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## Plenary Presentations

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### **Non-Invasive Assessment of Physiological Status: A 30-Year Contribution to Primatology**

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*Key Words:* Faeces · Hormone analysis · Reproduction · Stress · Field endocrinology

The ability to assess physiological status is important in helping to provide a more complete understanding of primate biology. Since primates are generally difficult to handle, potentially dangerous and sensitive to physical and social disruption, scientific and practical considerations emphasise the need for a non-invasive approach. Endocrine methods based on the measurement of hormones and their metabolites in urine and faeces have proven particularly useful since they do not require animal capture and/or restraint and samples can be collected on a frequent basis and for prolonged periods of time. There are three main areas where these methodologies have substantially contributed to primatology: (1) captive management/breeding programmes, (2) comparative studies and (3) integrating physiology and behaviour in field settings. The latter has led to a new discipline, field endocrinology, in which quantitative measures of physiological status are used to gauge the significance of observational data, thereby facilitating the testing of hypotheses concerning the adaptive value of behavioural and morphological traits. This has resulted in new insights into actions of physiological adaptation and behavioural and reproductive processes of wild primates in an evolutionary context. In this talk, the development and application of non-invasive endocrine assessment in primates will be reviewed. Examples from the three areas mentioned above will be presented to illustrate how non-invasive endocrine methodologies have contributed to primatology, with special reference to field-based research.

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## The Ant and the Chimpanzee: New Insights into Cultural Primatology

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*Key Words:* Chimpanzee · Tool use · *Dorylus* spp. · Culture · Development

Ant-dipping has been observed across several wild chimpanzee communities in Africa and is often cited as one of the best examples of culture in chimpanzees. This tool-use behaviour involves the use of a modified stick or stalk of vegetation to gather biting and gregarious army ants (*Dorylus* spp.). Since army ant consumption shows both intra- and inter-community variation, it provides a unique opportunity to investigate the respective influences of ecology, development and social parameters on individual and community-wide variations in behaviour. Recent data from Bossou, Guinea, and detailed entomological analysis of the army ant species available at different chimpanzee study sites, as well as direct observations of the behaviour, indicate that the aggressiveness and the density of the ant species influence tool length and the technique employed at each site. Behavioural differences persist, however, between the communities of Taï, Côte d'Ivoire, and Bossou, where the same species of army ants are consumed by the chimpanzees. A comparative study between these two long-term field sites indicates that these differences reflect conformism or conservatism within communities rather than ecological differences. A longitudinal study of the acquisition of ant-dipping among the chimpanzees of Bossou also reveals the importance of the role of the mother and the opportunity to observe and practice the behaviour in the learning process of young chimpanzees. Finally, such a comparative approach between study sites, combined with a detailed analysis of the behavioural acquisition in young chimpanzees, clearly demonstrates the narrow relationship existing between ecology, social learning and culture in primates.

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## A Genetic Perspective on the Evolution of Cooperation in Chimpanzees and Humans

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*Key Words:* Group selection · Competition · Reproductive skew · Genetic differentiation

The extent and complexity of human cooperation exceeds that seen in any other mammal. Darwin was the first to suggest that inter-group competition has played a key role in the evolution of altruistic cooperation in humans. Recently, Bowles (2006) used empirical data from hunter-gatherer populations in a model that suggested that such cooperation could evolve under conditions of high competition between groups, high genetic differentiation between groups, and low reproductive skew within groups. To test this model, we have assembled data on local genetic differentiation from multiple wild chimpanzee groups as well as published information from human populations sampled on a small geographic scale. Genetic data are also used to examine whether, despite the appearance of intense reproductive competition among wild chimpanzee males, the distribution of reproduction over the long term is not highly skewed. Preliminary results suggest that the present form of the group competition model may be insufficient to explain the evolution of human cooperation.

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## Wild Capuchin Monkeys Use Tools: Why and How It Challenges Our Ideas about Tool Use in Human Evolution

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*Key Words:* Wild capuchins · Nut-cracking · Tool selectivity · Transport

Wild capuchin monkeys living in Fazenda Boa Vista (Piauí, Brazil; a dry forest habitat) use hammers and anvils to crack open nuts, and then eat the nutritious kernels. I will discuss our team's studies of the cracking activities of two groups of capuchin monkeys in Boa Vista, together with our explorations of their hammers, anvils, and the nuts they crack. These monkeys crack nuts throughout the year using proportionally large stones (on average, 1 kg; an adult monkey weighs 2–4.5 kg). The nuts are very difficult to crack because they have a thick, tough shell, and stones suitable as hammers are very rare in the habitat where capuchins live. Our work shows that these monkeys display selectivity in their choice of stones, nuts, and anvil sites, and finely honed skill in cracking the nuts. These findings challenge notions that selectivity, transport and physical skill in tool use are characteristic only of humans, human ancestors and great apes. Stone tool use by capuchin monkeys opens up a new reference point for thinking about tool use across species and across evolutionary time.

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## Oral Presentations

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### Niche Overlap between Howler Monkey Species in a Contact Zone

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*Key Words:* Contact zone · Niche overlap · *Alouatta guariba* · *Alouatta caraya*

Ecological theory predicts that only niche differentiation allows the stable coexistence of similar species. However, little is known about ecological relationships between closely-related parapatric species in contact zones. We investigated niche overlap of syntopic brown howlers (*Alouatta guariba*) and black howlers (*A. caraya*) in a contact zone in the Atlantic Forest of Argentina to evaluate the potential for interspecific competition. During 12 months, along with data on food availability, we collected 1,394 hours of observational data on feeding behaviour and GPS-based data on ranging behaviour of two groups of each howler species using scan sampling. Both at the species- and group-level, we analyzed (1) feeding behaviour, in terms of daily time spent feeding, dietary diversity (Shannon index  $H'$ ), and use of different feeding strata; (2) dietary overlap (Morisita-Horn index  $C_H$ ); (3) home range size, use and overlap (fixed kernel method). Across months, black howlers fed at lower strata and had a more diverse diet (mean  $\pm$  S.E.,  $H' = 2.77 \pm 0.08$ ) than brown howlers ( $H' = 2.39 \pm 0.09$ ). However, both species spent

similar amounts of time feeding and their diets overlapped extensively ( $C_H = 0.6 \pm 0.05$ ). In particular, across months, heterospecific groups, which overlapped in their home ranges and core areas consistently more than conspecific groups, did not overlap in diet less than conspecific groups. Given the high degree of niche overlap, syntopic brown and black howlers are likely to be competing for food. This could explain the essentially parapatric distribution of howler species throughout the Neotropics.

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## Causal Knowledge about a Proto-Tool Task in Humans and Chimpanzees: Is Simple Association That Simple?

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*Key Words:* Cognition · Causality · Support problem · Great apes · Tool use

Both humans and chimpanzees are flexible tool-users, who discern the functionally relevant features of a tool in a certain context. Whereas causal comprehension is assumed in humans, it has been stated that chimpanzees' performance in tool-using tests emerges through learning perceptual regularities. Here, chimpanzees ( $n = 23$ ) from Leipzig Zoo (Germany) and children (2-year olds,  $n = 13$ ; 3-year olds,  $n = 19$ ) from Madrid (Spain) performed in two conditions a strip pulling task. In the causal condition, they could pull one of two parallel paper strips on a platform, baited on their distal end. One of the strips was cut into two pieces and therefore was not functional. In the perceptual condition, instead of paper strips there were stripes of the same shape, size, and colour painted on the platform. Here the subjects chose by touching a stripe and obtained the reward from the experimenter. All the subjects except half of the chimpanzees got the reward when they chose the continuous strip(e) (direct contingency). The remaining chimpanzees had to choose the discontinuous strip(e) (reverse contingency). Overall, both chimpanzees and children solved the direct contingency in the causal condition. In contrast, only two 3-year-old children solved the perceptual condition. Chimpanzees did not solve the reverse contingency in either condition. These results suggest causal understanding of the task by chimpanzees and children from at least 2 years of age, and difficulties in learning about perceptual arbitrary cues in the three groups, a capacity that seemingly starts to emerge in humans around 3 years of age.

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## Genetic Differentiation of Bornean Orang-Utan Populations

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*Key Words:* Genetic differentiation · Refugium · *Pongo pygmaeus* · Geographical barrier · Conservation

Historic levels of genetic isolation and gene flow shape current patterns of genetic diversity and point to the evolutionary significant units for conservation management. To date, sur-

prisingly little is known about genetic diversity patterns of Bornean orang-utans due to the fragmented picture provided by previous studies. While there is conflict regarding population structure throughout Borneo, local studies of the *P. p. morio* subspecies in Sabah detect high differentiation of populations across the Kinabatangan River, highlighting its role as a barrier to gene flow. The lack of a clear picture of population structure stems mainly from sample size limitations. The current meta-study is novel in that it capitalizes on the use of a large number of non-invasive samples from different populations across Borneo (Tuanan, n = 32, Sungai Lading, n = 26, Sabangau, n = 19, Gunung Palung, n = 6, Danum Valley, n = 14, and Kinabatangan, n = 20) and separated by various rivers. We used autosomal data from 15 microsatellite loci as well as control region mtDNA haplotypes. Our findings are consistent with high levels of population differentiation despite indications of a recent radiation within Borneo, possibly from a central refugium during the Last Glacial Maximum (~20 ka). MtDNA haplotypes point to at least 6 geographical clusters, with considerable substructuring within the *P. p. wurmbii* subspecies, particularly for populations in the south of the island where major rivers are not crossable. We discuss these results in the context of possible historical scenarios leading to current patterns and the future of conservation management policies.

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## The Effects of Forest Disturbance on the Population Density of the Bornean Orang-Utan in Tanjung Puting National Park, Central Kalimantan, Indonesia

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*Key Words:* Orang-utan · Tanjung Puting · Nest counts · Disturbance · Population density

The effects of forest disturbance on populations of the Bornean orang-utan (*Pongo pygmaeus*) are not fully understood. We used nest-count surveys conducted from June to August 2008 to compare orang-utan density across disturbed and undisturbed forest sites in Tanjung Puting National Park, Central Kalimantan, Indonesia. The results show higher population densities in well-established secondary peat-swamp forest (5.1 individuals per km<sup>2</sup>) than in primary peat-swamp forest sites (average of 1.7 individuals per km<sup>2</sup>), suggesting orang-utans are unaffected by disturbance when forest is left to recover. Very low population density was estimated in peat-swamp forest recovering from recent heavy illegal logging (0.7 individuals per km<sup>2</sup>), implying that orang-utans adapt less well in the short term following logging. No orang-utan nests were detected in any sites recovering from intense forest fires. A higher density of orang-utans was estimated in primary dry-ground forest (3.1 individuals per km<sup>2</sup>) than in primary peat-swamp forest sites, contrary to the general assumption that peat-swamp forest is preferred orang-utan habitat. This study is the first to survey primary peat swamp in Tanjung Puting and to investigate the effects of the 2006 fires. It presents only the second major assessment of the orang-utan population within Tanjung Puting National Park and estimates an overall population of 9,281 individuals.

