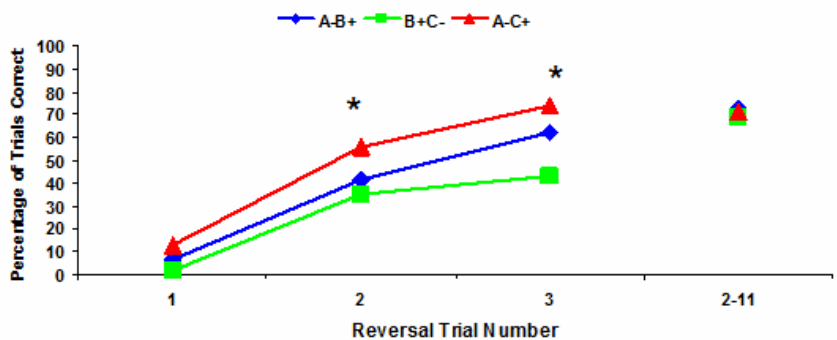
Figure 1. Performance in each condition by the two monkeys that responded using a touch-screen. The single A-B+ reversal trial that occurred between training and test trials is labeled here as Trial 1, and the 10 test trials are labeled as Trials 2-11.

B. If the animal has learned both to avoid the B stimulus and approach the A stimulus, performance should be poorest on the control (A-B+) condition because both associative processes (approach and inhibition) remain. These are all predictions based on associative learning as the primary force behind the animals' behavior. However, a more cognitive interpretation also exists. If the monkeys learn more than inhibitory and excitatory associations formed between specific stimuli and responses, they could discern all that they needed to know from the first reversal trial. Specifically, that trial illustrates that now the B stimulus is the correct stimulus and the A stimulus is the incorrect stimulus, and the subsequent introduction of the C stimulus would not disrupt performance. In the B+C- condition, the organism could continue to respond based on learning that B is now the correct response. In the A-C+ condition, the organism could respond based on learning that the A stimulus is no longer the correct response, and thus the C stimulus should be selected. The A-





Chewie - Joystick



Han - Joystick

Figure 2. Performance in each condition by the two monkeys that responded using a joystick. The single A-B+ reversal trial that occurred between training and test trials is labeled here as Trial 1, and the 10 test trials are labeled as Trials 2-11.

B+ condition would allow a continuation of the win-stay, lose-shift rule that emerged from the first reversal trial (see Rumbaugh & Pate, 1984a, 1984b).

Performance for all four animals was very similar, and in line with a previous experiment conducted with joystick-using capuchin monkeys (Beran et al., 2008). The touch-screen monkeys (Figure 1) each performed significantly differently on the three conditions across all trials after the reversal trial, Luke  $F(2, 305) = 4.56, p < .05$ ; Obi  $F(2, 150) = 12.92, p < .01$ . Luke also showed a significant difference in performance for Trial 3 after reversal and Obi showed a significant difference in performance for Trials 2 and 3 after the reversal trial. The joystick monkeys showed slightly more variability in performance (Figure 2). Chewie performed significantly differently on the three conditions across all trials after the reversal trial,  $F(2, 206) = 30.59, p < .01$ , but Han did not ( $2, 228 < 1.00, p = .63$ ). However, Han showed a significant difference in performance for Trial 2 and Trial 3 after reversal, and Chewie showed a significant difference in performance for Trial 3 after the reversal trial.

The touch-screen monkeys and joystick monkeys all appeared to learn the response contingencies of test stimuli faster in the A-C+ condition than in the A-B+ or B+C- condition. Thus, the monkeys performed the two-choice discrimination faster when the S+ was replaced with a novel stimulus, and the S- remained the same. This suggested that all of the monkeys learned to inhibit responding to the S- during training because this stimulus produced punishment (in the form of a time-out penalty).

These data also suggested that the input device used for testing, and thus the level of stimulus-response spatial contiguity included in the task, did not influence learning performance. In other words it made no difference whether the response occurred at the same location as the stimulus or at a different location. Performance was qualitatively similar with both types of response input.

## **Project 2. Acquiring Ordinal Sequences Quickly – Manual Versus Computerized Tasks**

Ordinality refers to the relative position of one entity with respect to other entities in a sequence. Some research programs have trained animals to associate various symbolic stimuli with discrete quantities. For example, Washburn and Rumbaugh (1991) trained rhesus monkeys to select among 2, 3, 4, or 5 Arabic numerals presented on a computer screen, and the monkeys received an equivalent number of food pellets to each numeral that was selected. Those monkeys selected the larger numeral when presented with pairs of numerals, and they succeeded when faced with novel arrays of 3, 4, or 5 different numerals at one time. Beran et al. (2008b) replicated these findings with capuchin monkeys and rhesus monkeys. Olthof, Iden, and Roberts (1997) also presented monkeys with two numerals and the monkeys received a number of food items equal to the numeral that they selected on each trial. Olthof and Santi (2007) used similar tests with pigeons, and they also showed that ordinal relations emerged from this pair-wise training paradigm with arbitrary stimuli.

In most studies that use this task, acquisition of the ordinal series required a large number of training trials. Washburn and Rumbaugh (1991a) reported that their monkeys needed more than 400 trials to reach high levels of performance on the ordinal task. Beran et al. (2008b) gave their monkeys 1,000 training trials before moving to the test phase. Olthof et al. (1997) reported that their monkeys required a large number of training trials, and pigeons required 45 multiple-trial training sessions to reach criterion in selecting the larger member of a pair of presented symbols (Olthof & Roberts, 2000). Other research projects that required nonhuman animals to select visible sets of non-food items (i.e., magnitudes) in ordinal sequences also reported that large numbers of training trials were required (e.g., Brannon & Terrace, 2000; Judge, Evans, & Vyas, 2005; Smith, Piel, & Candland, 2003).

One study, however, reported very rapid acquisition of an ordinal sequence of arbitrary stimuli. Beran, Beran, Harris, and Washburn (2005) reported that two chimpanzees and a rhesus macaque rapidly learned the ordinal relations between five colors of containers (plastic eggs) when all containers of a given color contained a specific number of identical food items. All three animals also performed at high levels when comparing sets of containers to sets of visible food items. In that paradigm, the animals were presented with two different colored plastic eggs, each containing some number of food items. The color of the egg indicated how many food items were inside, and so colors constituted the ordinal sequence. These primates exceeded chance levels within the very first 40-trial session, and they reached

near perfect performance within only 3 or 4 such sessions (<150 trials). In addition, the chimpanzees successfully selected among 3, 4, and 5 egg arrays in the correct decreasing quantity order from the very first presentations of such trials. Therefore, very rapid acquisition of the desired ordinal sequence was established.

In the present experiment, we first determined whether the chimpanzees and the monkey in the Beran et al. (2005) study remembered the learned ordinal sequence of these egg stimuli after a 9-month delay. These data would provide evidence of long-term memory for the ordinal sequence, matching other previous reports of such long-term memory in animals (Beran, 2004; Beran et al., 2000; Burdyn, Noble, Shreves, & Thomas, 1984; Patterson & Tzeng, 1979; Reichmuth Kastak & Shusterman, 2002). Then, we tested chimpanzees and monkeys on variations of the ordinal learning task. We used the manual test with plastic eggs that physically held food, and we compared performance on that test to performance on a computerized variation in which colored squares were selected on the screen (with resulting delivery of different quantities of food items as a result of the color that was selected). This experiment allowed us to determine whether the specific format of the Beran et al. (2005) ordinal training led to this rapid learning of the sequence in comparison to other kinds of tests that have been used (namely, those presented in a computer task).

## **9-MONTH RETEST WITH THE MANUAL TASK**

In the original project (Beran et al., 2005) two chimpanzees (Sherman and Lana) and a rhesus monkey (Gale) were presented with eggs in five different colors – red, blue, green, orange, and yellow. Those five colors always represented 5, 4, 3, 2, and 1 food reward contained within the respective eggs of those colors. Training took the form of presenting four trials in each session of all possible combinations of two of those eggs (with the larger value egg equally often on each side of the presentation apparatus). To reach the criterion for mastery of the ordinal sequence, an animal had to be correct on 90% of trials within a session. All three animals exceeded chance levels on the very first session. Sherman and Gale required only three sessions to reach the criterion, and Lana required four sessions.

In the re-test, each of these primates completed a single 40-trial session just like those used during training. The animals had not seen the eggs or performed this task for more than 9 months. Lana and Gale were perfect, choosing the larger-valued egg on all 40 trials. Sherman made a single error and was 97.5% correct overall. In a second session, the animals were presented with a single egg compared to a visible quantity of food (this condition was used in the original study to demonstrate that the animals had learned something about the absolute number of food items in each egg). Sherman was correct on 92.5% of these trials. Lana was correct on 85% of these trials, and Gale was correct on 72.5% of these trials. In all cases, performance exceeded chance levels as assessed with a binomial sign test,  $p < .05$ .

## **TRAINING ORDINAL SEQUENCES OF COLORED STIMULI ON THE COMPUTER**

In the next phase, we presented the exact same task in computerized format. Now, subjects chose between two colored squares on a computer screen, and the computer dispensed the relevant number of food items on the basis of the choice that was made. The critical difference, therefore, was the use of two-dimensional stimuli that were spatially discontinuous with the response loci of the animals (the joysticks), and food rewards were not

contained within those response stimuli (so, food, too was discontinuous with the response stimuli). However, the pacing of the task was the same.

We tested Sherman, Lana, and Gale, assuming they would show some transfer of learning from the egg task to the computer task because we used the same exact five colors in the same ordinal sequence. We also included two new chimpanzees (Panzee and Mercury), and two new monkeys (Willie and Hank), all of whom had no experience with the egg task, so that we could assess how much transfer actually occurred. The criterion for mastery of the ordinal sequence was the same - 90% correct over 40 trials.

The performance of each animal is shown in Figure 3. Sherman and Lana (chimpanzees) met the training criterion, although it took them many more 40-trial blocks than with the egg stimuli. In Sherman's case, performance was high from the first few blocks, although it took some time for him to finally reach the criterion (nine blocks with the computer task compared to three blocks with the egg version of the task). Lana, however, performed at chance levels for the first seven blocks, and it took her a total of 10 blocks to reach the criterion (compared to four blocks with the egg version of the task). Gale, who had met criterion quickly with the egg task and showed perfect 9-month retention, required 29 blocks of trials to meet the criterion on the computerized version of the task. He began to exceed chance levels at the 10<sup>th</sup> block of trials, but performance did not rise to criterion quickly as it had with the egg version of the task.

Of the new animals, the monkey Hank reached the criterion after 24 blocks, and he began to exceed chance levels after approximately 10 blocks. The monkey Willie reached criterion after 88 sessions although he began to exceed chance levels after approximately 60 sessions. Neither of the new chimpanzees reached criterion, although they were not given as much opportunity as the monkeys (Panzee was discontinued after 32 blocks and Mercury was discontinued after 27 blocks, because both chimpanzees only rarely exceeded chance levels of performance within a session). These results suggested that animals with no previous experience with sequencing these five colors had a difficult time learning to organize the ordinal sequence when presented with a computer version of the task. This does not mean that such a task is impossible, as primates have learned to sequence arbitrary stimuli using this paired-comparison method before (e.g., Beran et al., 2008b; Harris, Beran & Washburn, 2007; Washburn & Rumbaugh, 1991a). It just indicates that training takes substantially longer in the computerized format used here than in the more naturalistic format with the physical items that contained the food rewards.

Next, we gave the four best-performing animals (Lana, Sherman, Hank, and Gale) the same computer task again but with five new colors to be learned in a new sequence. All details were the same as in the previous experiment. Lana required 23 blocks to reach the criterion, and Sherman never reached criterion even after 23 blocks (in fact, he never exceeded chance levels of responding). Hank never reached criterion (after 115 blocks), and Gale reached criterion after 31 blocks. These data indicated clearly that Sherman, Lana, and Gale did not show the rapid acquisition that they had showed with the egg stimuli in the Beran et al. (2005) study, and this computerized task was very difficult.

Finally, we re-introduced the task with the eggs. We tested all four chimpanzees. Sherman and Lana, of course, were very familiar with the task, but Panzee and Mercury had not performed this task (and, recall, both of them rarely exceeded chance levels of responding when sequencing these colors in the computerized task). As expected, Sherman and Lana met the criterion in the first session (Sherman – 100% correct; Lana – 97.5% correct). However,

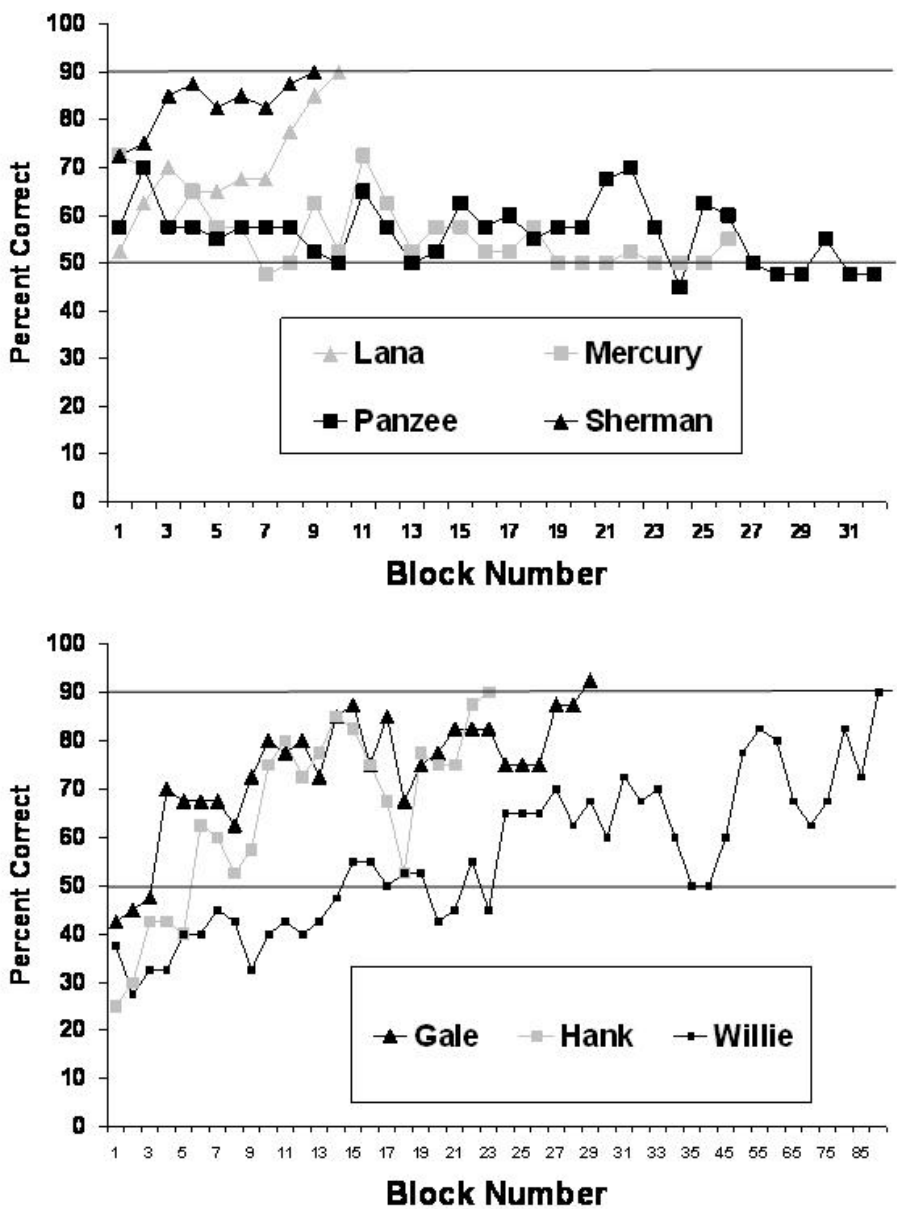


Figure 3. Performance of each animal on the computerized ordinality task. The top figure shows chimpanzee performance and the bottom figure shows monkey performance. The horizontal line at the 90% correct value indicates the criterion value, and chance is represented by the horizontal line at the 50% correct level in each graph.