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## Information Dissemination as an Explanation of Troop-Level Aggregation in Fission-Fusion Species with Varied Party Composition

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*Key Words:* Social structure · Fission fusion · Altruistic communication · Agent-based modeling

In Hamilton's (1971) explanation of aggregation, group size is constrained by the carrying capacity of an environment, but sustained by predation risk. However, for species exhibiting high levels of fission-fusion (FF) social dynamics, predation risk appears to affect the size of the travel parties, but not of the troop. FF affects the constraint on troop size by allowing an increased net dispersal during foraging (Lehmann et al., 2007). For some species, e.g. hamadryas baboons, the lower limit of troop size might reflect an increased risk of predation at night. But for other species, such as spider monkeys, chimpanzees and humans, the full troop rarely assembles. These species are also characterised by unstable party configuration – on different days different animals associate. One possible selective force supporting troop size is thus information sharing. This could apply to temporary food resources such as ripe fruit, and may also be a preadaptation for culture. If so, we would expect another constraint on troop size besides Dunbar's (1992) time-budget limits for relationships, but also from inclusive fitness (Hamilton, 1964). The altruistic dissemination of useful resources is known to require average relatedness proportional to the cost of this dissemination (Cace and Bryson, 2007). We present a social model where FF derives simply from oscillations in individually-assessed risk and hunger. This model also demonstrates emergent behaviour similar to border raids and border patrols. A further model shows FF without oscillating risk, but facilitating group exploitation of occasional resource bonanzas.

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## On the Neglected Behavioural Variation between Sympatric Primate Groups

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*Key Words:* Vervet monkeys · Variation · Social learning · Tradition

Primatologists have, for a long time, documented individual differences in behaviour. More recently, behavioural differences between groups belonging to different populations have been a research focus because several of these differences seem to be due to arbitrary traditions. However, we largely lack information on the degree of similarity in the behaviour of sympatric groups of the same species. How strong is within-site variation compared to between-site variation? Can within-site variation be readily explained with small scale variation in ecology or might we find local traditions on the level of individual groups? We will present observational and experimental data on six neighbouring groups of vervet monkeys at Loskop Dam Nature Reserve that address within-site variation. The data demonstrate significant variation between the groups with respect to a variety of social and foraging behaviours. These differences can partly be explained by ecological variables like group size and food availability. Several differences, however, including different responses to experimental manipulations, lack an ecological explanation and hence suggest local traditions.

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## Psychological Consequences of Cooperative Breeding in Primates

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*Key Words:* Cooperative breeding · Prosociality · Cognition

Broadly defined, cooperative breeding refers to any breeding system in which individuals other than parents help to care for and provision offspring. According to the Cooperative Breeding Hypothesis, the adoption of this breeding system played a crucial role during human evolution; it can account for many of our species-specific demographic and life-history traits and with them our ability to move into new habitats and our subsequent worldwide geographic distribution, and even our dramatically enlarged brains. Understanding the psychological, i.e. emotional/motivational and cognitive consequences of cooperative breeding in non-human primates is a necessary prerequisite for evaluating the explanatory power of the Cooperative Breeding Hypothesis in this domain. We present the results of a literature review suggesting that in non-human primates and other mammals, cooperative breeding is associated with emotional/motivational predispositions such as increased social tolerance and attentional biases towards conspecifics, as well as with increased socio-cognitive performance, indicating that cooperative breeding might also account for these features in humans. Less clear is whether cooperative breeding is also related to spontaneous prosociality, in part due to the use of divergent test paradigms. This issue is of particular relevance because spontaneous prosociality is a key ingredient of uniquely human cognition, and we suggest an experimental approach which can provide comparable data from various species with minimal experimental manipulation of the subjects. Finally, we propose questions which will have to be addressed in the future to understand fully the impact that cooperative breeding had during human evolution.

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## Conflict between Local Human Communities and Non-Human Primates in Guinea-Bissau, West Africa

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*Key Words:* Non-human primates · Conflict · Bushmeat · Conservation · Perceptions

Conservation strategies which do not consider cultural and economic variables and local participation are doomed to fail: wealth, gender or religion must be incorporated as many of these variables constitute identity factors of local communities and strongly influence perceptions of nature, biodiversity, landscapes and ecosystems. We present data collected in Guinea-Bissau via surveys and observation applied in tabancas (small villages) in isolated rural areas. Data were collected on non-human primates (NHP) such as chimpanzees, Guinea baboons, King colobus, western red colobus, Campbells' monkeys and vervet monkeys, as well as other wildlife. Conflicts between locals and NHP exist for several reasons: (i) resource competition; (ii) traditional taboos that used to protect primate species are losing their effect; (iii) the authority of old villagers is being challenged; (iv) deforestation, slash-and-burn agricultural technique and large cashew-tree plantations are responsible for habitat loss and (v) bushmeat consumption. Bushmeat consumption was not common among all religious groups, but hunting was



performed by locals with different religious backgrounds (Muslims, Christians and Animists). While gender is another factor that affects the perceptions of wildlife (e.g. intelligence and proximity ranking, aesthetic values, among others), age influences NHP bushmeat consumption. NHP survival is increasingly being threatened by new values transmitted by globalization and the dominant economic model. Conflict frequency is on the rise and conservation strategies organized by international and local NGOs still do not take into account cultural and economic variables.

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## **Behavioural Features of Baobab Smashing by Savannah Chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal: A Referential Model for the Origin of Human Material Culture**

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*Key Words:* Western chimpanzees · Baobab fruits · Material culture · Behavioural features · Evolution

Behavioural observations of savannah chimpanzees (*Pan troglodytes*) are important for understanding the evolution of early hominin material culture, which likely evolved under similar ecological conditions. Recent research indicates that percussive technology was widespread in the Oldowan, possibly originating in processing fruits, and preceding cracking, stone knapping and pounding. Use of natural anvils to open embedded food items is widespread among chimpanzees, but the simplest percussion has seldom been thoroughly investigated. This study focused on behavioural characteristics of baobab fruit pounding among Fongoli chimpanzees in south-eastern Senegal. The community of 35 individuals included 11 adult males, 9 adult females and 15 immature chimpanzees. Most baobab fruit smashing was arboreal: 64.8% on horizontal branches, 2% on trunks, 32.5% on terrestrial stone anvils, and 1% on earth. Right-handed pounding was most prominent (70%), although left hand use notably occurred among particular individuals (23%), whilst some immatures were ambidextrous (7%). Pounding positions included tripod (32.5%), sitting (42.6%), bipedal (15.7%), squatting (1.2%) and shifting postures (8%). Baobab fruit was held by the stem (72%) or by the fruit itself (28%) during smashing. Median number of hits to open fruits was 13 (range 2–172), although youngsters needed significantly more hits for success. Fongoli chimpanzees often transported baobab (maximum 5 fruits in mouth) up to 1 km to feeding sites. ‘Archaeological’ details were compared to neighbouring chimpanzee communities and to prehistoric hominin sites in East Africa. Findings have valuable implications for the reconstruction of early hominin land use, especially when behavioural and ethoarchaeological data are compared.



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## Food-Associated Calling Sequences in Bonobos, *Pan paniscus*

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*Key Words:* Bonobo · Vocalizations · Food · Call sequences · Chimpanzee

When encountering food, chimpanzees and some other primates produce specific calls, whose acoustic structure co-varies with the caller's food preference. For chimpanzees, there is evidence that listeners use these contingencies to guide their own foraging behaviour. Here, we investigated the vocal behaviour of another great ape, the bonobo (*Pan paniscus*), in response to food. We were able to distinguish acoustically five different call types given during interactions related to food. These calls were not given singly, but usually as part of long and complex call sequences. We established the food preference hierarchies for ten different individuals, housed at two different facilities. We found that the composition of call sequences produced by these individuals was not random, but related to the type of food encountered by the caller. Significant variation in call composition was explained by taking into account the caller's individual food preferences, suggesting that bonobo food calling sequences convey meaningful information to other group members.

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## Are Chimpanzees Good Ambassadors for Biodiversity Conservation in Tombali (Guinea-Bissau, West Africa)?

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*Key Words:* Flag-ship species · Sociozoologic scales · Social perceptions · Attitudes · Community-based conservation

The status attributed to different species – 'good' or 'bad' – can provide clues about the underlying attitudinal factors that determine which animals may act as flag-ship species for environmental conservation purposes. Such sociozoologic scales can be applied to assess people's perceptions towards biodiversity. This presentation considers how people from Tombali (Guinea-Bissau) perceive chimpanzees. Three hypotheses are considered: (i) A correlation between positive attitudes and edibility is expected, except for chimpanzees which are given other attributes; (ii) In general, chimpanzees are perceived as 'good' animals, due to their human-like appearance; (iii) Negative perceptions are due to a lack of knowledge regarding chimpanzee behaviour, as a consequence of a low number of encounters between humans and apes. A survey was conducted during two months. The sample (n = 257) included all adult inhabitants who could be contacted. Photos of the Guinean fauna (n = 27) were shown to subjects who were asked to rank these according to adjectives such as: 'good', 'bad', 'edible', 'inedible', 'pretty', and 'ugly', among others. Descriptive statistical analysis and principal component analysis were applied to these rankings. In general, apart from some religious beliefs that might protect chimpanzees from poaching and bushmeat exploitation, locals do not appear to be very fond of these primates. Fortunately for chimpanzees, their human resemblance has been protecting them from heavy hunting pressure. Chimpanzees are potentially good ambassadors for a conservation programme only if there is an understanding of why people hold negative attitudes and how these can be mitigated, as found for women and in some religious contexts.

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## What Mediates Personality Variation in Grey Mouse Lemurs (*Microcebus murinus*)?

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**Key Words:** Personality · Risk-taking · *Microcebus murinus* · Exploration · Boldness

Consistent individual differences in behaviour across time and context have been described for a variety of animals and are defined as temperament or personality. Personality traits are moderately heritable and have been shown to affect several components of fitness. However, the processes responsible for the maintenance of personality variation within populations are mostly unknown. One potential mechanism is a life-history trade-off resulting from a correlation between risk-taking and other personality traits. The aim of this study was to test if personality is related to risk-sensitive foraging, and might thus affect the survival component of fitness, in small nocturnal primates under high predation risk. This study was performed in Kirindy forest, western Madagascar, where individuals of a natural population of grey mouse lemurs (*Microcebus murinus*) have been regularly (re-)captured and individually marked since 2002. I measured personality in open field and novel object tests in 53 (22f, 31m) individuals within their home-range. Additionally, I exposed 12 of these individuals to low and high risk situations, while controlling for resource value at artificial feeding sites and tested for differences in individual risk-taking behaviour. These tests revealed: (1) consistent individual differences in exploration, boldness and activity and (2) a correlation between risk-taking behaviour in a feeding context and other personality traits. These preliminary results indicate that survival costs might mediate personality variation in grey mouse lemurs.

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## Brown Spider Monkeys (*Ateles hybridus*) in Fragmented Areas: Behavioural and Ecological Adaptations

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**Key Words:** Fragmentation · *Ateles hybridus* · Behavioural ecology · Population density

Conservation of threatened primates in the wild largely depends on the understanding of their behavioural ecology and population biology that may lead to the implementation of successful conservation strategies. Brown spider monkeys (*Ateles hybridus*) are nowadays facing a high risk of extinction due to habitat loss, fragmentation and hunting throughout Colombia and Venezuela. Data on the behavioural ecology and density of two populations of *Ateles hybridus* have been collected. We conducted line transects to estimate the population densities at two sites within Serrania de Las Quinchas and in small forest fragments at San Juan in Colombia. We also collected data on the monkeys' social behaviour and ecology. We found higher densities of spider monkeys in recently disturbed forests, evidencing the short term effects of habitat loss on these populations. As for most studies on *Ateles*, brown spider monkeys relied heavily on ripe fruits at both sites. Nevertheless, their diet in the fragmented forests included one of the highest percentages of leaves reported to date. Home range size at Quinchas reached the size reported for other studies on *Ateles*. In contrast, the home range size of groups living in the small forest fragments was much smaller (ca. 30 hectares) and there was a very low percentage

of overlap between neighbouring groups. This study provides evidence for some immediate effects of fragmentation on the behavioural ecology of spider monkeys and in the long term will elucidate the effects of fragmentation on the population dynamics and survival of these endangered primates.

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## Cladistic Analysis of Human Sociosexual Behaviour and Life Cycle

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*Key Words:* Hominoidea • Phylogeny • Behaviour • Sex • Life cycle

Modern primatology, anthropology and sociobiology deal with the problem of fundamental reproductive, developmental and behavioural differences between humans and the rest of the Hominoidea. Such attributes of human nature as parental care, monogamy, long-term male-female bonds, concealed ovulation, menopause or longevity are mentioned frequently. Humans are considered unique in many of these traits and generally the most derived species of the hominoids in terms of their life history and sociosexual behaviour. This would definitely be true only under the assumption that humans evolved from a chimpanzee-like ancestor. However, no serious attempts have ever been made to analyze the conspicuous diversity of the ape/human behavioural patterns phylogenetically. So far, human sociobiology is implicitly based on the linear, ladder-like reasoning ('from apes to human beings') rather than on explicit evaluation of the phylogenetic trees. In order to fill this gap, we analyzed phylogenetically the available information concerning reproduction, ontogeny, behavioural patterns, social relationships and ecological background (75 characters) in all species of extant and some extinct apes, in order to reconstruct the individual clades' ancestors and the actual level of evolutionary novelty of the individual species. Our study reveals that the common ancestor of the Hominini (*Pan* + *Homo*) as well as common ancestors of Hominidae and Hominoidea showed more or less gorilla-like behaviour, mating system and sociobiology. Ergo humans, despite the universal assumptions, should rather be regarded as 'slightly derived gorillas' than 'highly derived chimpanzees'.

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## On the Significance of the 'Tchi-Fak': A Reflection on Species-Recognition in Loud Calls of Malagasy Sifakas (*Propithecus* spp.)

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*Key Words:* Communication • Loud calls • Species recognition • Sifakas • Playback experiments

Madagascar is one of the top global biodiversity hotspots with extremely high endemism rates for both flora and fauna, and the diversity of its endemic primates is still not completely known. Traditionally, scientists divided the genus *Propithecus* into 3 species – *P. diadema*, *P. verreauxi*, and *P. tattersalli* – with 4–5 subspecies in each of the first taxa, but recent studies have suggested that a larger number of distinct species should be recognized. Because vocalizations of non-human primates are predominately innate, vocal variation may be important in characterizing population divergence. In this study, I characterized geographical variation in

the ‘Tchi-fak’ – loud calls among wild *P. verreauxi* and its subspecies as well as *P. tattersalli*. Acoustic analyses revealed subtle as well as striking differences in call structure between taxa. In order to test whether differences in the acoustic structure of the taxon-specific loud calls are also perceived by sifakas, I conducted playback experiments with these calls in four different populations. Results revealed no clear-cut recognition of taxon-specific loud calls, probably reflecting the relatively recent divergence process among taxa.

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## Barbary Macaque Infants Are Costly Social Tools

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*Key Words:* Barbary macaques · *Macaca sylvanus* · Infant · Stress · Glucocorticoid level · Network analysis

Male Barbary macaques (*Macaca sylvanus*) constitute one of the renowned exceptions to the rule that male mammals typically spend little time with infants. As neither paternal investment nor improved future access to females explained male investment in infant care, we set out to test whether male interactions with infants function as a signal of status or rather as a means to stabilize social relationships with other males. We combined behavioural observations with estimations of the stress response via faecal glucocorticoid analysis, to determine the costs and benefits of male caretaking behaviour. The study was conducted on 12 male Barbary macaques living in the enclosure ‘La Forêt des Singes’ at Rocamadour, France. As previous studies suggested that grooming affects glucocorticoid level, we also examined grooming patterns. Neither the amount of grooming given nor of grooming received varied with glucocorticoid levels. Infant care was not related to male rank, rejecting the assumption that infants are a rare commodity that males compete for. Social network analyses revealed that infant carriers had more elaborate social ties to other males than non-carriers. Importantly, the time spent with infants alone, but not the contact time with other males, was related to elevated glucocorticoid levels, suggesting that specific males use infants to gain access to the male-male network and to stabilize precarious relationships. Our findings support the view that Barbary macaque infants function as ‘social tools’ that come at a price.

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## Social Construction of the Feeding Niche in Orang-Utans: A Comparative Study

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*Key Words:* Social learning · Culture · Peering · Horizontal/oblique transmission · Food complexity · Independent exploration · Orang-utan

In primates, social transmission of behaviour has resulted in behavioural variation at geographically different sites. This study aimed to examine social learning in a wild population of Sumatran orang-utans, *Pongo abelii*. The target population at Suaq Balimbing, Sumatra, exhibits the largest known cultural repertoire of all orang-utan populations, including tool-use while foraging. Results show that young orang-utans selectively pay visual attention according to increasing processing complexity as well as rarity. Additionally we found more practicing of foraging skills after intense observation of other individuals using the particular technique. For

choice of role models, after their mother, Suaq infants tend to pay attention to closely associated individuals when opportunities occur. The results were compared to observations at a Bornean site, Tuanan, central Kalimantan. Focusing on 6 infants of Suaq and 4 of Tuanan we measured opportunities for social learning and found a significant difference in sociality between these two sites. Orang-utans at Suaq display great social tolerance. Hence offspring raised here are exposed to opportunities to learn socially from multiple role models from an early age. This comparative approach enables us to explore the reasons for cultural differences, and supports the hypothesis that social learning contributes to the construction of intelligence.

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## Reproductive Parameters of Wild Female Assamese Macaques (*Macaca assamensis*)

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*Key Words:* Faecal hormone analysis · Gestation length · Interbirth interval · Female cycles · Seasonality · *Macaca assamensis*

Information on basic reproductive parameters is crucial for the understanding of primate reproductive strategies. Macaques are of special interest, because, although sharing basic patterns of social organisation, they exhibit a high degree of variation in social structure and reproductive strategies. For example, macaque species vary in the degree of seasonality, number of cycles to conception, development of sexual signals, etc., all of which influence the mating strategies of the sexes. As a basis for investigating determinants of the observed variation in reproductive strategies among macaques, we report here information on reproductive traits for wild Assamese macaques (*Macaca assamensis*). During two consecutive reproductive seasons, data were collected from 15 adult females living in a multimale-multifemale group (~60 individuals) at Phu Khieo Wildlife Sanctuary, Thailand. In order to assess ovarian activity, timing of ovulation and to ascertain conceptions, 2,140 faecal samples were collected and measured for oestrogen (E1C) and progesterone metabolites (20a-OHP). Results indicate that reproduction in Assamese macaques is highly seasonal, with a mating season lasting from October to January and a birth season from mid-April to the end of June. Females showed no cyclic ovarian activity outside the mating season and conceived during the first or second menstrual cycle. Preliminary data indicate an average gestation length of 164 days (n = 6). Females usually give birth biannually; however, a small percentage of females who had given birth early in a birth season produced an infant the next year. Discussion will focus on the comparison of reproductive parameters among macaque species and its consequences for reproductive strategies.

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## The Hoolock Gibbon Status Review Project: First Results from Rakhine and Kachin States

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*Key Words:* Hoolock gibbon · Myanmar · Conservation · Deforestation · Hunting

Globally, hoolock gibbon populations are dwindling due to forest clearance, disturbance and hunting. Myanmar is believed to hold large intact areas of prime gibbon habitat and to support the largest remaining populations of hoolock gibbons. Yet there is no significant data on the conservation status of the gibbons in this country. The Hoolock Gibbon Status Review project was recently implemented jointly by the People Resources and Conservation Foundation (PRCF), Fauna & Flora International (FFI), the Myanmar Biodiversity and Nature Conservation Association (BANCA) and the Zoology Department of the University of Yangon, to assess comprehensively the conservation status of hoolock gibbons in Myanmar. This will help identify, prioritise and plan conservation interventions to boost options for the long-term conservation of these apes. The project will also identify major threats to gibbon populations in Myanmar and raise awareness among stakeholders regarding conservation needs for the species. We present the first results of our field surveys in Rakhine and Kachin states, i.e. the southwest and the northeast of Myanmar. Hoolocks were encountered in every survey area, but so were habitat destruction, habitat deterioration and hunting. Near the Chinese border in Kachin, we found massive ongoing deforestation throughout the survey area caused by Chinese timber companies. The occurrence of hoolock gibbons there is restricted to few relict forests, all of which may be cleared within the next two years. These preliminary results suggest that the status of hoolock gibbons in Myanmar may be more alarming than previously believed.

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## What's the Risk? Determining Predation Risk in a Baboon-Leopard System

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*Key Words:* Predation · Felid · Group size · Group spread · Vigilance · Baboon

The importance of predation in shaping the behaviour and ecology of primates has long been recognized. Nevertheless, the fact that actual predation was rarely observed led to many studies concluding that food acquisition played a more important role in primate evolution. More recently, studies have attempted to quantify how animals perceive and act upon predation risk rather than focussing on observing successful predation events. This approach presents challenges, however, most notably in identifying the precise factors that determine predation risk in natural populations. Here I take a modelling approach to determine the factors influencing risk of predation in a baboon-leopard system. The model illustrates that visibility and predator density are the key habitat parameters underlying variation in risk, with inter-individual distance as the main factor limiting prey ability to detect predators. Empirical data provide support for some of these results and I outline ideas for further research to examine other predictions from the model.