Mercury and Panzee also showed very rapid acquisition of the ordinal sequence. Mercury required three blocks to reach the 90% criterion, and Panzee required six blocks. Also, both new chimpanzees exceeded chance levels of responding by the end of their first session with the egg stimuli. Thus, we replicated the extremely rapid learning that occurs when these kinds of stimuli are used to present pair-wise training of an ordinal sequence of arbitrary stimuli.

So why should this advantage for learning occur for the manual test and not the computerized test? We believe that the manual test more likely taps into the natural salience structure of the animal's environment. Food items contained within "shells" (which the eggs were in a functional sense), and the choice of those things by direct pointing or contacting of those stimuli, more naturally mimics a foraging-like task or situation for animals such as these. This situation provides more natural salience in the association between the egg colors and the quantities that are contained within, making learning more likely on the basis of this salience (see Rumbaugh, King, Washburn, Beran, & Gould, 2007). Therefore, this research program indicates an advantage for the non-computerized format of the ordinal learning task. These results also provide further evidence for the need for careful and insightful consideration of the best methodology and stimulus presentation format when one tries to establish a behavioral competence in a nonhuman primate species.

## SUMMARY

These two new research projects illustrate the care that needs to be taken when designing methods for use with nonhuman primates. In some cases, one can see flexibility as reflected in consistent performance across testing methods (as with the touch-screens and joysticks used in the mediational test). In other cases, manual versus computerized tests can produce quite different levels of performance, speed of acquisition, and retention (as in the ordinal test). These kinds of results indicate that no single method should be relied upon solely as a means of determining whether a given individual or species does or does not have a certain behavioral trait or cognitive capacity. Rather, it is through varied and creative methodological assessments that a fuller picture of primate behavior and cognition will emerge.

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*Chapter 9*

## **PATTERNS OF DAILY MOVEMENT, ACTIVITIES AND DIET IN WOOLLY MONKEYS (GENUS *LAGOTHRIX*): A COMPARISON BETWEEN SITES AND METHODOLOGIES**

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### **ABSTRACT**

We estimated home range use, activity patterns, and diet in a group of woolly monkeys in Caparú Biological Station (Colombia) during 12 months. These patterns were correlated with fruit supply and compared with previous information reported for woolly monkeys. The comparison shows that the daily distance travelled and home range size were negatively correlated with fruit production. However, woolly monkeys seem to show different ecological strategies depending on the fruiting patterns at each study site. In general, woolly monkeys consume alternative resources (leaves or arthropods) when fruit supply is low, but at Caparú woolly monkeys did not decrease daily path length during periods of fruit scarcity as they do in other places. The activity patterns and diet composition seem to differ among populations, but part of the differences may be explained by the use of dissimilar methodologies. In general, studies which record behaviour by scan sampling tend to overestimate conspicuous behaviours such as movement and fruit feeding, and underestimate less conspicuous behaviours such as resting. The majority of comparative studies recommend the use of both continuous and instantaneous observations on focal individuals.

**KEYWORDS:** ecological strategies; focal animal sampling; fruit production; scan animal sampling; primate socio-ecology.

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## INTRODUCTION

Woolly monkeys (genus *Lagothrix*) are large frugivorous primates that complement their diet with young leaves, arthropods, flowers and some small vertebrates, but the relative importance of these items seems to vary at temporal and spatial scales (Stevenson *et al.*, 1994). The basic ecological characteristics of woolly monkeys such as home range, daily movement patterns, activity, and diet have been reported at different study sites (Defler, 1995, 1996; Defler and Defler, 1996; Dew, 2005; Di Fiore, 2004; Di Fiore and Rodman, 2001; Gonzalez, 2006; Peres, 1994; Stevenson, 2000, 2002, 2006; Stevenson *et al.*, 1994, 1998). Home range areas are among the largest reported for Neotropical primates, though there is large variation between populations (169 - 760 ha) (Defler, 1995; Stevenson *et al.*, 1994). Similarly, activity patterns and diet composition vary among studies. Possible explanations for these variations have previously been associated with differences in productivity and supply of fruits among study sites (Defler, 1995, 1996) or with differences in body size between groups or subspecies (Di Fiore & Rodman 2001). Here we address these explanations and emphasize an additional possible cause of variation related to the use of different methodologies. As reported by Stevenson and Quiñones (2004), the use of different sampling methods can have dramatic effects on the estimates of activity budgets and diet composition in woolly monkeys.

In this study we test three different hypotheses: First, woolly monkeys are energy-maximizers in periods of high fruit abundance and energy-minimizers in periods of fruit scarcity, as described for some of their populations (Di Fiore and Rodman, 2001; Stevenson 2006) and for other ateline primates (Strier, 1992). The main prediction from this hypothesis is that animals travel more in periods of fruit abundance, in order to accumulate energy in lipid tissues. In contrast, they move less in periods of fruit scarcity to avoid an excessive waste of energy. The second hypothesis is based on the supposition that frugivorous primates need large home ranges to meet the energetic demands imposed by the scattered nature of their resources (Clutton-Brock and Harvey, 1977; Defler, 1995). Thus, if home range size depends on available fruiting resources, we predict larger home range areas and longer daily path lengths at sites with low fruit productivity. Finally, we examine whether or not the reported differences in activity patterns and diet might be due to the use of different methodologies. According to this hypothesis, when scan sampling is employed we expect to find a higher proportion of conspicuous behaviours (e.g., moving and fruit feeding) and a low representation of cryptic behaviours (e.g., resting and insect feeding) when compared to focal sampling (Martin and Bateson, 1993; Stevenson and Quiñones, 2004).

## METHODS

### Study Site

The Caparú Biological Station, also known as *Mosiro Itajura*, is located at the south east of the Vaupés department, Colombia, near Lake Taraira, an ancient meander of the Apaporis River (69° 31' W and 1° 04' S, ca. 200 m; Defler, 1999). The Station is located on a terrace of Pleistocene origin. The warm super-humid climate has a slightly bimodal rain regime

(Rangel and Luengas, 1997) with average yearly precipitation of 4.000 mm (Defler, 1996). The month of maximum precipitation is May (386 mm) while the driest is September (258 mm) (Palacios and Rodríguez, 1995). The average yearly temperature is 25.1°C, with slight variations throughout the year, and soils are generally shallow and acid with low fertility (Defler, 1996).

## Study Groups

At least 4 groups of *Lagothrix lagothricha* were observed in the trail system, of which we studied two (SC and FCB). Group SC accounted for 84% of our observations, and was a large group of about 40 individuals. In this group we identified at least 4 adult females with dependant infants, 15 adult males, and 11 adult females without dependant young. Group FCB was a smaller group consisting of 15 individuals, including two females with dependant infants, three adult males, and one adult female without dependant young.

## Field Protocol

We estimated monthly fruit production using phenological transects (Stevenson, 2004). We searched for fruits on the ground along 9.6 km of trails (24 transects, 400 m each). Once a fruit was found, we located the parent plant, identified the species, and calculated the approximated crop size using binoculars. Usually, the number of fruits on several branches was counted, averaged, and then extrapolated to the total number of branches. To estimate the mass of fruit produced by each plant we collected, dried, and weighed 10 fruits from each species. We also registered the perpendicular distance from the tree to the trail to assess the effective sampling width of the transect, which varies depending on tree size and tree distance from the trail (Stevenson, 2004). With this information we calculated a community wide estimate of fruit abundance in units of production (fruit mass.ha<sup>-1</sup>.mo<sup>-1</sup>).

We followed woolly monkeys during 12 daytime hours, 5 days a month between July 2004 and June 2005 (720 h total). Using a compass and the trail system as reference, we delineated the route of the group on a map (1:12500 scale) and estimated daily path length (DPL) using a map measurer. We used daily path length estimates from twelve-hour diurnal follows. We estimated daily path length for two groups SC ( $n = 50$ ) and FCB ( $n = 6$ ), but we calculated the home range of a single group (SC). We considered all quadrants of one hectare where the group was seen at least once during the study as part of the home range, and we determined the variation in home range size as a function of increased sampling time from instantaneous samplings made each 30 minutes. We also estimated the home range area using the minimum convex polygon method (Mohr, 1974).

We recorded activity patterns and diet composition using instantaneous samples every 10 minutes on focal individuals (Altmann, 1974). We registered 4320 instantaneous samples during the study. We were unable to recognize all individuals in our study groups, therefore it was impossible to follow a protocol to choose focal animals. In general, when a focal animal was lost we followed an animal in our proximity. Accordingly, the number of instantaneous samples of each age sex class was proportional to the number of individuals of each age sex

class in the groups. As focal animals we used adult males ( $n = 2057$  point samplings), adult females with dependant infant ( $n = 677$ ), adult females without dependant offspring ( $n = 1202$ ), and juveniles ( $n = 384$ ). Follows of the focal were generally short (average 6.8 min; 5-182 min), but we always observed the focal individual at least 5 minutes before registering an instantaneous sampling. We classified the activities as resting, feeding, moving, and social interactions (Table I). When the animals were feeding, we distinguished among fruits, leaves, arthropods, and other minor items (flowers and vertebrates). The activity budgets and diet composition reported in this study are the percentage of observations from all sampled individuals pooling all records and then using the total to calculate percentages.

Statistical Analyses

We used an analyses of variance to assess monthly variation in fruit production, using 24 phenological transects as sampling units. We analyzed daily path lengths using Mann Whitney Test. We used G tests to look for the association in activity patterns along time (months) and the relationship between age/sex classes and both activities and diet. We used regression analyses to assess the effect of fruit production on several aspects of primate behaviour (i.e., daily path length, activities and diet).

RESULTS

Fruit Production

Fruit abundance varied considerably during different months of the year ( $F_{(11, 276)} = 9.4, p < 0.001$ , Figure 1). The lowest fruit production was observed between October and January. However, *a posteriori* Tukey analyses revealed the main differences in fruit production between a peak in fruit production (April and May) and the remaining months (June - March), which will be considered periods of fruit scarcity. The estimated fruit supply for the year was 106.3 kg.ha<sup>-1</sup>.

Table I. Behavioural categories and definitions used in the study.

Behaviour	Definition
Resting	To be inactive, either lying, sitting, or in standing postures. Included in this category time spent in vocalization, defecation, urination, and self-grooming.
Feeding	To handle, process, consume or actively search plant food items or animal prey.
Social interactions	To be engaged in grooming, playing, mating or aggressive behaviours involvig one or more partners. Included in this category was time spent scent marking.
Moving	Engaged in active spatial displacement not associated with social interactions or feeding.

**Table II. Comparison of the daily distance traveled and the home range of the woolly monkeys in four different studies.**

	DPL m	SD	Minimum distance	Maximum distance	Home range (ha)	N(days)	Group size
Caparú (1984-1987) <sup>1</sup>	2880	836	2016	3582	760	60	24
Tinigua <sup>2</sup>	2001	431	667	4145	200	149	14-30
Yasuni <sup>3</sup>	1792	247			124	~60	24
Yasuni <sup>3</sup>	1878	395			108	~43	23
Caparú (2004-2005) <sup>4</sup>	2503	778	1125	4375	>440	53	~ 41

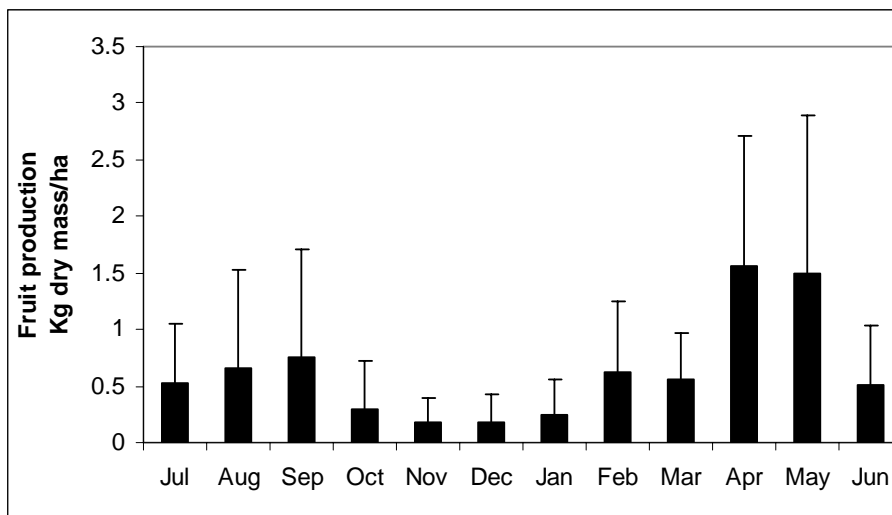
<sup>1</sup> Defler 1996<sup>2</sup> Stevenson 2006<sup>3</sup> Di Fiore 2003<sup>4</sup> This study

Figure 1. Monthly variation of fruit supply during July 2004 - June 2005 at Caparú Biological Station, Colombia. Error bars represent one standard deviation. As sample units, we used phenological transects, 400 m each. *A posteriori* Tukey tests revealed significant differences only between two discrete groups: 1) April and May and 2) the remaining months.