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## Factors Influencing Skill Transmission in Captive Chimpanzee Groups

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*Key Words:* Chimpanzee · Social learning · Two-action task · Conservatism · Peering

We studied the ways in which naïve chimpanzees (*Pan troglodytes*) employed social learning to acquire innovations performed by others. The extent of cultural evolution is critically dependent on whether naïve individuals deploy social learning and, if so, whom they choose as role models and whether they have opportunities to interact and, thus, learn from them. Two processes in particular may bring about stagnation in primate traditions: individual conservatism and active conformity. We examined whether conservatism in social learning and interactions with knowledgeable individuals, as assessed by peering and scrounging, actually affected the adoption of novel techniques. Innovation-and-transmission experiments with two-action food tasks were conducted in four different groups of captive chimpanzees (Sanctuary hopE, Austria: 5 and 9 chimpanzees; Abenteuerland Walterzoo, Switzerland: 11 chimpanzees; Leintal zoo, Germany: 33 chimpanzees). We recorded the distribution of the solutions varying over time and with different availability of the solutions. In all groups we found evidence for conservatism, which in fact slowed down or even prevented the transmission of novel alternatives. Chimpanzees showed a great interest in their group members' manipulations of the food tasks and especially less skilled chimpanzees had high rates of peering. Scrounging seemed to be a major factor explaining the adoption of alternative techniques in that skilled chimpanzees tended to use the technique that was less vulnerable to scrounging. Thus, not only conservatism, but also interactions among group members critically influenced the transmission of novel techniques within the groups.

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## Dispersal Patterns and the Influence of Social Status on Paternity Success in Six Free-Ranging Vervet Monkey (*Chlorocebus aethiops*) Groups

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*Key Words:* Priority of Access Model · Paternity concentration · Vervet monkeys · Microsatellites

The 'Priority of Access Model' (PoA) introduced by Altmann in 1962 suggests that a high-ranking male gains a reproductive advantage by monopolizing mating access to sexually attractive females. The basic prediction derived from this model is that in social groups with a linear dominance hierarchy the probability for each male to sire offspring decreases according to dominance rank, with paternity success being entirely concentrated in the dominant male when breeding synchrony is low and female mate choice restricted. To test this prediction properly, the number of oestrous females in a group and the duration of the overlap of their receptive period would have to be known at all times. So far, many studies have been unable to assess these parameters thoroughly, due to the high amount of time and effort that has to be invested. This study will investigate the effects of social status on reproductive success indirectly by assessing paternity concentration and therefore reconstructing dominance-reproductive success



relationships purely from genetic data. For this purpose, faecal samples have been collected from all individuals in six free-ranging vervet monkey (*Chlorocebus aethiops*) groups living in adjacent home ranges in the Loskop Dam Nature Reserve in the Mpumalanga province, South Africa. Each of the group's social rank history of the last two to three years is known. We genotyped the individuals at 16 human-derived microsatellite loci for subsequent paternity analysis and information on male dispersal. We present our preliminary findings on the relatedness patterns within and between the study groups.

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## Cooperative Breeding and Brain Size in Mammals and Birds

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*Key Words:* Comparative study • Brain size evolution • Life history

Previous analyses have found consistent support for the 'expensive brain' framework, which predicts that relatively large-brained animals either exhibit increased total energy flow or re-allocate energy from other expensive functions such as digestion or production (growth and reproduction). The expensive brain hypothesis also predicts that energetic support to breeding females would reduce energetic constraints and thus allow for brain enlargement, if selection would favour this. To test this prediction, we collected data on different aspects of breeding help in mammals, such as the amount of carrying, feeding, or protecting the offspring by the father or other group members, and the frequency of allonursing, huddling and nest-sharing. For bird species, we use a published classification of breeding systems together with information on whether hatchlings are fed before or after fledging, as a proxy for the amount of allomaternal help. Using a large, revised dataset on brain and body mass data (430 eutherian and 603 bird species) we confirm the predicted positive correlation between brain size and the extent of allomaternal help in both mammals and birds (controlling for both body mass influences and phylogenetic relatedness). In addition, we show that in mammals, different types of help correlate differently with brain size according to their energetic value. Because humans are also cooperative breeders, our findings imply an important role for cooperative breeding in the evolution of the very large human brain.

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## The Evolution of Voluntary Food Transfers among Primates

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*Key Words:* Food sharing • Reciprocal altruism • Costly signalling • Dominance • Kin selection

Voluntary food transfer among kin and non-kin is a human universal, despite the costs. To trace its evolution, we reviewed the available literature on food sharing among non-human primates ( $n = 150$  publications). By comparing the relative number of publications on food transfers, we show that they are particularly common among extractive foragers, where infants depend on food transfers to acquire nutrition and information. Using cladistic analyses we show that the evolution of food transfers among adults is significantly more likely in clades where transfers to infants are already common. In addition, the presence of allo-maternal care has facilitated the evolution of food transfers among adults. Thus, we suggest that difficulty of

diet first led to tolerated taking by infants. Food taking could then be used to test and demonstrate tolerance among adults in taxa where this trait was already present. This was possible when subordinates had some leverage over dominants, because they could choose other association partners, i.e. in fission-fusion (e.g. *Cebus*, *Pan*, *Pongo*) or modular societies (e.g. *Rhinopithecus*, *Pygathrix*). This scenario allows predictions as to which other taxa should show food transfers given the right conditions. Finally, while the most common form of transfers among all non-human primates is tolerated taking, we suggest that more active forms of transfers may evolve either among kin groups when the motivation to help is high (i.e. among cooperative breeders) or if active sharing can serve as a costly signal to potential cooperation partners and is thus reciprocated more than passive taking.

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## How Sexy Does a Girl Have to Be to Achieve Her Goals?

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*Key Words:* Mating strategies · Sexual signals · Colobines · Female mating competition · Sexual swellings

Sexual swellings are imprecise indicators of ovulation that allow females to attract males. The question remains why females of some species develop exaggeratingly large swellings when a less costly signal should suffice. We looked at one species, *Procolobus tephrosceles*, in Uganda, with small sexual swellings and a closely related species, *Procolobus badius badius*, in Ivory Coast, with large swellings. We investigated two possible reasons why females may require a large costly signal despite being considered the choosy sex in these primates. (1) Females could need a strong signal to outcompete other females in order to attract the right or the most males. (2) Large signals give females the opportunity to avoid male monopolisation allowing them to attract enough males to avoid infanticide risk or to achieve mate choice. To test these alternatives, we studied the length of the receptive period, operational sex ratio, female promiscuity, male interest in females and female proceptivity and choosiness in these two species with different sexual swelling sizes but similar social systems. Our preliminary results suggest that the species with the strongest female-female mating competition has the largest swellings, but that the duration of the receptive period and the occurrence of post-conception swellings is similar in both species. We suggest that the strength of the sexual signal (i.e. the species-specific size of the swelling) is determined by the intensity of female mating competition and male mate choice, while a long receptive period is sufficient to achieve promiscuous mating and avoidance of male monopolisation.

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## Identification and Prevalence of *Strongyloides* spp. in Wild, Semi-Captive and Captive Borneo Orang-Utans (*Pongo pygmaeus*) Based on PCR Using Targets in Ribosomal DNA and Coproscopy

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**Key Words:** Bornean orang-utan · *Pongo pygmaeus* · *Strongyloides f. fuelleborni* · rDNA sequencing · Infection risk factors

Nematodes of the genus *Strongyloides* which can cause potentially fatal infections are of major importance for the health of the endangered orang-utan (*Pongo* spp.). Since little is known about its infection dynamics in orang-utans, this study aimed to determine factors that significantly influence the infection risk for *Strongyloides* in orang-utans and to characterize the parasite genetically down to species and subspecies level. Faecal samples from 163 captive, 61 wild individuals and 38 captive groups of Borneo orang-utans (*P. pygmaeus*) were collected in Kalimantan, Indonesia, over six months in 2006. *Strongyloides* isolates from 1 human were additionally available. Larvae were identified by light microscopy, PCR amplification and direct sequencing of parts of 18S and ITS1 rDNA. Prevalences (assessed by microscopy) were 39% for captive, 33% for wild individuals and 58% for groups. In captivity, infant orang-utans had a significantly higher infection risk than adults (logistic regression model analysis; OR 3.05; 95% CI 1.39–6.73). Thirty of 31 investigated sequences, including the human isolate, displayed 98.5–100% identities of the 18S rDNA locus with *S. fuelleborni fuelleborni*. One isolate from a captive orang-utan had 98.7% sequence identity with *S. stercoralis*. Sequences of the ITS1 rDNA gene were 82.1–97.5% identical with *S. f. fuelleborni*, *S. stercoralis* and *S. procyonis*. The results suggest that a different genotype of *S. f. fuelleborni* with zoonotic potential exists in wild and captive Borneo orang-utans, which may transfer the nematode to humans. The findings can contribute to improve health management plans for Bornean orang-utans and Indonesian public health programmes.

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## Kinship and Social Bonds in Wild Female Chimpanzees at Ngogo, Kibale National Park, Uganda

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**Key Words:** Kinship · Kin selection · Social bonds · Chimpanzees

A large body of research suggests that kinship has a strong influence on the formation of social bonds in many group-living primates. Here we combine behavioural observations of party association, spatial proximity, grooming and space use with extensive molecular genetic analyses to determine whether female chimpanzees ( $n = 39$ ) form strong social bonds with unrelated individuals of the same sex. We compare our results with those obtained from male chimpanzees who live in the same community and have been shown to form strong social bonds with each other. We demonstrate that party association is as good a predictor of spatial proximity and grooming in females as it is in males, that the highest party association indices are consistently found between female dyads, and that the sexes do not differ in the long-term stability of their party association patterns, and that these results cannot be explained as a by-product of

the tendency of females to range selectively in particular areas of the territory. We also show that the vast majority of female dyads that form strong social bonds are not closely related, and that 'subgroups' of females who frequently associate with one another in similar areas of the territory do not consist of relatives. These results suggest that a passive form of kin-biased dispersal, involving the differential migration of females from neighbouring communities into subgroups, was unlikely to be occurring. Thus, as in males, kinship plays a limited role in structuring the intrasexual social relationships of female chimpanzees.