## Daily Path Length

Average daily distance traveled was higher for the largest group, however no significant difference was detected, perhaps due to the few data recorded for the small group (SC: 2503 m  $\pm$  778 SD,  $n = 50$ ; FCB: 2125 m  $\pm$  637 SD,  $n = 6$ ;  $U = 110$ ,  $p = 0.26$ ). Daily path length of SC group varied significantly throughout the year and fruit production was not a significant predictor of monthly mean DPL ( $F_{(1, 10)} = 3.45$ ,  $r^2 = 0.26$ ,  $p = 0.09$ ). The daily path length for the groups at Caparú was higher compared to estimates reported at sites with higher fruit production (Table II).



## Home Range

Using instantaneous samples, the SC group used 334 ha and individuals of this group were observed in a total of 440 ha during the study. Using the minimum convex polygon method (Mohr, 1974), we obtained an estimate of 596 ha. However, these seem to be underestimates of the real home range area, since a cumulative curve of number of new 1 ha quadrants entered per hour of observation does not reach a clear asymptote (Figure 2), showing that sample size was insufficient to determine the total home range.

## Activity Patterns

We observed woolly monkeys resting in 50% of the monthly records ( $SD = 6.2$ ), moving in 29.5% ( $SD = 0.8$ ), feeding in 18% ( $SD = 3.5$ ) and engaged in social behaviours in 2.5% ( $SD = 1.0$ ). Activity patterns varied throughout the year ( $G = 125.7$ ,  $p < 0.0001$ , d.f. = 33). Both monthly estimates of fruit supply and the percentage of time spend feeding were associated with feeding time ( $r^2 = 0.53$ ,  $p = 0.007$ ,  $n = 12$ ), since they feed more frequently in periods of fruit abundance. Activity patterns also varied significantly among the different age/sex categories ( $G = 14.2$ ,  $p = 0.1$ , d.f. = 9). The males and the females with dependant young showed the highest frequencies in resting activities, while juveniles spent more time in social interactions (typically playing) than other age/sex classes.

## Diet

Woolly monkeys fed on fruits more frequently (69% of monthly feeding observation  $SD = 22.9$ ) than leaves (16%,  $SD = 7.2$ ) and arthropods (13%,  $SD = 5.9$ ). In only 2% ( $SD = 2$ ) of the feeding cases individuals consumed other items (e.g., frogs, flowers, lichens, and water taken from bromeliads). These percentages vary significantly throughout the year ( $G = 372$ ,  $p < 0.01$ , d.f. = 33,  $n = 804$  feeding observations). For example in November, during the season of fruit scarcity, leaf and arthropod feeding surpass fruit feeding (Figure 3). The composition of the diet did not vary significantly among the different categories of sex and age ( $G = 14$ ,  $p = 0.12$ , d.f. = 9). However juveniles show a slight tendency to eat more arthropods and females with dependant young tend to eat the least amount of fruits.

We found a positive relationship between the frequency of fruit feeding (number of instantaneous observations per month) and fruit production (fruit mass.ha<sup>-1</sup>.mo<sup>-1</sup>) ( $F_{(1, 10)} = 8.54$ ,  $p = 0.02$ ,  $r^2 = 0.46$ ). We found a slightly negative relationship between fruit production (fruit mass.ha<sup>-1</sup>.mo<sup>-1</sup>) and arthropod feeding (number of instantaneous observations in arthropod feeding per month) ( $F_{(1, 10)} = 2.74$ ,  $p = 0.12$ ,  $r^2 = 0.21$ ). A similar negative relationship was found between fruit production and the consumption of other minor items ( $F_{(1, 10)} = 5.0$ ,  $p = 0.12$ ,  $r^2 = 0.22$ ). The consumption of leaves peaked just before the season of fruit scarcity, thus, fruit production was not a good predictor of leaf eating ( $F_{(1, 10)} = 0.17$ ,  $p = 0.69$ ,  $r^2 = 0.02$ ; Figure 3).

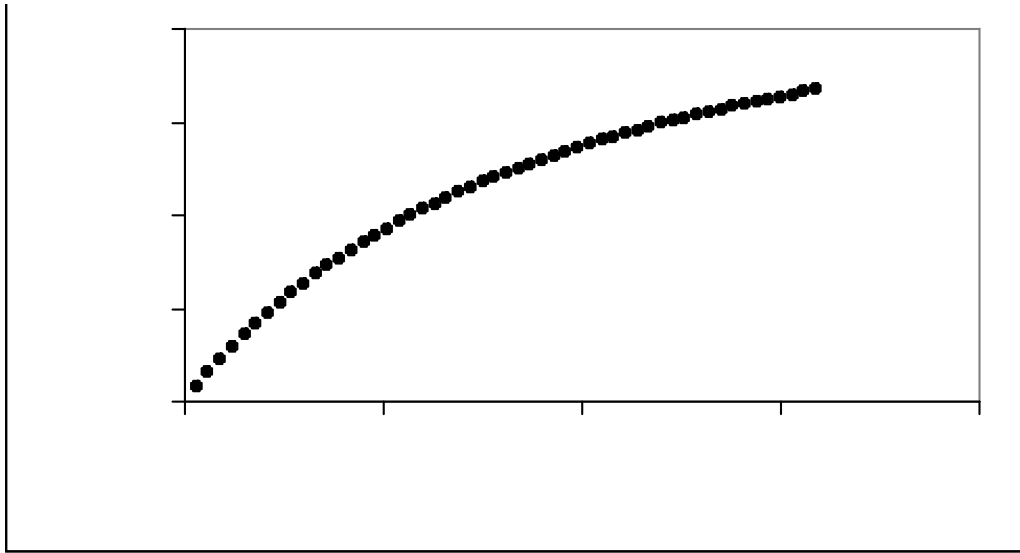


Figure 2. Cumulative number of hectares used by the woolly monkeys as a function of sampling time ( $n = 636$  h). Data obtained using instantaneous location samples taken each half hour at Caparú, Colombia (calculated from 50 simulations using the EstimateS software; Colwell 2005).

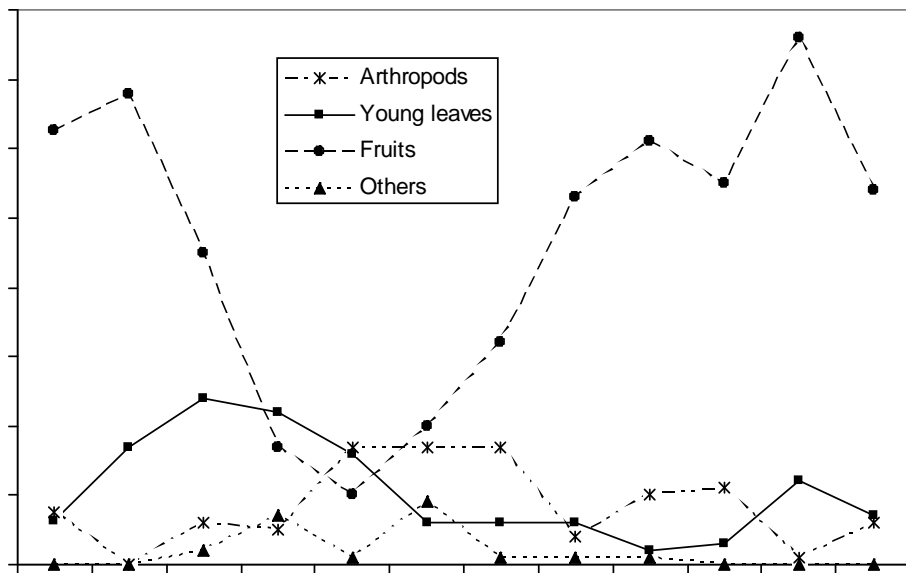


Figure 3. Annual variation in the amount of instantaneous samples registered in different feeding categories used by woolly monkeys in Caparú Biological Station, Colombia.

## DISCUSSION

### Fruit Production

Similar to the results from this study, Defler (1996) and Palacios and Rodríguez (2001) reported a peak in fruit production between April and May in Caparú. Annual fruit production estimated in Caparú ( $106 \text{ kg} \cdot \text{ha}^{-1}$ ) was very low compared to Tinigua National Park ( $930 \text{ kg} \cdot \text{ha}^{-1}$ ,  $\text{SD} = 105$ ; Stevenson, 2004), where fruit supply was determined during three years using the same methodology. This result supports the idea that the low fruit production in Caparú may be due to the low soil fertility and high rainfall, typical of Amazonian black water basins (Defler, 1996). The soils at Tinigua National Park, in comparison, are associated with younger sediments and the basins of white water rivers (Botero, 1998). Such differences may also explain the differences observed in woolly monkey home range size and population densities between Caparú and Tinigua (Palacios and Rodríguez, 2001). The results of this study confirm large differences in fruit production, and confirm the strong correlation observed fruit production and the abundance of primate populations (Stevenson, 2001).

**Table III. Percentages of time spent on each category of activity of woolly monkeys in five different studies.**

	Movement	Rest	Feeding	Social	Method
Yasuní <sup>1</sup>	34.5	23.2	36.2	4.7	Scan
Caparú (1985-1987) <sup>2</sup>	38.8	29.9	25.8	5.5	Scan
Caparú (2004-2005) <sup>3</sup>	29.5	50	18	2.5	Focal
Tinigua <sup>4</sup>	26	35	36	3	Focal
Yasuní <sup>5</sup>	37	23	37	3	Focal

<sup>1</sup> Di Fiore and Rodman 2001

<sup>2</sup> Defler 1995

<sup>3</sup> This study

<sup>4</sup> Stevenson 2006

<sup>5</sup> Dew 2001

### Fruit Production and Patterns of Habitat Use

Daily distance traveled and home range of fugivorous primates may be positively correlated to group size and negatively correlated to fruit supply (Defler, 1995, 1996; Palacios and Rodríguez, 2001; Stevenson, 2006). Despite the large variation in daily path length and home range size found for the groups of woolly monkeys in Caparú, they tend to travel longer distances and to have larger home ranges than in Tinigua National Park (Table II), supporting the hypothesis that groups in less productive sites need to travel more to get comparable resources. Similar results were found in previous studies, suggesting that larger groups of frugivorous primates need to travel longer distances in order to fulfill their energetic requirements (Janson and Goldsmith, 1995; Stevenson, 2006). Our comparison between the two groups also suggests that group size affects daily path length. However, the differences

were not significant, which may be due to the small sample size for the small group. Overall, the results of this study support the hypothesis that average daily path length and home range size are negatively correlated to fruit supply.

Stevenson (2006) reported that woolly monkeys spend a great part of the day resting during periods of fruit scarcity, reducing daily path length. In contrast, in this study daily path length was negatively correlated with fruit production ( $F_{(1, 10)} = 3.45$ ,  $p = 0.09$ ,  $r^2 = 0.26$ ), suggesting that woolly monkeys follow a different strategy in Caparú. We believe that the relationship between daily path length and fruit supply may depend not only on overall fruit production, but also, on feeding patch characteristics (i.e., size and density of patches). We found that fruit patches (i.e., individual fruiting trees) in Tinigua were more productive than in Caparú. Additionally the average fruit crop size per tree in Tinigua did not vary much between months with high supply ( $2.1 \text{ kg} \pm 5.8 \text{ SD}$ ) and months of fruit scarcity ( $2.6 \text{ kg} \pm 10.3 \text{ SD}$ ) (Stevenson, 2004). In contrast, at Caparú fruit crop size during the period of fruit abundance was more productive ( $1.3 \text{ kg} \pm 2.0 \text{ SD}$ ) than in periods of fruit scarcity ( $0.8 \text{ kg} \pm 1.4 \text{ SD}$  between June and February). Therefore, the density of fruiting trees (32 vs. 2 fruiting plants per km) determines the difference between the months of high and low fruit supply in Tinigua and not the average size of the crop. At Caparú, the season of scarcity exhibits both low average crop production and low density of fruiting trees (7 vs. 14 plants per km in abundance period), and average crop size is considerably lower than during the season of high productivity. An explanation for why woolly monkeys at Caparú move more during the season of fruit scarcity may be that the food in one tree is not sufficient to satisfy feeding requirements. In support, we found that the average time length of feeding bouts was shorter in the season of fruit scarcity compared to the season of fruit abundance ( $4.7 \text{ min} \pm 0.5 \text{ SD}$  vs.  $9.4 \text{ min} \pm 5.3 \text{ SD}$ ), suggesting that they must visit several trees each day. Given that the distance between trees is far, woolly monkeys at Caparú must travel more during scarcity periods.

Woolly monkeys at Tinigua can accumulate energy (as fat) during the season of high productivity by visiting several productive trees, and then they minimize their energetic expenditure during the scarcity season (Stevenson *et al.*, 1994). A similar seasonal fattening process was reported by Peres (1991 & 1994b), Di Fiore & Rodman (2001) and Di Fiore (2003). Di Fiore (2003) found no relation between the daily path length and the consumption of ripe fruits, even though he found a significant positive association between insect abundance and moving time. His results suggest that ranging behaviour in Yasuní may be more immediately tied to foraging for insect prey, than to foraging for ripe fruit. The results from Di Fiore (2003) and this study do not support the hypothesis that woolly monkeys are energy minimizers in all ecological settings.