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## **A Unified Account of the Primate Tolerance Spectrum**

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*Key Words:* Social structure · Macaque · Tolerance spectrum · Socio-ecological theory · Agent-based modeling

We propose an account for macaque social structure which reconciles two dominant theories, the socio-ecological theory [SE, van Schaik, 1989] and the phylogenetic inertia theory [PI, Thierry, 2007], and includes aspects of the DomWorld theory [DW, Hemelrijk, 2002]. From PI we take the model that structure evolves as a complex of tightly-correlated behaviour patterns, which are adaptively sculpted to be generally robust to selective pressure, but ease adaptation along 'variable axes'. Such variation in evolutionary rates is hypothesized by evolutionary developmentalists [Kirschner and Norton, 2006]. The oldest version of the macaque behaviour complex is exhibited by the Barbary macaque, placed at 3 of 4 on the tolerance spectrum by Thierry [2004]. From SE we take that the primary selective pressures generating this complex have been infant mortality, predation and food availability. The tolerance spectrum reflects a variable axis, with increased predation pressure resulting in less tolerance. The evidence of Isbell [2008] agrees with DW that increased violence in individual interactions motivates the shift to more despotic social structures, with fewer social interactions and a better-specified dominance hierarchy. However, in keeping with SE we argue that dominance rank also facilitates adaptation via reproductive advantage. The extent of this role is determined by inclusive-fitness tradeoffs. In our model, fit males have greater reproductive success, though females allocate some fecundity to variation. Selection acts more weakly on females, amounting to greater resource access for the most productive matriline. We describe our theory through a series of agent-based models demonstrating its plausibility and consequences.

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## **Orang-Utan's Flexible Deployment and Cumulative Build-Up of Techniques in a Problem Solving Task**

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*Key Words:* Behavioural flexibility · Cumulative build-up · Cumulative culture · Orang-utan

Some human cultural traditions change over time and accumulate modifications in the direction of greater complexity, which has been described as cumulative cultural evolution. While striking cultural variation in behaviour from one site to another has been described in

chimpanzees and orang-utans, cumulative culture seems to be limited to humans. In recent experiments, captive chimpanzees were found to be rather conservative, as they maintained the technique they had learned initially. Behavioural flexibility in the sense of continued interest in acquiring new solutions to a task after having learned a solution is a vital prerequisite for cumulative build-up of techniques. Our aim was therefore to investigate experimentally how flexible captive orang-utans would be in applying techniques in a problem solving task. We provided nine Sumatran orang-utans in Zurich Zoo with two types of transparent tubes partly filled with syrup, along with potential tools, such as sticks, twigs, wood wool and paper. In the first phase of the experiment the orang-utans could reach inside the tubes with their hands (regular conditions), in the second phase tubes were too narrow for their hands to fit in (restricted conditions). We found that orang-utans showed high behavioural flexibility, applying ten different techniques under regular conditions and switching techniques under restricted conditions if this was advantageous. Additionally our experiment yielded two more complex techniques building on previous ones. This suggests that orang-utans have some power for cumulative build-up of techniques, and possibly modest cumulative culture, in order to deal with novel exigencies.

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## Effects of Predation Risk on the Grouping Patterns of Spider Monkeys

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*Key Words:* Predation risk • Antipredator strategies • *Ateles*, mineral licks • Fission-fusion

Predation risk is considered one of the driving forces underlying the evolution of gregariousness in diurnal primates. Studying the influence of predation risk on primate grouping patterns is difficult, however, as predation events are seldom observed and many primates have evolved effective anti-predator strategies. Spider monkeys (genus *Ateles*) have very fluid grouping patterns, and subgroups change frequently in size and composition, providing an opportunity to assess directly the effects of predation risk on grouping behaviour. In northwestern South America, spider monkeys come to the ground at mineral licks to practice geophagy, where they are exposed to predation by large felids. Using video camera traps, we monitored all mineral licks visited by three groups of spider monkeys (*Ateles belzebuth*) at the Tiptuni Biodiversity Station in Amazonian Ecuador to document visitation patterns at these 'risky' sites, and we collected observational data on social behaviour and grouping patterns from two of these groups. We found that maximum subgroup size was higher on days of salt lick visitations and that subgroup size increased during salt lick visits, reaching its peak when monkeys were in the salt lick area. Spider monkeys spent several hours in the trees surrounding the salt lick prior to descending to the ground (typically for <2 min per individual). Also, spider monkeys would descend only if males were present in the subgroup and if weather conditions were sunny with no wind. Our results support the hypothesis that diurnal primates adjust group size in response to the perceived risk of predation.

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## Chemical Mate-Guarding in Wild Saddle-Back Tamarins, *Saguinus fuscicollis*

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*Key Words:* Mate-guarding · Scent-marking · Sexual selection · Callitrichidae

Mate-guarding of fertile females is a male strategy to monopolize matings and thus to ensure paternity. Since in tamarins and other callitrichids, female reproductive status is advertised through scent-marks, one may ask whether males would also try to 'guard' by chemical means, i.e. overmarking. During a field study on the function of scent-marking in saddle-back tamarins (*Saguinus fuscicollis*) in north-eastern Peru, the opportunity arose to address this question during an episode of mate guarding observed in a polyandrous group of 1 female and 2 male tamarins. We compared the pattern of copulations, scent-marking and responses to scent-marks in both periods. Copulation frequency increased for the guarder, who monopolised 91% of the copulations. Scent-marking frequency decreased for all individuals, but the guarder increased the proportion of suprapubic marking. The guarder also marked more than the other male during mate-guarding, while there was no difference in the previous period. Female scent-marks were more frequently investigated by the guarder than by the other male. The guarder overmarked female scents more often than during the no-guarding period, and more than the other male. During mate-guarding, almost 50% of female scents were overmarked by the guarder, and more than 56% of the guarder's scent marks were employed to overmark the female's scents. Therefore, the other male had limited access to female scent-marks. These results demonstrate that mate-guarding has a chemical component in tamarins, and suggest that olfactory communication plays an important role in mate attraction and mating competition.

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## Population Genetic Structure of Chimpanzees from the Gulf of Guinea Region

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*Key Words:* Chimpanzee · Gulf of Guinea region · Genetic diversity · Geographic origin · Paleodemographic history

Studies of intraspecific variation among chimpanzees (*Pan troglodytes*) have revealed that the partitioning of genetic diversity in chimpanzees varies across Africa. The Gulf of Guinea region encompasses portions of Cameroon and Nigeria, and is home to two chimpanzee subspecies (*P. t. ellioti* [formerly *P. t. vellerosus*] and *P. t. troglodytes*). The ranges of these subspecies converge at the Sanaga River in central Cameroon, but little is known about the paleodemographic history of chimpanzees across this region. Here, we present multilocus genetic data from 47 captive chimpanzees housed at the Limbe Wildlife Centre (LWC) in Cameroon. A geographic origin of each LWC chimpanzee was inferred using smoothed and continuous assignment tests based on allele frequency maps constructed from 10-locus microsatellite genotypes of >100 geo-referenced chimpanzee samples. These assignment tests were robust in inferring an origin

for each chimpanzee as originating either north or south of the Sanaga River in Cameroon. After inferring a putative origin for each chimpanzee, we tested alternative scenarios of genetic history within a hierarchical hypothesis-testing framework using complete mtDNA genomes, Y-chromosome microsatellite genotypes and 26 intergenic autosomal loci. Our hypothesis-testing framework was designed to (1) explore how different population parameters have influenced chimpanzee paleodemographic history and (2) infer how rivers and forest history have affected the partitioning of chimpanzee genetic diversity. The results of our analyses suggest that both forest history and riverine barriers (particularly the Sanaga) have played a key role in shaping the unique paleodemographic history of chimpanzees across the Gulf of Guinea region.

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## Is Variety the Spice of Capuchins' Life? An Experiment on Token Value Representation and Food Choice

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*Key Words:* Variety seeking • Token • Value • Choice • Evolution of money

Money can be exchanged for a potentially unlimited variety of goods and services. Being 'the' medium of exchange, money is devoid of a direct hedonic value and its representation requires a high level of abstract thinking. In this study, we explored the processes involved in this one-to-many mapping in capuchin monkeys trained to exchange tokens for goods. We aimed to evaluate how eight capuchins (a) represent the value of a token (Multi-token) that allows them to choose one among 10 different foods (one high-preferred food and nine less preferred foods), in comparison with a token (Mono-token) that allows them to choose one among 10 pieces of the same high-preferred food, and (b) whether the quality of the less preferred foods affects capuchins' choices. In a first condition, the Multi-token was exchangeable for a variety of mid-preferred foods (B-foods), whereas in a second condition the Multi-token was exchangeable for a variety of low-preferred foods (C-foods). Both conditions involved 20 sessions, each consisting of (i) 20 binary choices between one Mono-token and one Multi-token, (ii) exchange of the selected token, and (iii) choice of one piece of food from a tray. In both conditions, capuchins consistently preferred the Multi-token, and after their choice they often opted for one of the less preferred foods – suggesting that the value of the Multi-token is mostly based on its ability to provide access to a higher variety of foods.

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## Locomotor Behaviour of Wild Orang-Utans (*P. p. wurmbii*) in Disturbed Peat Swamp Forest, Sabangau, Central Kalimantan, Indonesia

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*Key Words:* Locomotor behaviour • Orang-utan • *Pongo pygmaeus wurmbii* • Torso-orthograde suspension • Support use

This study examined the locomotor behaviour of a population of wild Bornean orang-utans (*Pongo pygmaeus wurmbii*) in disturbed peat swamp forest in the Sabangau Catchment,



Indonesia. The main objectives were to identify key associations between orang-utan locomotion and support use and to identify any major differences in locomotor repertoires between orang-utan species. The study took place between March and September 2007. A total of 6,599 instantaneous observations of positional behaviour were obtained, with 1,074 of locomotion. Thirteen individuals were observed, including all age-sex categories. The study revealed that torso-orthograde suspension dominates orang-utan locomotion, concurring with previous studies in dipterocarp forest. However, comparison with previous studies showed that whilst the overall locomotor repertoire of orang-utans does not differ substantially between species, the relative frequency of observed locomotor behaviours does differ. The subjects of the current study were found to exhibit substantially higher frequencies of tree-sway than observed in previous studies, suggesting this energetically efficient mode of locomotion is an important aspect of traversing the canopy in a disturbed peat swamp forest. Log-linear modelling was used to identify key associations between orang-utan locomotion, body size, height in the canopy, and support use. Whilst all variables included in the model were found to influence locomotion to a varying degree, support type and support diameter were found to have the strongest associations with locomotor repertoire. This supports the hypothesis of Thorpe and Crompton [2005] that orang-utans have evolved specific modes of locomotion in order to solve problems associated with traversing a complex arboreal environment.

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### **Tool Selection Based on Rigidity in Great Apes**

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*Key Words:* Problem solving · Tool selection · Tool properties · Causal knowledge · Primates

Wild chimpanzees use tools to solve a variety of tasks. Some tasks require pliable tools while others require rigid ones. Individuals consistently select appropriate tools for the task at hand. However, little is known about whether those choices are based on familiarity with the materials or some abstract knowledge about tool properties is also implicated. It is also unclear what type of information is required to select tools. Is manipulation of unfamiliar objects required or can observation alone suffice? We investigated whether chimpanzees ( $n = 9$ ), bonobos ( $n = 4$ ), orang-utans ( $n = 6$ ) and gorillas ( $n = 2$ ) at Leipzig Zoo selected new tools based on their rigidity. Subjects were confronted with an out-of-reach reward and a choice of three tools differing in colour, diameter, material and rigidity. We used a total of 10 different 3-tool sets (1 rigid, 2 flexible). Subjects were unfamiliar with the tools included in each set. Subjects were required to select and use the rigid tool to retrieve the reward. Experiment 1 showed that subjects chose the rigid tool from the first trial with a 90% success rate. Experiment 2 addressed the role of manipulation and observation in extracting information about rigidity. In the manipulation condition, subjects manipulated the tools before choosing, whereas in the observation condition, they only watched the experimenter manipulating the tools. Subjects performed equally well in both conditions (about 80% correct). We found no species differences in performance in either experiment. We conclude that great apes can spontaneously select unfamiliar rigid tools even after gathering only minimal observational information.