## Effects of Fruit Supply on Patterns of Activity and Diet

The strong variation in proportions of different dietary items throughout time (Figure 3) was partially explained by the estimates of fruit production ( $F = 11.3$ ,  $p = 0.007$ ,  $r^2 = 0.53$ ). An increase in leaf consumption was observed during the season of fruit scarcity (September-October), the same period for which Defler and Defler (1996) and Palacios and Rodríguez (2001) reported a peak in the production of young leaves. During the second part of the season of fruit scarcity (November-February) we observed an increase in arthropod

consumption. These results suggest a strategy in which woolly monkeys consume more available non-fruit dietary items during periods of fruit scarcity (Stevenson *et al.*, 1994). This defines woolly monkeys as fruit-eaters that vary the composition of their diet depending mainly on fruit production, and secondarily on the abundance of other resources. Both Stevenson *et al.* (1994) and Di Fiore and Rodman (2001) found that woolly monkeys consume more arthropods when the fruit supply is high, suggesting that the availability of the arthropods they feed upon is seasonal and positively correlated with fruit abundance. Information on arthropod availability would be necessary to assess the importance of insects in the diet of woolly monkeys.

Stevenson *et al.* (1994) reported a strong correlation between fruit production and the amount of time feeding by woolly monkeys ( $p = 0.015$ ,  $r^2 = 0.46$ ). However, Di Fiore (2004) reported a low correlation between these variables. An explanation for this difference is that the variation of fruit supply over time is much lower in Yasuní than at Caparú or Tinigua. Woolly monkeys at Yasuní, unlike Caparú and Tinigua, are not obliged to have particular strategies to adjust to periods of fruit scarcity (Di Fiore, 2004).

We used a very similar methodology as the one used in Tinigua (Stevenson, 2006), therefore the differences between these studies can be attributed to the actual behaviour of groups under study (Tables III and IV). In Tinigua, woolly monkeys spend more time feeding, less time resting, and invest more time feeding on arthropods than in Caparú. All these differences may be associated with differences in food supply. Woolly monkeys at Caparú have to invest less time feeding and more time searching for food, because there are fewer resources such as fruits, and we also might expect fewer insects in places with low soil fertility (Kito *et al.*, 1996).

## Methodological Effects

The activity patterns and diet composition of the woolly monkeys reported in different studies showed considerable differences (Tables III and IV). The first source of apparent difference among studies is the definition used for each category of behaviour. Not all studies used the same categories, or defined them in the same way. This is particularly critical when arthropod feeding is estimated, since behaviors like active search of arthropods in leaves are classified by some authors as foraging (Di Fiore & Rodman, 2001; Dew, 2005) and as feeding by others (Stevenson, 2006; this study). In other cases, the inspection of leaves was not considered foraging or feeding (Peres 1994). Therefore, some differences in activity budgets and diet may result from the use of dissimilar categories, but for comparative purposes we included foraging and feeding as one category.

Comparing the two studies carried out at Caparú, we see that Defler's (1995) estimates of movement, feeding, social activities, and fruit feeding were considerably higher for this study. Defler's calculations for resting and arthropod feeding are much lower. These differences may be related to the use of different methodologies. In this study we used instantaneous samplings on focal individuals, while Defler used scan sampling. According to Altmann (1974); Harcourt and Stewart (1984); Martin and Bateson (1993), and Stevenson and Quiñones (2004), the use of scan sampling to record behaviour in large groups, where it is impossible to observe the whole group during a single scan, underestimates less conspicuous behaviours and overestimates the more evident ones. Therefore, movement, feeding on fruit

(especially when parts of the fruits eaten may fall to the ground), and conspicuous social behaviours may be overestimated by this method, and this is exactly the type of difference found for the estimates in Caparú. The scan method systematically disregards a portion of the group members on each scan and it is more probable to ignore a resting monkey in the closed canopy than one moving along branches. In contrast, registering activity using instantaneous sampling on a focal individual avoids this problem, since the activity noted depends exclusively on the activity done by the focal monkey at a particular instant, and not on the crypticity of the behaviour. Therefore, the differences between Defler's (1995) data and those reported in this study may be due primarily to methodological differences. Furthermore, Di Fiore and Rodman (2001) also used the scan methodology and, as in Defler's study, movement, feeding, social activities and fruit feeding are more frequent than those reported in this study or by Stevenson (2006), who used instantaneous samplings on focal individuals. However, the comparison of data from Yasuni collected using scans (Di Fiore 2004) and focal sampling (Dew 2001), which were collected during the same time period, actually seem to argue that both methods provide comparable estimates.

**Table IV. Comparison of the diet composition (%) reported for woolly monkeys in six studies.**

	Fruits	Leaves	Arthropods	Others	Recording method
Caparú (1985-1987) <sup>1</sup>	84	11	5	< 1	Scan
Yasuní (1995-1996) <sup>2</sup>	77	8	9	6	Scan
Urucu River <sup>3</sup>	81	16	<0.1	3	Scan
Caparú (2004-2005) <sup>4</sup>	69	16	13	2	Focal
Yasuní (1995-1996) <sup>5</sup>	73	10	6	5	Focal
Tinigua <sup>6</sup>	59	13	25	3	Focal

<sup>1</sup> Defler & Defler 1996

<sup>2</sup> Di Fiore 2004

<sup>3</sup> Peres 1994

<sup>4</sup> This study

<sup>5</sup> Dew 2001, 2005

<sup>6</sup> Stevenson 2006

Fruit feeding is a more conspicuous behaviour than leaf feeding, which is in turn more conspicuous than arthropod feeding. Therefore, we expected that arthropod feeding would be underestimated in studies using scan sampling, and our comparison confirmed this pattern (Table IV). Studies carried out in Yasuní (Dew, 2005; Di Fiore, 2004) offer another possibility for comparing studies done at the same place with different methodologies. In these cases, fruit feeding was again more common when scans were used (Table IV). In fact, we found significant differences (Man-Whitney  $U = 9$ ,  $p = 0.025$ ,  $n = 6$ ) in the frequency of fruit feeding between studies that used scans and studies that used instantaneous samplings on focal individuals (Table IV). It is also possible that these discrepancies could be due to differences in the ecological conditions present when the studies were conducted. However, the inter-annual variation (1990, 1996, and 2000) in activity patterns in the Tinigua population was remarkably low (Stevenson, 2006).

The idea that scan sampling is biased against cryptic behaviours is not new. Martin and Bateson (1993) affirmed: “An obvious danger with scan samplings is that results will be biased because some individuals or some behaviour patterns are more conspicuous than others... Focal sampling is generally the most satisfactory approach to studying groups”. Harcourt and Stewart (1984) used the same argument to explain why feeding time reported in gorillas was so low in some investigations when compared to others. Stevenson and Quiñones (2004) collected data on activities and diet on the same group of woolly monkeys over the same period of time using scan sampling and focal sampling. They found that moving and social interactions were more frequent when scan sampling was used, and resting was more common when using focal sampling. In only one comparison we found that focal and scan sampling provided similar results, therefore it seems valid to state that, in general, these methods provide different estimates. Despite these results, many researchers use scan sampling, making direct comparisons difficult. We recommend the use of both continuous and instantaneous observations on focal individuals for recording behaviour of woolly monkeys and other animals that live in large groups and have differences in the detectability of behaviours.

### **Additional Potential Explanations for the Variations in Diet and Activity Patterns**

As we previously said, the activity patterns and diet composition of the woolly monkeys reported in different studies show considerable differences (Tables III and IV). In the previous section we exposed how these differences may be due to the use of different methodologies. However, there are other non exclusive explanations. According to Di Fiore & Rodman (2001) differences in body size between species or subspecies of woolly monkeys partially explain the variation in diet between studies. This hypothesis is difficult to test now since there is a limited data set on body weight of wild woolly monkeys (Fooden 1963, Peres 1994b).

Independently of size, it is possible that woolly monkeys have different activity patterns or different diet between sites. The activity patterns and diet of woolly monkeys may vary between sites since each woolly monkey population is subject to particular ecological pressures. Food quantity and quality, density of inter and intraspecific competitors, or differences in size may affect the activity patterns and diet. However, we believe that before finding elegant ecological explanations for the differences reported in the diet and activity patterns of wholly monkeys, we need to ask ourselves if differences actually exist, or if they reflect the use of dissimilar methodologies. We believe that it is very difficult to answer these questions based on the limited information available until now. Therefore, we recommend unifying methodologies before making ecological comparisons between sites. As Harcourt and Stewart (1984), Martin and Bateson (1993) and Stevenson and Quiñones (2004) advise, the use of continuous and instantaneous observations on focal individuals is an appropriate way to quantify the behavior of animals that live in large groups and have differences in detectability.

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*Chapter 10*

## **“HOW CLOSE SHOULD WE GET”– RESEARCHERS’ ROLE IN PREVENTING THE ANTHROPOZOONOTIC OUTBREAKS IN GROUPS OF FREE RANGING CHIMPANZEES AND GORILLAS**

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### **ABSTRACT**

Chimpanzees and gorillas are the closest relatives of humans living on the Earth. Due to this fact they are susceptible to most of human infectious diseases, but the outcome of infection is often very different than in humans.

Chimpanzees can be infected with the HIV virus, but they never develop the actual disease. Opposite situation happens with some other human viral diseases. Common Flu, Metapneumovirus or Respiratory Syncytial Virus, which in post-infant humans are rarely considered the serious diseases, have been recorded to be fatal when transmitted to Great Apes.

In various countries in Africa researchers have witnessed numerous outbreaks of infectious, mostly respiratory diseases in ape communities, which could be traced back to humans as the source. Often most of the ape group would be affected with mortality reaching over 20%.

Gorillas in Rwanda are visited daily by the KARISOKE research team and by the trackers and tourists, which on average adds up to 2000 human visits to each gorilla per year. The numbers of respiratory cases monitored/treated by the Mountain Gorilla Veterinary Program team are at the very top on the list of the infectious diseases affecting gorillas in Virunga NP.

According to the field experience from 3 East African countries, researchers can play positive or negative, but always significant role in following the preventive visitation rules themselves and assisting the National Park offices in doing the same for the tourist visits.

## COMMENTARY

In recent years there has been an increase in awareness of disease transmission between humans and apes in their natural environment. Research programs in African forests include veterinary findings in their methodology. Many such research programs have changed or are currently changing the ape viewing policies that are applied in the field. In some sites (Gombe, Virungas) researchers and trackers undergo regular health checks, vaccination and quarantine in order to protect apes from potential human disease outbreaks, which can affect most and kill up to 20% of the ape group[1,4,6,8,13] Jane Goodall Institute (JGI) supervises the basic program in Gombe and MGVP (Mountain Gorilla Veterinary Program) overlooks the staff health through its well developed Employee Health Program in Rwanda and Congo<sup>9,16</sup>. In other sites at least some of these rules are applied.

Gombe Stream Research Center JGI (GSRC) was one of the first to admit and practically address the problem that occurred in Gombe in the 90s and in the year 2000 substantial changes in protocols have been introduced. Changes included increasing the minimal distance between humans and chimps in the forest routine health screening and basic hygiene training for the staff and quarantine for the incoming researchers. Also the artificial food provision of bananas, which had been administered to chimpanzees daily since early 60s, was abandoned entirely **by** the end of 2000.

GSRC also became more involved in monitoring and reporting about the tourist activities in the Park. [2,8,12] . This task was easy to introduce because research assistants are almost always present with the group of chimpanzees when the tourists arrive. Tourism in Tanzania is under control of TANAPA (Tanzanian National Parks), but their good long-term relationship with and appreciation of GSRC allowed the Center to become the advisor in the issues of disease risk to chimpanzees from tourism. The situation was relatively easy to control prior to 2005 because tourists were few and there was no permanent tourist lodge present in the forest. The number of respiratory outbreaks and resulting deaths **considerably decreased after the new protocols were established**.

General TANAPA attitude about the researchers' involvement in tourist management was always positive, but the situation became more complicated with the additional pressure due to a tourist company which has built the lodge inside the Park.

Tourist companies bring money to the Government and therefore have an influence concerning the areas they operate in. For most tour operators, the satisfied tourists – whatever the cost on wildlife and forest, are the main concern and because tourists often desire the close and prolonged contact with apes, the companies will break the rules if not supervised.

TANAPA authorities are not often present in the forest and therefore are often unaware of rules being broken in order to please the tourists. Researchers who spend all day with the groups of chimpanzees have a much better chance to observe the situation, but some of them are reluctant to report mistakes in order to keep good relationships with Wildlife authorities. Also, to point out other peoples' mistakes constructively, researchers should have the opinion of strictly following the rules themselves.

There are valid points why following rules makes the field work more difficult and the flow of data interrupted. In Gombe the "BO" (Bad Observation) symbol is used for the data sheets when chimpanzee actions cannot be clearly seen from the regulated 7 meters distance.

Researchers and assistants have been informed that they are not to break the distance rule in order to get better observation, using the BO mark instead.

In Mahale, at least until the year 2007, young researchers understood that if they cannot have the good observation from 7 meters (due to thick vegetation, big group of chimps present or a difficult terrain) they should move closer, sometimes **less than 1** meter from animals. This was not done with negative intentions, but the combination of numerous factors.

One important factor is how and by whom the new researchers are trained in their forest work. It is understandable that for most Research Institutes, the uninterrupted flow of data, best collected within the same methodology over decades, is the main concern. This situation combined with still inefficient scientific proof about the anthroponozoonotic disease transmission to apes causes the health rules often become the secondary issue.

Secondly, the field researchers are often overwhelmed to collect their data within their time frame. If the young PhD student approaches the final weeks of the field work and does not seem to have enough data for the final paper, he or she would try to get more observation even for the price of rules being broken.

A third factor is a big problem in Gombe, Mahale and Virungas. Throughout the decades of habitation within very close contact (including food provision and sometimes even encouraging the physical contact) the apes became over-habituated and many of them do not mind or even seek the proximity of people. In this situation not only do researchers have to follow the proper protocols not get too close, but also react immediately when the animals approach themselves.

Another important issue is the awareness of the anthroponozoonotic disease transmission among behavioral researchers and even among veterinarians **working in Parks**.

Unfortunately, very few cases of forest outbreaks involve a veterinary team for investigation and the means of sample transport from the remote forest within short time are not always available. **Therefore** the number of cases where the disease transmission was proved by laboratory findings is very limited due to field logistics.

**Some** veterinary teams (including the long term MGVP efforts in Rwanda, Uganda and Congo and the recent Max Planck Institute work in Western Africa) are working hard to increase this evidence, the epidemiological facts suggest that many, if not most of the recent serious outbreaks in habituated free ranging apes, are of the human origin[3,8,13,14].

The fact of anthroponozoonotic disease transmission to captive primates has been generally accepted for many years. Primate colonies in Zoos, Research Centers and Rehabilitation Centers are under strict health management, which covers also all the staff in contact with animals. If the captive chimps and gorillas are susceptible to the multiple human bacteria, viruses and parasites, it means that biologically they are the potential host of these pathogens. In cage or in the forest, if apes come to contact with the person who carries infection (and contact in forest is **often** physically closer than it ever happens with the captive chimps and gorillas), they can fall ill.

And because of their naive immune status towards the foreign pathogens, disease emerging from this contact can be much more serious in apes than **it is** in the human host.

The epidemiological patterns (morbidity, rate of transmission, mortality, age groups affected, etc) of the disease outbreaks observed in free-ranging apes vary and at least two marginal types can be identified.

Initially there are mild outbreaks with morbidity of 5-10%, affecting mostly young/sub adult (but usually not the nursing infants) and old/otherwise immunosuppressed animals, with mild to moderate symptoms. Such outbreaks are observed every 1-2 years between two chimp communities in Gombe (*pers. observation*)<sup>8</sup> and more frequently in Mahale, where in 18 months 2 such outbreaks were witnessed (November 2006 and October 2007) in only one habituated community of chimps. **Similar mild respiratory infections are observed among Virunga gorilla groups quite regularly and without negative consequences for the affected individuals.**

Another category would include the markedly more severe outbreaks with 50-100% morbidity, affecting males and infants most severely and with mortality reaching as **high** as 20% of the community [1,4,6,13].

A **possible** scientific explanation for the differences between these outbreaks is that in the first group the pathogen is local and the good immunity protects most of the apes from the serious symptoms. The **new-borns** are probably protected by the mother's antibodies which disappeared in older animals.

The second category of outbreak is **likely** caused by the introduced (likely by humans) foreign pathogen to the immunologically naïve community of apes.

With global human travel becoming more frequent, research has been conducted in USA and Europe indicating that airplanes can be the frequent mean of infectious disease transmission[15,16,17].

It was summarized by Zitter and Mazonson (Am Med Association, 2002)

*“Aircraft cabins may be high risk environments for transmission of infectious diseases. Space confinement, limited ventilation, prolonged exposure times and recirculating air, all common to air travel, have been demonstrated to be risk factors for transmission of upper respiratory tract infections in other settings”.*

Most of researchers and tourists arrive to the ape sites after at least one international flight, during which they were likely exposed to high risk of respiratory infection from some of few hundred passengers they shared the aircraft with. Within few days from their flight, sometimes before they show any symptoms, the travelers can already shed the respiratory virus. At the same time tourists are in close contact with the guides, lodge managers and the other tourists. They also pay daily, sometimes multiple visits to the habituated **apes in a forest.**

This combination of evidence seems strong enough reason to make antropozoonotic disease transmission to free-ranging habituated apes highly possible.

Added to the fact of an increasing mortality associated with respiratory outbreaks among habituated apes and laboratory findings from Mountain Gorilla Veterinary Program[7,9] and Kondgen [4] this means of global transmission becomes highly probable .

This fact has gradually been accepted by increasing number of ape researchers over the recent years and many forest sites policies have been changed, including the distances of observation, health management of staff and quarantine. In **three sites**: Tai, Mahale and PNVi DRC surgical masks were introduced for everyone in proximity of 100 meters from **apes** (unfortunately this rule is impossible to apply when **apes** visit the camps located within their range or when people walking in forest are not aware that **apes** are nearby)[3,4,8,10,13,14]

Surgical masks decrease the risk of respiratory disease transfer, but they should be of right quality and regularly replaced. Another potential problem observed in Mahale was that sometimes people understood that if they wear masks they are entirely safe for the chimps; therefore they abandoned the general health rules like distances and quarantine. According to extensive medical research on the various masks efficiency, surgical masks **alone** do not protect 100% of pathogen transmission.

At the same time they decrease the risk considerably especially when combined with at least two main health rules to be observed at all times: only healthy people should visit the apes and the distance of observation should be kept at minimal 7 meters (*F.Leendertz, pers. Communication*).

Even at locations where the rules are official and well established their implementation is often not efficient.

The rule acceptance, understanding and observation are generally better among researchers, than it is among the guides and managers of tourist companies [8,11,14].

The recent research on tourist rules efficiency conducted in Bwindi by Sandbrook<sup>11</sup> confirmed the long-term observations from Mahale, Gombe and Virunga Volcanoes NP in Rwanda. In all these forests health rules have been made official for many years (Gombe and Mahale since 2001, Virungas and Bwindi since 1999-2000) but in all these places their **practical** implementation is far behind the official policies.

In Rwanda Park authorities put substantial effort to the guide training and thank to the ongoing efforts of MGVP, there is considerable increase of the anthroponozoonotic disease awareness among the Park staff. On the other hand **increasingly** numerous tourists and extensively over-habituated gorillas often make the rule implementation **very difficult**. For reduced disease potential the researchers, apart from understanding and following health protocols themselves, should be involved in advising and reporting to the authorities about the tourism management around the chimps and gorillas.

From experience in Tanzania, Rwanda and Uganda, Park authorities are usually appreciative about such feedback, especially from the long-term research centers with good experience and international reputation.

Park authorities in many forests face the on-going problem of not receiving the current and honest updates from the field. Researchers are required to submit the regular (usually yearly) reports on their main activities and to immediately inform the Park management about the serious problems among animals. Still it does not provide the authorities (who are usually based in some distance and do not visit apes regularly) with the daily account of human activities around habituated apes.

In most places tourist companies are not required to report about their field activities at all. In theory they are required to follow the official rules and during the scheduled visits the Park Guide should accompany the quests, **but these regulations are frequently broken**. Also because in Mahale, Gombe and Bwindi some camps are located within the chimpanzee or gorilla territory, the un-scheduled contact without control is possible and happens on regular base (*pers. observation in all three sites*).

In short, if Park authorities are not aware of the current problem, they cannot react to it.



Most of them would probably appreciate the agreement with researchers about the current information supply, providing that it is done without threatening and pushing Park Authorities towards certain actions they do not want or cannot undertake.

If such MOU could be signed between researchers and Park Authorities at all sites, it has the potential to significantly decrease the number of life threatening disease outbreaks among the free ranging habituated chimps and gorillas in Africa.

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# INDEX

## A

- accidental, 79
- accidents, 84
- accountability, 151
- accounting, 139, 151
- accuracy, 155, 156
- acid, 33, 173
- acoustic, 3, 8, 9, 12, 13, 15, 18, 23, 24, 25, 26, 28
- acoustic signals, 3, 8, 13, 15, 18
- ACTH, viii, 30, 33, 35, 36, 38, 41, 43, 44, 45, 46, 50
- activation, 30
- acute, viii, 29, 30, 31, 32, 34, 40, 42, 43, 44, 45, 46
- acute stress, 31, 32, 40, 42, 44, 45, 46
- adaptation, 30, 57, 68, 119, 134, 135
- administration, viii, 29, 32, 33, 37, 38, 39, 40, 41, 42, 44, 45, 46
- adolescence, 117, 118
- adolescents, 77, 85, 86, 87
- adrenal cortex, 30, 31, 35, 36, 39, 40, 43, 44, 45, 46, 48, 49, 51
- adrenocorticotrophic hormone, 30
- adult, 7, 18, 23, 27, 31, 33, 57, 58, 63, 76, 78, 79, 81, 82, 83, 84, 85, 89, 92, 113, 118, 120, 122, 127, 131, 132, 134, 142, 144, 145, 151, 155, 166, 173, 174, 190
- adulthood, 18, 78, 117, 118
- adults, x, 9, 43, 50, 57, 59, 65, 77, 78, 85, 86, 129, 131, 132, 144, 147
- advertisement, 17
- advertising, 4
- Africa, xi, 83, 88, 91, 119, 122, 187, 189, 192
- afternoon, viii, 30, 34, 36, 38, 40, 43, 44, 45, 46, 143
- agent, 151
- aggression, 2, 24, 76, 81, 84, 90, 134, 140, 145, 150
- aging, vii, viii, 29, 30, 35, 36, 43, 44, 45, 46, 47, 48, 49, 50, 51, 118
- aging process, 50
- agriculture, x, 113, 121
- aid, vii, x, 1, 59, 67, 129, 135
- aiding, 138
- air, 13, 76, 122, 123, 132, 190, 193
- air travel, 190, 193
- aliens, 97
- ALL, 70
- alternative, xi, 16, 17, 62, 100, 103, 105, 171
- alternatives, 103, 154
- alters, 50
- Alzheimer disease, 50
- Amazon, 15, 19, 183
- Amazonian, 20, 178, 183
- amino acid, 33
- amplitude, 15, 44, 48
- AMS, 48
- analog, 167
- analysis of variance, 33
- anatomy, 76, 80, 115
- Andes, 171, 184
- androgens, 48
- animal communication, 8, 20, 24
- animal models, 155
- animal welfare, 18, 21, 23
- animals, vii, viii, x, 1, 2, 8, 12, 17, 18, 25, 30, 31, 32, 33, 34, 36, 37, 38, 39, 40, 42, 43, 44, 45, 46, 56, 57, 76, 79, 100, 111, 113, 114, 115, 116, 117, 118, 119, 120, 121, 123, 125, 129, 132, 134, 136, 140, 147, 151, 153, 154, 155, 156, 157, 159, 160, 161, 162, 163, 165, 170, 172, 173, 182, 189, 190, 191
- ANOVA, 33
- antagonist, 45
- anterior pituitary, 30, 36, 44, 49
- anthropological, 117

anthropology, 115  
 anticoagulant, 33  
 antioxidant, 31, 48, 49  
 ants, 119, 121, 122, 124, 125  
 appendix, 66  
 application, 18, 32, 55, 152, 183  
 arginine, viii, 29, 45, 49, 51  
 argument, viii, ix, 53, 68, 69, 73, 96, 103, 105, 116, 120, 182  
 arrest, 116  
 arthropods, xi, 171, 172, 174, 176, 180  
 ash, 77  
 Asia, 114, 130, 131, 152  
 Asian, 23  
 assessment, 9, 18, 21, 125, 170  
 assessment procedures, 18  
 assumptions, ix, x, 53, 69, 115, 129  
 astrocytes, 123, 127  
 attitudes, 120  
 attribution, 27  
 autonomic nervous system, 47  
 autopsy, 81  
 availability, 116, 134, 180, 185  
 avoidance, 135  
 awareness, 69, 136, 167, 188, 189, 191

## B

babbling, 9  
 babies, 9  
 bacteria, 189  
 bananas, 188  
 Bangladesh, 131, 149  
 barrier, 149  
 basic research, 18  
 batteries, 13  
 battery, 14  
 behavior, ix, x, 19, 23, 24, 27, 54, 76, 79, 80, 83, 85, 86, 90, 91, 92, 95, 101, 113, 116, 119, 121, 124, 126, 129, 159, 165, 167, 168, 169, 182, 183  
 behaviours, xi, 10, 23, 57, 62, 68, 69, 107, 171, 172, 174, 176, 180, 182  
 beliefs, 96  
 benefits, 12, 73, 135, 157  
 bias, 18, 98, 128  
 biochemistry, x, 113, 121  
 biodiversity, 17  
 biological rhythms, 31  
 biomarker, 50  
 bipedal, 68, 84, 114  
 birds, 116, 118, 119, 120, 127  
 birth, 60, 91  
 births, 85

bleeding, 32  
 blocks, 163, 164  
 blood, 30, 32, 33, 36, 121  
 blood flow, 121  
 body shape, 84, 92  
 body size, 10, 22, 76, 79, 80, 81, 89, 92, 116, 172, 182, 184  
 body weight, 8, 23, 24, 32, 79, 87, 89, 91, 182  
 bonding, ix, 73, 75, 76, 79, 80, 89  
 bonds, 58, 68, 134  
 booms, 132  
 boredom, 135  
 Borneo, 131, 147  
 boys, 80, 126  
 brain, 46, 81, 86, 116, 119, 120, 121, 122, 126, 127  
 brain development, 116  
 brain growth, 119  
 brain size, 81, 116, 119, 122  
 Brazil, 1, 25  
 breakdown, 76  
 breeding, 78, 85, 91, 131  
 broad spectrum, 54  
 by-products, 118

## C

calorie, 89  
 Cameroon, 110  
 Canada, 20  
 candidates, 18, 100, 107, 121, 133  
 capacitance, 12  
 carbon, 85, 93  
 case study, 99  
 catecholamine, 46  
 catecholamines, 50  
 categorization, 61, 154, 169, 170  
 category a, 79  
 category b, 104  
 cattle, 33  
 cave, 86  
 cell, 45, 116, 123  
 Central Asia, 114  
 central nervous system, 19, 30, 51  
 cerebral cortex, 127  
 child abuse, 120  
 childhood, 67, 86, 91, 117, 118, 119, 120, 125  
 children, 55, 57, 58, 65, 67, 68, 69, 72, 73, 96, 100, 101, 102, 118, 119, 120, 122, 124, 155, 157, 167, 168  
 chimneys, 78  
 chimpanzee, 56, 73, 81, 83, 87, 88, 93, 106, 152, 164, 166, 168, 170, 188, 191, 192