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## Molecular Phylogeny and Biogeography of Leaf Monkeys (genus *Presbytis*)

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*Key Words:* *Presbytis* · Leaf monkeys · Taxonomy · Phylogeny · Biogeography

With more than 50 taxa described already, the Asian leaf monkeys of the genus *Presbytis* represent one of the most diverse genera within the Old World monkeys. The classification of *Presbytis* taxa, their phylogenetic relationships and the biogeographic patterns that have led to the current distribution are, however, still unclear and controversial. Previous studies have been based predominantly on the examination of anatomical features, particularly pelage colouration. Moreover, the only molecular genetic study undertaken so far relied heavily on material collected from captive animals. The main objectives of the present study are to clarify the taxonomy, phylogeny and biogeography of *Presbytis* using a combination of genetic, morphometric and bioacoustic data. Here we present the first genetic analysis of samples from wild animals representing major parts of the geographic range of the genus. Faecal samples were collected from 21 selected populations on Java, Sumatra and the Mentawai Islands. Additional samples from museum specimens from Borneo were used to supplement the dataset. Phylogenetic reconstructions are based on the complete cytochrome b gene and the hypervariable region I of the mitochondrial genome. The evolutionary and biogeographic history of the genus, on the basis of these phylogenetic reconstructions, will be discussed. The results of this study will also contribute towards assessing the conservation status of *Presbytis*.

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## Play Behaviour and Social Interactions of Infant, Juvenile and Sub-Adult Wild White-Bearded Gibbons (*Hylobates albibarbis*) in Sebangau National Park, Indonesia

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*Key Words:* Hylobatidae · Grooming · Ethology · Peat swamp forest

The study of juvenile gibbon social behaviour is a relatively new area of research and we have limited understanding of the dynamics of inter- and intra-group social behaviours. We aimed at quantifying the social and play behaviour displayed by juvenile wild white-bearded gibbons (*Hylobates albibarbis*); testing differences in age, sex, social partner choice, effects of group makeup, between group differences and their interactions. The gibbons studied were members of four groups of habituated gibbons at the Natural Laboratory Research Area (LAHG) in the Sebangau National Forest; consisting of two infants, four juveniles and five sub-adults. We found marked difference in play behaviour between the sexes and juveniles exhibited higher levels of play behaviour than either infants or sub-adults. Differences between groups were relatively small. The conducted study highlights the social needs of young gibbons. The findings suggest that juvenile gibbons would benefit from being kept in family groups, when possible. This study will be useful to zoos and rescue centres that care for gibbons, as the findings have implications for the husbandry of captive gibbons and highlight the huge impact that taking juvenile wild animals away from their familial groups may have on their development and welfare.

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## Recording Complex Positional Behaviour in Orang-Utans

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*Key Words:* Gap crossing · Tree sway · Movement notation · Locomotion · Posture · Orang-utan

Arboreal primates face numerous problems in their forest habitat that hinder effective movement, particularly gaps in the canopy and flexible supports. Habitat constraints influence body size and morphology of arboreal species, which has resulted in the evolution of diverse positional behaviours (locomotion and posture), particularly in large bodied mammals, such as orang-utans (*Pongo* spp.). Orang-utan positional behaviour is highly complex and to move successfully through the forest they have developed characteristic gap crossing behaviours (sway and ride) not observed in smaller species. These behaviours involve the oscillation of a support (e.g. a tree) either backwards and forwards, or in one direction only, until the amplitude of the oscillation is large enough to reach another support and cross the gap. Oscillatory behaviours are performed using a range of body postures; but due to the intricacy of the movements these variations have not been recorded previously. The aim of the current study was to develop a method to record accurately complex positional behaviour in primates, in particular gap crossing in orang-utans. A suitable method was developed from a movement notation technique, Sutton Movement Writing, and used in a study of 12 wild orang-utans at Ketambe Research Station, Sumatra, Indonesia. This method successfully enabled a detailed description of the postures during sway and ride and allowed the variation within gap crossing behaviours to be studied. It also resulted in the creation of new categories to define the postures observed, which can be incorporated into pre-existing classification systems used to describe primate positional behaviour.

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## Disentangling the Complex Population History of Orang-Utans (*Pongo* sp.)

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*Key Words:* *Pongo* sp. · Population history · Phylogeography · Sundaland · Dispersal

Conflicting scenarios of orang-utan population history have been proposed in recent studies. There is a general consensus that orang-utans colonized the islands of the Sunda Shelf from the southeast Asian mainland through the Thai-Malay Peninsula throughout glacial periods during which the Sunda Shelf was exposed. A detailed analysis of migration events, in particular colonization patterns of Sumatra and Borneo, as well as subsequent potential gene flow, has been limited by the uneven distribution of samples from orang-utans with known provenance. We collected non-invasive faecal samples from different Sumatran populations to complement a comprehensive collection of samples from different Bornean populations in order to reconstruct the phylogeography and population history of orang-utans. Preliminary mtDNA data (16S rDNA, cytochrome b and ND3 coding regions) suggest that Sumatran and Bornean orang-utans have been separated for at least 1.5 million years without the occurrence of gene flow between the islands. However, the current southernmost Sumatran population of Batang-Toru forms a link be-

tween the populations on the two islands, being clearly separated from the other Sumatran populations and basal to all Bornean populations. Sumatran orang-utans show a clear structuring into at least four major geographical clusters with deep divergence compared to Borneo orang-utans. However, preliminary X-chromosomal data, while confirming the special position of Batang-Toru, do not demonstrate this particular pattern and they also indicate a more recent divergence between Borneo and Sumatra. These findings let us postulate the occurrence of wide-ranging male-mediated gene flow within Sumatra and possibly also between Sumatra and Borneo.

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## Testing the Validity of the Expensive Tissue Hypothesis in Mammals

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*Key Words:* Comparative study · Brain size evolution · Organ mass · Diet

The Expensive Tissue Hypothesis (ETH) suggests that, assuming equal energy input, enlargement of the brain can be achieved as the size of other expensive organs is reduced. Initially, published data show a significantly negative correlation between brain mass and gut mass in anthropoids, but other studies found mixed support for the ETH. A revision of the ETH in anthropoids, using gut surface and sex-specific brain size data of 30 anthropoid species, showed that the negative correlation is valid in catarrhines, but not in platyrrhines. Moreover, an analysis of published organ mass data of 39 species from 8 mammalian orders showed only a weak negative trend between brain mass and gut mass. In conclusion, evidence for the general validity of the ETH in mammals is rather weak and warrants a broad comparative study in which sources of error are reduced as much as possible. In the present study, we collected organ mass data of healthy adult, non-domesticated mammals. We also controlled for the influence of preservation techniques. We present preliminary results of 51 mammalian species from our new dataset and discuss possible links with diet and basal metabolic rates.

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## Male Sexual Signals in Crested Macaques (*Macaca nigra*)

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*Key Words:* Sexual signals · *Macaca nigra* · Sexual selection · Loud calls · Ornamentation

Males may increase their reproductive success through the display of sexual signals. In crested macaques (*Macaca nigra*), males exhibit loud calls and scrotum colouration, both signals which have likely evolved through sexual selection. In a previous study, we have shown that the intensities of these signals are related to male dominance rank. How these two traits relate to each other and how they help to increase male reproductive success, however, remains unclear. Our study therefore aims to test the hypotheses that the two signals (1) correlate with each other, (2) play a role in the intensity of male-male contest, (3) attract females and (4) that their intensity relates to male access to fertile females. The study was carried out over a period of 14 months on two

groups of crested macaques living in the Tangkoko-Batuangus Nature Reserve, North Sulawesi, Indonesia. Data were collected, using focal animal sampling, from 22 males (mean: 120 h/male), and 16 females (mean: 23 h/female) during the fertile phase of their conception cycle. In addition, digital pictures of the scrotum of each male were taken once a week and colour intensity measured using the RGB method. Detailed acoustic analysis was carried out on 173 loud calls from 14 males and selected calls were used for playback experiments. Our results will contribute to a better understanding of the evolution of sexually selected traits in male primates.

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## Orang-Utan Phylogeny Derived from Male-Specific Markers

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*Key Words:* Orang-utan · Phylogeography · Y chromosome · Dispersal · Phylogeny

Orang-utans were widespread in south-east Asia during the Pleistocene. Nowadays, orang-utans are restricted to the islands of Borneo and Sumatra. The Sumatran orang-utans (*Pongo abelii*) show twice the genetic diversity of Bornean orang-utans (*Pongo pygmaeus*), although the latter are distributed over a much larger area. Mitochondrial, autosomal, and X-chromosomal phylogenies do not always find monophyly within Sumatra. There are several hypotheses to explain the high diversity and lack of monophyly within Sumatran orang-utans: (i) Sumatran orang-utans may form a relic of either several monophyletic populations or one mixing population spread over south-east Asia during the Pleistocene; (ii) immigrating orang-utans from Borneo may have increased the diversity on Sumatra; (iii) the populations on Sumatra have been isolated for a long time. To be able to resolve the phylogeography and phylogeny of orang-utans, it is necessary to compare evidence from as many independently inherited marker systems as possible. In this study, we apply human-derived polymorphic Y-specific microsatellite markers and newly discovered single nucleotide polymorphisms on the Y chromosome to a representative number of orang-utan populations. This will further our understanding of orang-utan phylogeography.

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## Monogamy, Polyspecific Associations and Group Sizes in Relation to Environmental Variation in Grizzled Langurs (*Presbytis comata*)

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*Key Words:* *Presbytis comata* · Group size · Monogamy · Polyspecific associations

The grizzled langur (*Presbytis comata*) is cited as one of the relatively few monogamous Old World monkey species. We investigated whether monogamy indeed forms a significant part of the species' social system, and whether habitat variation affects social structure and tendency to form polyspecific associations. We found the species to be restricted to the last remnants of rainforest on the island of Java, Indonesia, from sea level to >2,500 m a.s.l., in groups ranging from 1–13 individuals. Groups consisted of one adult male and several females with offspring or contained only males. Groups were only occasionally observed in polyspecific associations. There was no annual or seasonal variation in group sizes, nor did group size differ geographically. Group size was negatively correlated with altitude and forest size and positively with increasing distance into the forest. All-male groups, and bisexual groups found as part

of a polyspecific association, contained fewer individuals and occurred more frequently at higher altitudes than bisexual groups. Two out of 55 groups comprised one adult pair with offspring. Group size in the one area (a small high-altitude forest patch) where monogamy was purported ranged in fact from 4–9 individuals, all comprising one adult male and several adult females. We conclude that there is little evidence for frequent monogamy in this species, although, especially in high altitude forests, groups of two adults plus offspring do occur.