- 
- chimpanzees, vi, xi, 85, 88, 90, 109, 110, 111, 136, 151, 166, 187  
 China, 91, 130, 131, 148  
 chromosome, 80, 88  
 circadian rhythm, vii, viii, 29, 30, 31, 33, 38, 40, 43, 44, 45, 46, 48, 51  
 circadian rhythmicity, 31, 44, 51  
 circadian rhythms, viii, 29, 30, 31, 38, 44, 46, 48, 51  
 CITES, 132  
 classical, 136  
 classical conditioning, 136  
 classification, 2, 63, 155, 168  
 clay, 67, 78  
 cleaning, 142, 144  
 close relationships, 46  
 Co, 21, 24, 25, 51, 93, 183, 184  
 coding, 28, 49, 114  
 cognition, 12, 19, 22, 27, 28, 50, 55, 56, 58, 59, 66, 72, 73, 74, 92, 98, 119, 121, 135, 149, 155, 157, 165, 169, 170  
 cognitive abilities, vii, ix, x, 96, 129, 133, 135, 140, 149  
 cognitive capacities, vii, x, 73, 153, 168  
 cognitive capacity, 165  
 cognitive development, 69, 74, 134, 147, 149  
 cognitive function, 31  
 cognitive performance, vii, x, 153, 157  
 cognitive process, 153  
 cognitive research, 60  
 cognitive tasks, 55, 56  
 cohesion, x, 58, 129  
 coil, 13  
 Colombia, xi, 24, 26, 171, 172, 175, 177, 183, 184, 185  
 colors, 121, 161, 162, 163, 165  
 communication, vii, 1, 2, 4, 6, 7, 8, 10, 12, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 54, 59, 61, 62, 65, 67, 68, 72, 73, 81  
 communication systems, vii, 1, 8  
 communicative intent, 66  
 communities, xi, 187, 190, 192  
 community, 16, 92, 97, 130, 173, 190  
 community support, 130  
 competence, 55, 67, 73, 155, 165  
 competition, 21, 22, 75, 76, 79, 81, 85, 87, 88, 89, 91, 92, 184  
 complement, 172  
 complexity, 56, 60, 96, 99, 101, 103, 107, 115, 121, 125  
 components, 108  
 composition, ix, 75, 77, 85, 172, 174, 176, 180  
 comprehension, 10, 73  
 computer software, 15, 155  
 concentration, 34, 35, 36, 37, 40, 41, 42, 43  
 conception, 124  
 concrete, 138  
 confinement, 132, 190  
 conflict, 57  
 conjecture, 88  
 consensus, 80  
 conservation, 18, 20, 24, 25, 26, 27, 130, 131, 132, 151, 192, 193  
 consolidation, 47  
 constraints, ix, 17, 95, 106, 108, 185  
 construction, 119, 120  
 consumption, 176, 179  
 contiguity, 156, 161, 168, 169  
 continuity, 56  
 control, 9, 14, 40, 42, 55, 64, 65, 69, 119, 155, 156, 159, 167, 169, 188, 191  
 control group, 55  
 convergence, 103  
 conversion, 131  
 convex, 173, 176  
 cooling, 84  
 copulation, 88, 143  
 correlation, 90, 178, 180  
 cortex, 30, 31, 35, 36, 39, 40, 43, 44, 45, 46, 48, 49, 51, 116  
 corticosteroids, 30, 48, 50  
 corticosterone, 30, 50, 51  
 corticotropin, viii, 29, 49, 52  
 cortisol, viii, 30, 34, 35, 37, 39, 40, 41, 42, 43, 46, 47, 48, 49, 52  
 costs, 184  
 Côte d'Ivoire, 83  
 cotton, 10, 12, 17, 22, 26, 28  
 craniofacial, 81  
 cranium, 93  
 credibility, 18  
 CRH, viii, 29, 30, 32, 37, 38, 44, 45, 46  
 crimes, 124  
 crop production, 179  
 cross-cultural, 89, 93, 118, 120  
 cross-cultural comparison, 118  
 cues, 72, 154  
 cultural differences, 69  
 cultural psychology, 58  
 culture, viii, ix, 53, 55, 57, 64, 67, 68, 69, 72, 73, 74, 95, 96, 97, 98, 99, 100, 101, 102, 106, 107, 108, 118  
 curiosity, 76  
 currency, 73  
 curriculum, 123  
 cycles, 32, 118

**D**

danger, 9, 14, 182  
 data collection, 70, 154, 165  
 data set, 101, 155, 182  
 database, 155  
 dating, 77, 82, 83  
 death, 77, 81, 86, 118, 135  
 deaths, 77, 85, 188, 192  
 deciduous, 85  
 defecation, 174  
 defects, 86  
 defense, 49  
 defenses, 107  
 definition, 61, 68, 115, 118, 180  
 deforestation, 133  
 degradation, 24  
 dehydroepiandrosterone, 31  
 delivery, 162  
 dementia, 48  
 demographic structure, 117  
 demography, 117, 131  
 density, 116, 117, 118, 122, 179, 182  
 dentist, 58  
 deposition, 86  
 depression, 50  
 deprivation, 96, 97, 101  
 desensitization, 45, 49  
 destruction, 131  
 developmental process, 114, 120  
 diaphragm, 12  
 dichotomy, 90  
 diet, vii, xi, 32, 76, 83, 85, 89, 90, 120, 122, 123, 138, 141, 171, 172, 173, 174, 176, 180, 181, 182, 184  
 diet composition, xi, 171, 172, 173, 180, 181, 182  
 dietary, 179  
 diets, 85, 120  
 dimorphism, ix, 75, 79, 80, 81, 82, 84, 89, 92, 93  
 directionality, 13, 68  
 discourse, 63, 67, 72  
 discrimination, 17, 154, 156, 157, 161, 168, 170  
 discrimination learning, 168  
 discrimination tasks, 156  
 diseases, xi, 187, 192  
 disorder, 47  
 displacement, 174  
 distribution, 21, 61, 86, 87, 116, 125, 151  
 divergence, 20, 79  
 diversification, 119  
 diversity, x, 20, 76, 113, 122  
 division, 98  
 DNA, 80, 91, 114, 124

dogs, 84, 117  
 domestication, 119, 123  
 dominance, 8, 23, 26, 73, 76, 81, 166  
 donor, 123  
 dopamine, 46, 47  
 dopaminergic, 47  
 drinking, 139, 143, 151  
 drinking water, 151  
 DSL, 33  
 DSM, 15

**E**

East Asia, 152  
 eating, 85, 103, 107, 176  
 ecological, xi, 23, 134, 171, 172, 179, 181, 182, 185  
 ecology, vii, 1, 8, 12, 19, 23, 27, 76, 79, 125, 131, 132, 149, 150, 171, 183, 184  
 economic status, 117  
 ecosystem, 85  
 Ecuador, 10, 183  
 egg, 87, 88, 161, 162, 163, 164, 165  
 Egypt, 81  
 elderly, 43, 50, 86  
 electrodes, 13  
 ELISA, 33  
 e-mail, 75  
 embryology, 115  
 emission, 4  
 emotional, viii, 29, 30, 31, 32, 34, 40, 43, 45, 120  
 emotional state, 8  
 encoding, 10  
 enculturation, 60  
 endocrine, 26, 31, 46, 48, 51  
 endocrinology, 51  
 energy, 13, 15, 89, 172, 179  
 engagement, 66  
 England, 140, 141  
 enterprise, 55, 96  
 entertainment, 17  
 environment, x, 60, 83, 98, 99, 102, 103, 106, 121, 122, 129, 134, 135, 136, 147, 152, 155, 165, 188  
 environmental conditions, 3, 8, 12, 119  
 environmental context, 9  
 enzymes, 48, 49  
 epidermis, 121  
 epiphyses, 83  
 episodic memory, 154  
 erythrocyte, 49  
 erythrocytes, 31  
 Ethiopia, 77, 80, 90, 91, 93  
 ethology, 25  
 Europe, 86, 89, 91, 104, 120, 190

European Union, 19  
 Europeans, 114, 116, 122  
 evaporation, 122  
 evening, 30, 33, 38, 39, 43, 44, 45, 46  
 evolution, ix, 8, 18, 22, 23, 24, 26, 27, 56, 69, 72, 73,  
     75, 76, 88, 89, 90, 91, 92, 96, 97, 101, 114, 115,  
     116, 117, 118, 119, 121, 124, 125, 126, 169  
 evolutionary principles, 9  
 evolutionary process, 96  
 exaggeration, 115  
 execution, 16  
 executive function, 167  
 executive functioning, 167  
 exercise, 62, 122, 135  
 experimental design, 49  
 exploitation, 131  
 exposure, 25, 39, 45, 49, 60, 190  
 external constraints, 108  
 extinction, 18, 25, 130  
 eyes, 69, 97, 115, 121, 127

## F

facial expression, 2, 4  
 faecal, 134  
 failure, 14, 114  
 fairness, 57  
 family, 78, 79, 82, 131, 136  
 fat, 179  
 fauna, 119  
 fear, 124  
 feedback, 30, 191  
 feeding, xi, 2, 102, 103, 104, 105, 106, 108, 118,  
     119, 135, 136, 138, 143, 150, 152, 171, 172, 174,  
     176, 177, 179, 180, 181, 182, 183, 184, 185  
 feet, 114, 122  
 females, 34, 35, 36, 37, 39, 40, 41, 42, 43, 76, 78, 79,  
     81, 82, 83, 85, 86, 87, 88, 90, 118, 123, 131, 173,  
     174, 176  
 fertility, 118, 173, 178, 180  
 fertilization, 88, 124, 184  
 fertilizer, 122  
 fibers, 122  
 fidelity, 12, 80  
 film, 55, 61, 71  
 flexibility, 56, 165  
 flow, 121, 188, 189  
 fluvial, 78  
 food, x, 9, 22, 26, 57, 62, 63, 67, 72, 73, 76, 78, 81,  
     83, 86, 91, 102, 103, 113, 118, 119, 120, 133,  
     134, 135, 136, 137, 138, 140, 141, 142, 143, 144,  
     145, 146, 147, 149, 150, 151, 152, 158, 161, 162,  
     163, 166, 169, 174, 179, 180, 183, 188, 189

food intake, 138  
 forest fires, 133  
 forest fragments, 130  
 forests, 20, 68, 130, 131, 149, 184, 188, 191  
 fossil, ix, 75, 76, 77, 79, 80, 81, 82, 83, 84, 85, 86,  
     89, 91, 92, 114, 119  
 founder effect, 100  
 freedom, 106  
 fruits, 102, 172, 173, 174, 176, 179, 180, 181

## G

gametes, 87  
 garbage, 120  
 gender, 9, 25, 116  
 gene, 47, 50, 51, 124  
 gene expression, 50, 51  
 generation, 83, 96  
 genes, 51, 69, 88, 121, 122  
 genetic factors, 125  
 genetic traits, 88  
 genetics, 100  
 genome, 83, 88, 93, 121  
 genomes, 88  
 genomic, 88  
 genomics, 88  
 Germany, 32, 33, 80, 95, 104  
 germination, 184  
 gestures, 54, 59, 61, 62, 63, 65, 66, 67, 72, 73  
 gland, 48  
 glia, 124  
 glucocorticoid receptor, 30  
 glucocorticoids, 30, 31  
 glucose, 51  
 glucose regulation, 51  
 goals, 106  
 government, iv  
 grafts, 123  
 granules, 126  
 grapes, 141, 142, 143, 144, 145, 146, 147  
 graph, 164  
 grasslands, 85  
 gravity, 78, 84  
 Greece, 91  
 group size, 9, 77, 178, 184  
 grouping, 131  
 groups, x, 20, 24, 32, 35, 36, 37, 40, 41, 42, 44, 58,  
     60, 76, 77, 78, 79, 82, 86, 99, 104, 105, 123, 129,  
     131, 134, 148, 149, 158, 172, 173, 175, 178, 180,  
     182, 188, 189, 190  
 growth, ix, 46, 75, 76, 80, 83, 86, 114, 117, 118, 119,  
     122, 123, 125, 126, 127  
 growth rate, 117, 123, 125



growth spurt, 83, 117  
 guidelines, 133  
 Guyana, 28

## H

habitat, 12, 83, 131, 151  
 habitation, 189  
 habituation, 17, 149  
 hair follicle, 123  
 hands, xi, 6, 68, 84, 114, 153, 156, 158  
 hanging, 130, 143  
 harm, 132  
 harmonics, 9, 15  
 health, 30, 137, 188, 189, 190, 191, 192  
 hearing, 9, 27  
 heart, 103  
 heat, 84, 122  
 height, 8, 79, 147  
 hemisphere, 23  
 Hepatitis A, 134  
 herbs, 102  
 herpes, 151  
 herpes simplex, 151  
 high risk, 190  
 hip, 176  
 HIV, xi, 187  
 hominids, ix, 18, 75, 76, 77, 79, 80, 82, 83, 84, 85, 88, 89, 90, 91, 114, 117, 118, 119, 123  
 hormone, viii, 10, 29, 30, 33, 44, 46, 51, 52  
 hormones, 33, 44, 47, 48, 122  
 horse, 117  
 host, 189  
 housing, 31, 139  
 HPA, vii, viii, 29, 30, 31, 32, 33, 34, 36, 38, 39, 40, 42, 43, 44, 45, 46, 47  
 HPA axis, viii, 29, 30, 31, 32, 33, 34, 36, 38, 39, 40, 42, 43, 44, 45, 46, 47  
 human, ix, xi, 10, 18, 20, 21, 22, 26, 48, 49, 50, 51, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 72, 73, 74, 76, 77, 79, 80, 82, 84, 85, 86, 88, 89, 91, 92, 93, 95, 96, 97, 98, 99, 106, 107, 114, 115, 116, 117, 118, 119, 120, 121, 122, 123, 124, 125, 126, 127, 139, 151, 155, 168, 187, 188, 189, 190, 191, 192  
 human animal, 26  
 human brain, 126  
 human cognition, 55, 56, 58, 60  
 human condition, 79  
 human development, 117  
 human genome, 88, 93  
 human subjects, 55  
 humanity, 120, 122

humans, vii, viii, ix, x, xi, 18, 29, 30, 31, 33, 39, 44, 47, 48, 51, 53, 54, 55, 56, 57, 58, 59, 60, 62, 64, 65, 68, 69, 74, 75, 76, 77, 79, 80, 82, 83, 84, 86, 87, 88, 89, 91, 92, 96, 97, 107, 114, 115, 116, 117, 118, 119, 120, 121, 122, 123, 132, 134, 138, 139, 143, 145, 153, 166, 167, 170, 187, 188, 190  
 humidity, 13, 14  
 hunter-gatherers, 86  
 hunting, 85, 86, 119, 184  
 hygiene, 188  
 hyperactivity, 48  
 hypertension, 51  
 hypothalamic, vii, viii, 29, 38, 44, 47, 48, 49, 50, 51  
 hypothalamic-pituitary-adrenal axis, 47, 48, 49, 51  
 hypothalamus, 30, 46, 47, 48, 52  
 hypothalamus-pituitary-adrenal, 48  
 hypothesis, ix, 59, 68, 91, 95, 99, 102, 105, 118, 119, 172, 178, 179, 182

## I

id, 176  
 IDEA, 19  
 identification, 2, 12, 24, 61, 87  
 imagination, 136  
 imitation, ix, 95, 98, 99, 102, 103, 105, 106  
 immersion, 67, 69  
 immobilization, viii, 29, 32, 33, 34, 35, 36  
 immune system, 50  
 immunity, 190  
 implants, 47  
 implementation, 154, 191  
 in situ, 47, 137  
 in vitro, 45, 46, 51, 52, 57  
 in vivo, 57, 58, 60  
 inactive, 143, 174  
 incisor, 85  
 inclusion, 114  
 independence, 16, 118  
 India, 148  
 indicators, 18, 86  
 individuality, 24, 27  
 Indonesia, x, 129, 132, 148, 150, 151  
 industrialization, 83, 120  
 infancy, 4, 65, 68, 72, 117, 118  
 infants, 9, 10, 27, 54, 57, 58, 59, 68, 72, 77, 78, 110, 119, 120, 155, 173, 190  
 infection, xi, 187, 189, 190  
 infections, 190, 193  
 infectious diseases, xi, 187, 190, 193  
 inferences, 59  
 ingestion, 102, 104, 105  
 inherited, 107

inhibition, 52, 158, 159  
 inhibitory, 159, 167  
 initiation, 73  
 injection, viii, 29, 30, 33, 38, 39, 40, 42, 45, 49  
 injections, 32  
 innovation, 154  
 insects, 119, 180  
 insertion, 104  
 insight, x, 129, 136, 149  
 inspection, 55, 180  
 instinct, 132  
 institutions, 17  
 insulation, 122  
 insulin resistance, 47  
 integration, 49, 167  
 intelligence, 68, 170  
 intentionality, 27, 56, 59, 60, 66, 69  
 intentions, 189  
 interaction, 27, 57, 59, 65, 74, 82, 120, 143, 144  
 interactions, viii, ix, x, 2, 9, 51, 53, 55, 57, 58, 60, 62, 69, 75, 76, 77, 81, 83, 84, 88, 124, 129, 134, 147, 148, 149, 151, 174, 176, 182  
 interval, 9, 16, 32  
 intramuscularly, 33  
 intravenously, 32, 33  
 invasive, 17  
 inventions, 96, 98, 99, 106, 107  
 inventiveness, 97, 98  
 Investigations, 53, 74  
 investment, 89  
 ions, 66  
 isolation, 10, 17, 27, 88, 96  
 isotope, 85, 93  
 isotopes, 91  
 IUCN, 131, 151

## J

Japanese, 9, 10, 17, 23, 24, 27, 125, 126  
 Java, 131  
 journalists, x, 113  
 joystick, 154, 156, 157, 158, 160, 161, 170  
 juveniles, 77, 78, 79, 174, 176

## K

Kenya, 192  
 killing, 81, 132

## L

laboratory method, 22

lactation, 118  
 land, 78, 119  
 language, viii, 10, 18, 21, 22, 24, 26, 53, 54, 55, 57, 58, 59, 60, 63, 67, 68, 69, 72, 73, 74, 96, 97, 101, 102, 103, 122, 150  
 laptop, 13  
 large-scale, x, 129  
 latency, 155  
 Latin America, 19  
 laughter, 117  
 leaf blades, 104  
 learners, 99  
 learning, vii, ix, x, 8, 20, 23, 26, 47, 54, 58, 95, 97, 98, 99, 100, 103, 105, 106, 107, 108, 118, 119, 125, 134, 147, 149, 150, 153, 154, 155, 156, 157, 158, 159, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170  
 learning process, ix, 95, 97, 98, 154, 157, 169  
 learning skills, 170  
 learning task, x, 153, 155, 157, 162, 165  
 lens, 114  
 lenses, 78  
 lesions, 50  
 life cycle, 117  
 life quality, 140  
 lifestyle, 83, 85, 123, 134  
 lifetime, 96  
 likelihood, 85, 108, 157  
 limitations, 120, 167  
 linear, 14  
 linguistic, 54, 55, 57, 58, 59, 60, 67, 69  
 linguistically, 68  
 linguistics, 21  
 links, 76  
 lipid, 172  
 locomotion, 114  
 logging, 131  
 logistics, 189  
 London, 20, 22, 25, 28, 72, 109, 111, 112, 125, 128, 136, 151  
 long distance, 4, 10, 11, 28  
 long period, 13, 82, 117  
 long-distance, 84  
 longevity, 117  
 long-term memory, 154, 162  
 long-term retention, 166  
 losses, 16  
 love, 125  
 L-shaped, 141  
 lumbar, 80  
 lying, 174  
 lymphocytes, 50

# M

M1, 118  
 major depression, 52  
 males, 10, 76, 78, 79, 81, 82, 83, 84, 85, 86, 87, 88,  
     90, 123, 131, 147, 173, 174, 176, 190  
 mammal, 76, 77, 83  
 mammalian brain, 116  
 mammals, 12, 20, 23, 30, 76, 77, 117, 118, 119, 120,  
     121, 184, 192  
 management, 18, 130, 188, 189, 190, 191  
 mandates, 82  
 mandibular, 81  
 manipulation, x, 129, 136, 141, 150  
 man-made, 23  
 manufacturer, 16  
 market, 14, 132  
 marketplace, 132  
 marriages, 89  
 mask, 64, 65  
 mastery, 162, 163  
 matching-to-sample, 158  
 maternal, 27, 124  
 matrix, 60, 78  
 maturation, ix, 75, 82, 83, 86, 123, 126  
 Maya, 124  
 measures, 43  
 meat, 83  
 median, 77, 117  
 medicine, 49  
 Mediterranean, 91  
 melancholic, 52  
 melatonin, viii, 29, 30, 31, 33, 38, 39, 40, 41, 42, 45,  
     46, 48, 49, 50, 51, 52  
 memory, 13, 47, 154, 162, 167, 169, 170  
 men, 45, 51  
 mental state, 59, 60  
 mental states, 59, 60  
 metabolic, 32, 47, 119  
 metabolic syndrome, 47  
 metabolism, 46, 51  
 metacognition, 154, 169, 170  
 meteorological, 8, 24  
 mice, 46, 50  
 microenvironment, 50  
 middle class, 115  
 milk, 86  
 mineralocorticoid, 48, 51  
 Miocene, 77, 91, 127  
 mirror, 140, 151  
 misleading, 59  
 mitochondria, 123, 124  
 modalities, 6, 158

models, viii, 18, 29, 31, 58, 155  
 modernity, 83  
 moisture, 122  
 money, 188  
 monkeys, vii, viii, x, xi, 2, 6, 7, 9, 10, 12, 17, 18, 19,  
     20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32,  
     33, 34, 35, 36, 38, 39, 40, 44, 45, 46, 47, 48, 49,  
     50, 72, 76, 78, 92, 117, 120, 126, 140, 150, 152,  
     153, 154, 155, 156, 157, 158, 159, 160, 161, 162,  
     163, 166, 167, 168, 169, 170, 171, 172, 173, 175,  
     176, 177, 178, 179, 180, 181, 182, 183, 184, 185  
 morbidity, 189, 190  
 morning, viii, 30, 31, 34, 36, 38, 43, 44, 46, 142, 144  
 morphological, 2, 10, 23, 89, 125  
 morphology, 68, 81  
 mortality, xi, 86, 87, 187, 189, 190  
 mothers, 51, 68, 120, 132  
 motion, 12  
 motivation, 68, 99, 101, 107, 135, 149  
 motives, 66  
 motor coordination, 156  
 MOU, 192  
 mouse, 17  
 mouth, 69, 72, 81, 104, 105  
 movement, xi, 99, 119, 156, 170, 171, 172, 180  
 mRNA, 45, 47, 49  
 muscle, 76, 114  
 muscle mass, 76  
 music, 18, 22, 24, 25, 27, 151  
 myopic, 114

# N

NaCl, 33  
 NASA, 169  
 nation, 115  
 National Academy of Sciences, 73, 91, 92, 93, 110  
 natural, 9, 10, 17, 25, 45, 69, 83, 84, 86, 96, 118,  
     122, 126, 132, 135, 136, 165, 170, 188  
 natural environment, 17, 136, 188  
 natural science, 118  
 natural selection, 84  
 nature conservation, 17  
 negative consequences, 190  
 negative relation, 176  
 neglect, 116  
 neocortex, 116  
 Netherlands, 104  
 network, 49  
 neurobiology, 18, 169  
 neuroendocrine, viii, 29, 30, 47, 50, 51  
 neuroendocrine system, viii, 29, 30, 51  
 neurohormone, 51

neurons, 44, 45, 49, 50, 116, 122, 124  
 neuropeptides, 44  
 neurosecretory, 47  
 neurotransmitters, 46  
 neutralization, 104  
 noise, 13, 14, 20  
 non-human, 9, 10, 18, 20, 22, 23, 26, 28, 48, 50, 76, 77, 81, 86, 114, 152  
 non-human primates, 10, 18, 20, 48, 50, 76, 77, 152  
 non-invasive, x, 17, 129  
 norepinephrine, 46  
 normal, 71, 126, 136  
 nuclear family, 79  
 nucleus, 30, 47, 49, 51  
 nursing, 7, 51, 143, 190  
 nutrient, 47, 93  
 nuts, 101

## O

object permanence, 140  
 observations, x, xi, 10, 54, 55, 79, 101, 107, 129, 135, 136, 142, 143, 148, 171, 173, 174, 176, 182, 191  
 obsolete, 14  
 odors, 23  
 oil, 133  
 old age, 45, 86  
 olfaction, 23  
 olfactory, vii, 1, 2, 4, 8, 19, 21, 27, 143  
 olive, 82  
 omission, 123  
 omni-directional, 13  
 open-field, 167  
 operant conditioning, 152  
 opsin, 121  
 optimization, 121  
 organism, 30, 87, 106, 123, 159  
 ovum, 123  
 oxygen, 31  
 oxytocin, 49, 50

## P

pacemaker, 30, 44  
 pacing, 163  
 pain, 103  
 paleontology, 76, 77  
 PAN, 72  
 pancreas, 48  
 parabolic, 13  
 paradox, 26

parasites, 102, 122, 134, 189  
 paraventricular, 30, 47, 49, 51  
 paraventricular nucleus, 30, 47, 49, 51  
 parental care, 76, 79  
 parent-child, 80  
 parenting, 120  
 parents, 65, 120  
 Paris, 125  
 partition, 143  
 partnerships, 130  
 passive, 125, 143  
 pathogenesis, 45, 47  
 pathogens, 189  
 pathology, viii, 29, 30, 31, 48  
 pathophysiological, 48  
 pathways, 49, 56, 91  
 patients, 45, 50  
 peat, 150  
 pedestrian, 59  
 pelvis, 80, 84, 93  
 penalty, 158, 161  
 pendulum, 131  
 penguins, 122  
 peptide, 33, 46, 49  
 peptides, 48, 50  
 perception, 4, 18, 22, 28, 154, 166  
 periodicity, viii, 29, 30, 38, 43, 44, 45, 46  
 peripheral blood, 30  
 permit, 149  
 perturbations, 47  
 pests, 12  
 pets, 132  
 pharmacopoeia, 33  
 Philadelphia, 127  
 philosophical, 60, 62  
 photographs, 170  
 phylogenetic, 76, 114  
 phylogeny, 8, 23, 79, 127  
 physical sciences, 49  
 physiological, 10, 30, 38, 43, 45, 48, 86, 91  
 physiology, 49, 51, 115, 118, 119, 121  
 piloerection, 2  
 pineal, viii, 29, 31, 33, 38, 39, 45, 46, 47, 48, 49, 50  
 pineal gland, 33, 38, 39, 45, 46, 48, 49, 50  
 pinealectomy, 47  
 pituitary, vii, viii, 29, 38, 44, 45, 46, 48, 49, 51  
 placebo, viii, 29, 33, 39, 40, 41, 42  
 planning, 132, 154, 166, 167  
 plants, ix, 77, 95, 102, 103, 104, 105, 106, 107, 179  
 plasma, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46  
 plastic, 12, 45, 131, 137, 141, 161, 162  
 plasticity, 18, 51, 116, 119, 131

play, viii, xi, 2, 4, 9, 29, 30, 64, 86, 107, 143, 187  
 Pleistocene, 78, 85, 86, 90, 91, 92, 172  
 Pliocene, 91, 120  
 pollution, 133  
 polygamy, 88  
 poor, x, 8, 114, 129, 133, 135  
 population, ix, 10, 17, 21, 25, 26, 27, 69, 77, 85, 87, 89, 95, 96, 100, 103, 105, 115, 116, 117, 118, 122, 124, 130, 178, 181, 182, 184, 192  
 population density, 21  
 population group, 87  
 positive relationship, 176  
 potatoes, 119  
 power, 12, 14, 98, 99  
 precipitation, 173  
 predators, 9, 10, 12, 22, 28, 85, 119, 134  
 predictability, 10  
 prediction, 172  
 predictors, 26  
 preference, 147  
 prefrontal cortex, 168  
 Pretoria, 91  
 preventive, xi, 187  
 prior knowledge, 97  
 private, 88, 116, 130  
 problem solving, x, 99, 129, 135  
 production, viii, xi, 3, 10, 18, 28, 29, 31, 46, 48, 96, 98, 122, 171, 173, 174, 175, 176, 178, 179, 180, 184  
 productivity, 172, 179  
 program, 102, 103, 104, 105, 106, 108, 165, 188, 192  
 propagation, 8, 24, 28  
 prophylaxis, 31  
 protected area, 130  
 protein, 89, 124  
 protocol, 173  
 protocols, 188, 189, 191  
 psychological assessments, 156  
 psychological processes, 135  
 psychological stress, 47  
 psychological well-being, 150  
 psychology, 58, 153, 167, 168  
 pubertal development, 51  
 puberty, 79, 117  
 pulse, 49  
 punishment, 161  
 purification, 33  
 PVC, 152  
 PVN, 30, 44, 45