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## **Social Constraints upon Group Movements of Japanese Macaques (*Macaca fuscata yakui*) on Yakushima Island**

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*Key Words:* Collective movements · Consensus decision · Social style · Leadership · *Macaca fuscata*

Studies performed on decision making in primates all point to a shared or partially shared consensus even in despotic species. However, they have been mainly conducted under semi-free ranging conditions. Therefore, one could argue that the stronger the ecological constraints, the less shared the consensus decision. Indeed, in the wild, the most experienced individuals (supposedly the philopatric sex) would be predicted to be the most suited to take decisions on behalf of the whole group. Another hypothesis, relying on social system, is that the most dominant individuals would be the ones expected to lead in a rather despotic species like Japanese macaques. To assess these hypotheses, we followed a group of 60 wild Japanese macaques on Yakushima Island and recorded their group movements. Among the 28 adult individuals, 24 initiated group movements. There was no significant effect of the sex of the initiator upon the number of individuals joining the movement (Mann-Whitney-Wilcoxon,  $N_f = 79$ ,  $N_m = 83$ ,  $W = 1498.5$ ,  $p = 0.143$ ). There was a significant correlation of the dominance rank of the initiator and the number of followers among males (Kendall's rank correlation,  $n = 83$ ,  $z = -2.714$ ,  $\tau = -0.324$ ,  $p = 0.007$ ) but not in the female hierarchy ( $n = 79$ ,  $z = -0.134$ ,  $p = 0.894$ ). Moreover, a matrix correlation between the associations observed during group movements and the social network of the group was highly significant (Dietz R-test,  $\rho = 0.75$ ,  $p < 0.0001$ ). These results correspond to a partially shared consensus as found in rhesus macaques and highlight the crucial influence of the species' social system upon mechanisms underlying group movements whatever the environmental constraints.

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## **Female Expression of Mating Interest in Chimpanzees of Kanyawara, Kibale National Park, Uganda**

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*Key Words:* *Pan troglodytes schweinfurthii* · Mating interest · Sexual behaviour · Reproductive strategies · Sexual swelling

Sexual interactions can be initiated by either males or females in chimpanzees. Yet, the expression of mating interest varies between the sexes. While males display a variety of behav-

hours from a distance to invite females for copulations, females are, so far, not known to advertise their sexual willingness from a distance. Instead, female chimpanzees typically initiate copulations by first approaching the male and then presenting their sexual swellings. In this study, I examined whether females actively position their sexual swellings from a distance towards certain males to attract them for mating. Data come from 664 copulations observed among chimpanzees in Kanyawara over a 2.5-year period. To estimate mate preferences, I analyzed female proceptivity rates of 6 oestrous females towards a total of 13 males. Further, I calculated sexual swelling visibility rates for each female per male. Females pointed their swellings significantly longer towards preferred males compared to eschewed males only during the periovulatory period (POP), when conception was more likely. These higher sexual swelling visibility rates towards preferred males suggest that females may have strived to influence which males sire their offspring. In contrast, eschewed males had a higher swelling visibility rate during non-POP, when females were less likely to conceive. These female attempts to draw attention to non-preferred males may have functioned to confuse paternity. My results indicate that female chimpanzees point their sexual swellings strategically across oestrus. This may play a crucial role in expressing their mating interests which are in compliance with their reproductive strategies.

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## Social Games between Bonobos and Humans: Evidence for Shared Intentionality?

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*Key Words:* Communication · Gestures · Social games · *Pan paniscus* · Shared intentionality

Triadic social games are interesting from a cognitive perspective because they require a high degree of mutual social awareness. They consist of two agents incorporating an object in turn-taking sequences and require individuals to coordinate their attention to the task, the object and to one another. Social games are observed commonly in domesticated dogs interacting with humans, but they have received only little empirical attention in non-human primates. Here, we report observations of bonobos (*Pan paniscus*) engaging in social games with a human playmate. Our behavioural analyses revealed that the bonobos, in many ways, behaved similarly to human children during these games. They were interested in the joint activity, rather than the play objects themselves, and used communicative gestures to encourage reluctant partners to perform their role, suggesting rudimentary understanding of others' intentions. Our observations thus may imply that shared intentionality, the ability to understand and share intention with other individuals, emerged in the primate lineage before the origins of hominids.



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## Conflict Management in Six Groups of Wild Vervet Monkeys

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*Key Words:* Conflict management · Population level · Individual level · Redirection · Alliances · *Chlorocebus aethiops*

Conflicts are inevitable in social groups but have to be solved in order to avoid fission. Conflict management has been a research focus in primatology, providing evidence that primates use diverse mechanisms to cope with aggression: reconciliation, consolation, alliance formation and redirection. While we know that different species may use each mechanism to varying degrees, few studies have focused on the relative importance of the mechanisms within a species and on the variation that may exist between groups of the same species. In this study, we investigated conflict frequencies and post-conflict behaviours in six groups of wild vervet monkeys, *Chlorocebus aethiops*, in Loskop Dam Nature Reserve, South Africa. We found that groups differed both with respect to frequency of aggressive interactions and conflict management. Most importantly, individuals in some groups use more affiliative mechanisms (reconciliation and consolation) while individuals of other groups may mainly use escalatory strategies (alliance formation, redirection of aggression). A more detailed analysis of escalatory strategies revealed that alliances with kin occur independently of the rank of the opponent while individuals preferentially join the dominant if they are unrelated to both conflict partners. Redirection is used primarily against weak targets (juveniles) that were typically unrelated to the aggressor. This study highlights the multidimensionality of conflict management in vervets and cautions against generalisation of results obtained in one group to the population or species level.

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## A Test of Anticipatory Strategies in Capuchin Monkeys (*Cebus apella*): Coping with Expected Feeding Time

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*Key Words:* Conflict management · Anticipation · Reassurance · *Cebus apella*

Several studies have shown that primates might use post-conflict strategies such as reconciliation in order to repair damaged relationships. Beside post-conflict strategies, anticipatory mechanisms of conflict prevention can also be hypothesised to play a role in maintaining and preserving valuable relationships. If monkeys could foretell a contentious forthcoming situation (e.g., competition over food), we can expect that they will attempt to pre-emptively reduce the likelihood of conflict by employing tension reduction strategies. Nevertheless, these pre-conflict behaviours are cognitively more demanding than post-conflict strategies as they imply that individuals possess the ability to anticipate future conflicts. A type of conflict that can be anticipated, because of its predictability, is that occurring over food in captive animals subject to fixed feeding schedule. We collected data on grooming and play as well as on aggressive interactions on a group of twelve capuchin monkeys housed at the CNR Primate Centre in Rome during three different periods: Pre-feeding, Feeding, and Control. If the monkeys were able to use some form of conflict prevention strategy we might expect a higher level of sociopositive interactions selectively directed towards specific mates, such as kin, allies or more dominant

individuals, during Pre-feeding as opposed to Control, leading to lower levels of aggressive interactions in the Feeding period. Our results show that, despite an increase in pre-feeding grooming, individuals did not alter their social preferences when expecting a stressful event. Most of the increase in pre-feeding grooming was done by the alpha male, who also refrained from aggression during Feeding if he had groomed during Pre-feeding, suggesting the occurrence of some form of reassuring behaviour towards the rest of the group during tense situations. Capuchins seem thus able to anticipate feeding time, but they were not able to cope with it actively by using conflict prevention strategies.

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## Nutrient and Energy Digestibility in Captive Crowned Lemurs (*Eulemur coronatus*)

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*Key Words:* Lemuridae · Digestibility · Energy intake · Obesity · Frugivores

For many lemur species it is not known to what extent they use the energy and nutrients in their diets, which makes it difficult to predict how much food they need to meet their requirements. In captivity, lemurs tend to be fed diets rich in sugars and low in fibre year-round, which is thought to result in high obesity rates. The objective of this study was to assess the role of dietary energy density and feeding regimes in the aetiology of obesity in captive crowned lemurs. We examined the energy and nutrient intake and digestibility in four groups of crowned lemurs (n = 15) in two European zoos with comparable enclosure size and structure. During seven 14-day digestibility trials carried out at different times of the year, food and leftovers were weighed and all faeces collected daily. Food and faecal samples were freeze-dried and analysed for gross energy (GE), dry matter (DM), crude protein (CP), crude ash (CA) and ether extract (EE) as well as for neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL). Non-fibre carbohydrates (NFC) were calculated as 100 - (CP+CA+EE+NDF). Body weights of all lemurs were taken prior to and during the trial periods. Mean body weights of male and female crowned lemurs in both zoos exceeded those of wild conspecifics. Obesity was associated with high dry matter and energy intake. Dietary energy density as well as DM and nutrient digestibility were high in both zoo diets. We conclude that DM amount and energy density need to be controlled in zoo diets for crowned lemurs to avoid obesity.

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## Emerging from Long-Term Deprivation: Bonding and Tolerance of Social Stimulation in Ex-Laboratory Chimpanzees

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*Key Words:* Trauma · Social competence · Rehabilitation · Chimpanzee

Great apes reared in captivity have often been separated from their mother and other social companions at an early age. Onset of deprivation during infancy affects both poles of social attraction, the security complex regulating attachment behaviour and the arousal complex ex-

pressed in exploration and play. We monitored severely deprived ex-laboratory adult chimpanzees from prior re-socialisation through group building until one year into rehabilitation. Early deprived (from 1.2 years of age: ED) and later deprived chimpanzees (from 3.6 years of age: LD) developed different security-to-arousal target values: ED were more timid, more idiosyncratic, less socially initiative and stress tolerant than LD. Social compatibility was influenced by chimpanzees' similarity of deprivation history. Contrary to assessment theory, symmetric dyads established compatibility more readily than dyads with asymmetric deprivation histories. Affiliation competence, measured on a 6-grade scale of increasingly intense social contact, remained low in groups with an ED majority, but increased when LD predominated. When in minority, only LD chimpanzees adjusted to the majority, by down-scaling their stimulation seeking, whereas ED immersed in a LD majority hardly up-scaled their stimulation tolerance. Therefore, recovery was best in LD-LD combinations. Our results show that traumatic life events and chronically adverse conditions lastingly affect chimpanzees' personalities, stimulation thresholds and social competence. Thus the interpretation of experimental results on captive chimpanzees should take individual rearing history into account. In addition, our results are relevant for captive management, as well as any efforts to rehabilitate individual great apes into a more natural setting.