## Q

qualitative differences, 169

quality of life, 140  
 quarantine, 134, 137, 188, 190, 191  
 questioning, 58

## R

radiation, 21  
 radio, 17  
 rain, 13, 21, 131, 172, 183  
 rain forest, 13, 21, 183  
 rainfall, 77, 178  
 rainforest, 83  
 random, 65  
 range, vii, ix, xi, 2, 13, 15, 17, 24, 63, 65, 70, 76, 80, 95, 116, 171, 172, 173, 175, 176, 178, 190  
 rat, 50, 51, 52, 124  
 rats, 45, 47, 48, 49, 50, 51, 124  
 reactivity, viii, 30, 31, 38, 40, 43, 44, 46, 48  
 reading, 116  
 reality, 192  
 reasoning, 56, 106  
 recall, 163, 168  
 receptors, 30, 45, 46, 48, 49  
 recognition, 5, 17, 26, 27, 140  
 reconcile, 106  
 reconstruction, ix, 75, 80, 82, 85, 88, 89  
 redundancy, 23  
 refractory, 48  
 regression, 174  
 regular, 188, 191  
 regulation, viii, 20, 29, 30, 31, 33, 42, 45, 46, 50, 51, 125  
 regulations, 191  
 regulators, 46  
 rehabilitate, 141  
 rehabilitation, vii, x, 129, 132, 133, 134, 135, 136, 137, 138, 139, 141, 149, 150  
 Rehabilitation Center, 189  
 rehabilitation program, 135  
 reinforcement, 169  
 relationship, 52, 121, 122, 123, 168, 174, 176, 179, 188  
 relationships, 28, 46, 73, 76, 80, 114, 140, 188  
 relatives, xi, 79, 187  
 relevance, 17, 48  
 reliability, 31, 46, 49, 103  
 replication, 16  
 reproduction, 19, 76, 86, 120, 123  
 reptiles, 119  
 reputation, 191  
 reserves, 93  
 resistance, 47  
 resolution, 130

resources, xi, 81, 171, 172, 178, 180  
 respiration, 84  
 respiratory, xi, 187, 188, 190, 191, 193  
 response time, 156  
 responsiveness, viii, 30, 32, 33, 36, 38, 39, 40, 42, 43, 44, 45, 46, 49  
 retention, 163, 165, 166  
 returns, 58, 120  
 reversal learning, 155, 157, 166  
 rewards, 146, 151, 162, 163  
 rhythm, viii, 29, 30, 31, 44, 45, 47, 50, 51, 131  
 rhythmicity, 30, 44  
 rhythms, viii, 29, 30, 31, 38, 44, 46, 48, 49, 51  
 right hemisphere, 168  
 risk, 20, 76, 86, 188, 190, 191, 192, 193  
 risk factors, 190  
 risks, 184  
 rivers, 178  
 rocky, 78  
 rodent, 51, 123  
 rodents, viii, 29, 30, 31, 45, 125  
 rods, 121  
 role-playing, 64  
 rolling, 143  
 Royal Society, 22, 28, 109, 111, 112  
 RTS, 15  
 Russia, 29, 31, 33  
 Russian, 29, 48  
 Rwanda, ix, xi, 95, 102, 187, 188, 189, 191, 192

## S

sample, 78, 80, 86, 87, 92, 158, 175, 176, 179, 189  
 sampling, xi, 13, 14, 33, 143, 171, 172, 173, 174, 177, 180, 181, 182  
 sanctuaries, x, 129, 132  
 scalp, 122  
 scarce resources, 81  
 scarcity, xi, 136, 171, 172, 174, 176, 179, 180  
 scientific community, 16  
 sclera, 115  
 SCN, 30, 31, 44, 45, 46  
 search, 59, 140, 174, 180  
 searching, 58, 180  
 sebaceous glands, 122  
 Second World War, 115  
 secretion, viii, 29, 31, 38, 39, 44, 45, 46, 48  
 sediments, 77, 78, 85, 178  
 selecting, 161  
 Self-control, 169  
 self-recognition, 140  
 SEM, 33, 34, 35, 36, 37, 39, 40, 41, 42  
 semantic, 28

senescence, 50  
 senile, 48  
 senile dementia, 48  
 sensitivity, 43  
 sensitization, 51  
 sentence comprehension, 71  
 sentences, 54  
 separation, 88, 114  
 sequencing, 157, 163  
 SES, 117, 118  
 sex, vii, 1, 8, 9, 22, 25, 26, 49, 78, 79, 85, 86, 87, 92, 115, 116, 121, 122, 124, 125, 146, 173, 174, 176  
 sex differences, 25, 26  
 sex ratio, 85, 86, 87, 92  
 sexual behavior, 116  
 sexual dimorphism, ix, 10, 75, 80, 81, 84, 89, 92, 93  
 shape, 10, 19, 51, 54, 81, 117, 122, 170  
 shaping, 69  
 sharing, 62, 63, 67, 68, 72, 73, 76, 91  
 sign, 54, 96, 143, 162  
 signalling, 10, 17, 20, 25  
 signals, 2, 4, 8, 9, 10, 13, 14, 15, 16, 18, 21, 23, 24, 26, 30, 126, 169  
 signs, 73, 132  
 similarity, 23, 114  
 simulations, 177  
 single test, 101  
 sites, 77, 78, 83, 85, 91, 172, 175, 178, 182, 188, 190, 191, 192  
 skills, vii, ix, x, 12, 55, 56, 57, 58, 59, 60, 65, 95, 99, 100, 102, 103, 107, 129, 132, 134, 135, 151, 153, 170  
 skin, 79, 103, 115, 120, 121, 122, 123, 134  
 sleep, 30, 47, 51  
 SME, 14, 15  
 Smithsonian Institution, 25, 26  
 social activities, 6, 68, 147, 148, 180  
 social behavior, x, 21, 76, 92, 129  
 social behaviour, 91, 147, 149, 176, 181  
 social cognition, 68, 69  
 social context, 12, 23, 26, 152  
 social development, x, 129  
 social group, 9, 76, 77, 78, 79, 81, 82, 149  
 social learning, 97, 98, 99, 102, 103, 104, 106, 107, 119  
 social organization, 86, 183  
 social relations, 90, 140, 150  
 social relationships, 140  
 social skills, vii, x, 129, 132  
 social status, 26, 65  
 social stress, 49, 88  
 social structure, ix, 2, 75, 81, 131  
 social support, 78

social systems, vii, 1, 8, 76, 78  
 socialisation, 143  
 socialization, 134  
 sociocultural, 74  
 sociology, 127  
 software, 15, 154, 155, 156, 177  
 soil, 178, 180  
 soils, 173, 178  
 sounds, 2, 13, 15, 17, 19, 25, 28  
 South Africa, 28, 78, 85  
 Southeast Asia, 131  
 spatial, 156, 161, 166, 168, 169, 172, 174  
 specialization, 115  
 speciation, ix, 75  
 species, vii, ix, x, 1, 2, 6, 8, 9, 10, 12, 15, 17, 18, 19, 20, 54, 55, 56, 58, 69, 73, 75, 76, 77, 79, 80, 81, 83, 84, 87, 88, 89, 95, 97, 98, 99, 100, 101, 102, 104, 105, 106, 107, 113, 114, 115, 116, 118, 121, 124, 130, 131, 132, 136, 138, 141, 149, 151, 152, 153, 155, 156, 157, 165, 167, 173, 182, 183, 185  
 species richness, 183  
 spectrum, 14, 54  
 speculation, 80  
 speech, 18, 22, 27, 57, 58, 66, 70, 101, 117  
 speed, 13, 131, 155, 165  
 sperm, 75, 79, 87, 88, 118, 123  
 spermatogenesis, 88  
 spines, 102  
 sponges, 119, 126  
 Sri Lanka, 21  
 SRS, 15  
 St. Louis, 124  
 St. Petersburg, 33, 48, 50  
 stability, 24, 84  
 stages, 63, 72, 117, 118  
 standard deviation, 175  
 standardization, 96, 103  
 standards, 137  
 starvation, 86, 120  
 statistics, 16  
 stereotyping, 115  
 steroids, 117  
 stimuli, 162  
 stimulus, x, 16, 43, 98, 135, 153, 156, 157, 158, 159, 161, 165, 166, 168, 169, 170  
 stings, 104, 105, 106  
 storage, x, 113  
 strategies, xi, 20, 21, 23, 87, 124, 171, 180, 185  
 stress, vii, viii, 20, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 51, 86, 88, 91, 120  
 stressors, 36  
 stress-related, viii, 29, 30

stretching, 68  
 strontium, 91  
 structuring, 157  
 students, 114, 115, 116, 123  
 substrates, 22  
 sulfate, 31, 50  
 supply, xi, 118, 171, 172, 174, 175, 176, 178, 179, 180, 192  
 suppression, 19  
 suprachiasmatic, 30, 47, 49, 50, 51  
 suprachiasmatic nucleus, 30, 47, 49, 51  
 suprapubic, 5  
 surgical, 190, 191  
 surprise, 122  
 survival, 30, 86, 116, 117, 118, 119, 135  
 swallowing, 102, 105, 106, 107  
 sweat, 84  
 Sweden, 15  
 swelling, 116  
 symbolic, 61, 67, 161, 166, 167  
 symbols, 55, 67, 161, 169, 170  
 sympathetic, 50  
 symptoms, 190  
 syntax, 65  
 synthesis, 30, 48  
 systematics, 19, 27, 131

## T

tactile stimuli, 2  
 Taiwan, 93  
 Tanzania, 10, 77, 83, 188, 191, 192, 193  
 taxa, 76, 130, 140  
 taxonomic, vii, x, 1, 8, 21, 28, 79, 113  
 taxonomy, 18, 27  
 teaching, 17, 149  
 teeth, 81, 83, 84, 85, 86, 91, 92, 143  
 temperature, 31, 173  
 temporal, 172  
 tenure, 78  
 termites, 85, 93  
 territorial, 2, 18  
 territory, 87, 132, 134, 191  
 testicle, 87  
 testis, 87  
 textbooks, 76, 123  
 Thailand, 79, 131, 148  
 therapy, 52  
 thinking, 101  
 thorns, 102  
 threat, 22  
 threatened, 18, 192  
 threatening, 2, 192

three-dimensional, xi, 153  
 threshold, 100  
 throat, 132  
 tissue, viii, ix, 29, 47, 75, 79, 87, 123  
 T-lymphocytes, 50  
 tolerance, 26  
 torture, 120  
 tourism, 188, 191, 192  
 tourist, xi, 187, 188, 191  
 tracking, 192  
 trade, 131, 132, 133, 134, 135, 140, 141  
 tradition, 114  
 Traditional Medicine, 110  
 training, 67, 130, 132, 135, 155, 157, 158, 159, 160, 161, 162, 163, 164, 168, 188, 191  
 traits, 56, 81, 114, 117, 122  
 trajectory, 100  
 transcript, 64, 70  
 transcription, 51, 70  
 transcripts, 60  
 transfer, 163, 191  
 transitions, 117  
 transmission, vii, ix, 23, 24, 27, 31, 49, 95, 97, 99, 126, 188, 189, 190, 191, 192, 193  
 transport, 31, 78, 84, 189  
 traps, 56  
 trauma, 77, 83  
 travel, 172, 178, 179, 190  
 trees, 126, 131, 135, 179, 184  
 tufted, 17, 21, 22  
 turtles, 118  
 twinning, 78  
 tyrosine hydroxylase, 50

## U

Uganda, 189, 191  
 uncertainty, 166, 169, 170  
 underlying mechanisms, 19  
 undernutrition, 124  
 uniform, 122  
 upper respiratory tract, 190

## V

vaccination, 188  
 values, 33, 35, 36, 38, 39, 42, 43, 89, 166  
 variability, 77, 115, 160  
 variables, 61, 76, 89, 157, 168, 180  
 variance, 33, 174

variation, 21, 23, 33, 52, 89, 92, 114, 115, 116, 117, 121, 124, 162, 172, 173, 174, 175, 177, 178, 179, 180, 181, 182  
 vasopressin, viii, 29, 32, 45, 49, 50, 51  
 vegetables, 32  
 vegetation, 77, 184, 189  
 ventilation, 190  
 vertebrates, 115, 116, 117, 123, 125, 172, 174  
 veterinarians, 189  
 veterinary medicine, 18  
 Vietnam, 130, 131  
 violence, 84, 88  
 violent, 85  
 viral diseases, xi, 187  
 virus, xi, 151, 187, 190  
 viruses, 189, 192  
 visible, 72, 121, 136, 161, 162  
 vision, 121  
 visual stimuli, 156, 168  
 vocalisations, vii, 1, 2, 8, 9, 10, 12, 13, 17, 18, 22, 24  
 vocalizations, 20, 21, 22, 23, 24, 25, 27, 28

## W

walking, 68, 77, 84, 143, 190  
 warfare, x, 113  
 water, 15, 33, 78, 132, 138, 151, 176, 178  
 wavelengths, 13  
 weapons, 84, 85  
 wear, 64, 65, 191  
 websites, 17  
 welfare, vii, 1, 8, 18, 19, 150  
 well-being, 120, 150  
 West Africa, 76, 83, 88, 92  
 WHO, 193  
 wildlife, 188  
 wind, 23  
 withdrawal, 47  
 women, 43, 45  
 wood, 137  
 woodland, 77, 83  
 woods, 63  
 wool, 127  
 writing, 79  
 written records, 85

## Y

Y chromosome, 88  
 yes/no, 143  
 yield, 79, 81  
 young adults, 43