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## Emergence of Reconciliation in a Virtual World

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*Key Words:* Reconciliation • Self-organization • Macaques • Grooming • Social structure

Reconciliation is defined as the affiliative interaction that occurs between former opponents immediately after a conflict. According to de Waal and Yoshihara (1983), the cognitive abilities necessary to reconcile are to recognize individuals, remember former opponents, and have a conciliatory disposition. However, using an individual-based model we show that reconciliation can emerge using simpler behavioural rules. In our model, individuals group together in space, they fight and groom. Initially, they are identical. Their winning capacity changes depending on the self-reinforcing effects of winning and losing. Upon encounter, individuals decide not to fight when they think they will be defeated. In such a case, their tendency to groom the other is greater the greater their stress; stress increases after a fight and decreases with grooming. Using these rules, reconciliation emerges in our model as measured by the PC-MC and the time rule method. Moreover, individuals reconcile more with those with whom they groom relatively more (i.e. they conform to the valuable relationship hypothesis). In addition, by increasing intensity of aggression, the society switches from egalitarian traits to despotic ones, and the percentage of fights reconciled decreases. This resembles the differences between despotic and egalitarian macaques. Hence, our model shows that patterns supposedly indicating reconciliation may emerge without memorizing former opponents and without a conciliatory tendency. Therefore, to confirm cognitive processes of reconciliation other types of evidence are needed. We explain how our model can be used as a null model to guide studies on reconciliation.

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## Human Impact on *Microcebus* spp. and *Lepilemur* spp. in Northwestern Madagascar – Insights from Genetics

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**Key Words:** Conservation · Abundance · Genetic bottleneck · Hunting · Fragmentation · Madagascar

Forest loss and habitat fragmentation are major environmental pressures in Madagascar, with hunting posing an additional threat to larger species. It is of major conservation concern whether signatures of these disturbances can already be detected in forest-dwelling animals. I will compare the influence of hunting, forest loss and fragmentation on abundance, genetic diversity and genetic differentiation in four *Microcebus* species and three *Lepilemur* species occurring in northwestern Madagascar. Furthermore, I will investigate whether populations already show signs of genetic bottlenecks. Species of both genera are nocturnal, solitary foragers but differ considerably in body size. The analyses are based on surveys in 26 forest fragments, ranging in size from 0.2 km<sup>2</sup> to 40.8 km<sup>2</sup>, and from 13 sites in the 1,040 km<sup>2</sup> Ankarafantsika National Park. Genetic sampling was performed in 29 sites on a total of 671 individual *Microcebus* spp. and 137 individual *Lepilemur* spp. Genetic results are based on multilocus genotypes and on sequence data. Mouse lemurs occurred in all study sites, whereas sportive lemurs were absent from 69.2% of the fragments, but from only 7.7% of the park sites. Genetic diversity was generally higher in the park than in the fragments. Forest fragmentation increased the genetic differentiation between populations beyond the effect of isolation-by-distance. Signatures of past genetic bottlenecks could be identified, which most likely started within the last few hundred years. The data indicate that *Lepilemur* spp. is particularly threatened probably due to hunting and that species of both genera already show clear genetic signatures of human impact.

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## Testing the Ecological Constraints Model with Ranging Data from Wild Gibbons

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**Key Words:** Territoriality · Ecological constraints model · White-handed gibbon · Day range · Polyandry

The ecological constraints model predicts that as primate group size increases, day range length and/or home range size also increases due to the energetic needs of more individuals. Support for the hypothesis comes from within-group studies of fission-fusion primate communities, with far less evidence from primates living in stable groups. We evaluate the ecological constraints model with ranging data from pair-living and multimale white-handed gibbon (*Hypobates lar*) groups by testing the prediction that pairs should travel significantly less than multimale groups, because each additional adult significantly increases energetic demands. Data come from 10 well-habituated groups studied at Khao Yai, Thailand, from 2002–2008 that were consistently followed from night-tree to night-tree. Every ten minutes, group location was marked on a trail map and day range length was calculated cumulatively as the distance travelled between marked locations. Using AutoCAD, group day ranges were digitized to evaluate between-month and between-year variation in home range size and day range length. We found great variation in all parameters: home range size varied from close to 15 ha to >50 ha, day range

length from around 500 m to nearly 2,000 m, and group composition from no time spent multemale to nearly 80% of the time spent multemale. Our preliminary analyses fail to confirm the ecological constraints model for gibbons, as multimale groups did not consistently have larger home ranges and longer day ranges than pairs. These results are significant for the evolution of gibbon foraging patterns and social structure, as well as questioning the broader application of the ecological constraints model.

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## The Social Model Hypothesis Tested on Vervet Monkeys

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*Key Words:* Vervet monkeys · Social learning · Social model hypothesis

Social learning plays an important role in primates. The ‘social model hypothesis’ [F. de Waal, 2005] states that individuals will not randomly learn from any social partner but mainly from preferred role models: the mother and high ranking group members. Such directed social learning could be caused by group members more often paying attention to the actions of preferred role models than to other group members. We tested this possibility in a field study on six groups of vervet monkeys (*Chlorocebus aethiops*) at Loskop Dam Nature Reserve, South Africa. During focal samples, we quantified the frequencies with which adult individuals were observed by other group members of known age, class, rank, sex and degree of relatedness. Data were collected on naturally foraging and grooming individuals as well as during food experiments designed to test for social learning. We found that group members pay more attention to females than to males and that dominant females are more often observed than subordinate females. As females are the philopatric sex with a matrilineal hierarchy in vervet monkeys, we propose that not only relatedness and rank but also philopatry plays a role in determining the likelihood that other group members will learn socially from an individual’s actions.

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## Symbolic Stimuli Facilitate Capuchin Monkeys to Solve the Reverse-Reward Contingency Task

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*Key Words:* Inhibition · Reverse-reward contingency · Token · Symbol

Capuchin monkeys (*Cebus apella*) can operate on symbolic objects to combine quantities and employ similar cognitive mechanisms to choose between symbolic objects and between real foods. However, it is still unclear whether symbolic stimuli ameliorate their performance in an inhibition task, as is the case for humans and chimpanzees. In this study, we tested eight capuchins in a reverse-reward contingency procedure, in which they have to indicate the smaller stimuli between two arrays to obtain the larger reward. Subjects were presented with binary choices between: (1) food (two vs. five pieces of peanut), (2) low-symbolic stimuli (two vs. five tokens, corresponding to one reward each), (3) high-symbolic stimuli (two high-value tokens, corresponding to two and five rewards, respectively). Control conditions were introduced to rule out the possibility that reversal learning could account for success. Only one subject could hold back from choosing the larger quantity of food and generalized to novel combinations of food. Three

subjects solved the task when faced with the high-symbolic stimuli and generalized to novel combinations of tokens. However, no subject transferred the rule acquired in the food condition to the symbolic ones or vice versa. Thus, the use of symbols is beneficial to attain success in the reverse-reward contingency task, as previously reported in chimpanzees and 3-year-old children.

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## Evolutionary Roots of Social Norms in Chimpanzees

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*Key Words:* Chimpanzees · Social norms · Empathy · Perception · Morality

Universally, social norms guide human social life. Since social norms generate social expectations of the appropriate behaviour within a group, their violation may provoke strong negative emotional reactions in victims and, most importantly, also in unaffected bystanders. Although chimpanzees also protest when their social expectations are violated (e.g. food stolen), such protests are primarily based on 'egoistic' norms (i.e. the individual's selfish social preferences). To establish the presence of social norms in chimpanzees, we have to investigate whether they, like humans, also show reactions to norm violations as unaffected bystanders. A possible norm violation in chimpanzees could be the killing of infants by adults. To address this question, we conducted video experiments with captive chimpanzees ( $n = 11$ ) housed in Gossau, Switzerland. In the habituation phase, we showed the whole group video clips of unfamiliar conspecifics performing socially neutral behaviours (i.e. tool use, walking around). In the experimental phase, the chimpanzees could watch unfamiliar conspecifics performing infanticidal attacks (treatment), or performing hunts or showing excitement in another context (controls). If killing infants violates chimpanzees' expectation, then they should show stronger reactions (e.g. looking time, distress behaviour) towards infanticidal attacks than to the other stimuli. Preliminary analyses confirm this prediction. Our experiments therefore suggest that chimpanzees differentially perceive and evaluate social events even as completely unaffected bystanders and that chimpanzees, therefore, satisfy a basic precondition for the existence of social norms. As for humans, however, chimpanzees may not always be able to act upon perceived norm violations.

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## Analogical Reasoning in Tool Use in Tufted Capuchin Monkeys (*Cebus apella*)?

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*Key Words:* Analogy · *Cebus apella* · Tool use · Functional features · Distracting features

Analogical abilities in animals have been primarily studied in chimpanzees. Here we investigated how capuchin monkeys (*Cebus apella*) solve tool problems requiring the appreciation of the length(s) of the tools in relation to tube length(s). Eight capuchins were required to select the longest stick from different sets of three sticks differing in length (functional feature) to retrieve a reward placed inside a horizontal tube. Phase 1 included (a) a training session in which each stick had a different handle and (b) a transfer test in which the handles were switched among sticks, so that the functional tool was the same length but had a different handle than in the training. Only one subject succeeded in this transfer. Phase 2 included (a) a training ses-

sion in which the same sticks of Phase 1 were used with handles switched in every trial, and (b) a transfer test in which the baited tube was longer than previously and all sticks had the same new handle. Here, the longest tool during the training becomes the intermediate one in the transfer. Three out of eight subjects passed this transfer possibly because during the training of Phase 2, they learnt about the functional feature of the sticks irrespective of the perceptual characteristics of the handles. These results show that capuchins might apply analogical structures in tool using tasks after having learnt to ignore distracting irrelevant features.

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## **Olive Baboons (*Papio h. anubis*) Perform Better in Abstract than in Food Quantity Discrimination Tasks**

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*Key Words:* Analogue magnitude system • Cognition • Impulse inhibition • Non-food items • Relative numerosness judgment

In order to maximize their food intake, animals should be able to discriminate between different quantities. In addition, number discrimination is of interest from a comparative perspective, as it is considered to be the foundation of mathematical understanding in humans. Quantity discrimination tasks have been conducted in various primate and non-primate species. A large body of studies have used different food amounts to test whether the subjects possess numerical competencies. In this study, however, we found that baboons perform significantly better in discrimination tasks when the animals have to choose between two arrays of non-edible items compared to edible ones. We tested five olive baboons housed at the German Primate Centre, Göttingen, in different two-choice tasks using either different quantities of raisins or coins (i.e. little black stones or pieces of cardboard). The baboons chose the larger number of pieces more accurately when it was represented by non-food items, and when the difference between the two arrays was larger. Further experiments revealed that the surface covered also affected the subjects' choices. Notably, the baboons also passed a reversal task in which they were rewarded for choosing the smaller quantity of pieces. Our findings are in line with previous observations that a lack of impulse inhibition may interfere with making accurate quantity judgments. Future studies should therefore not only concentrate on food quantity discrimination as this may conceal the real numerical capabilities of a species.

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## **Conflict Characteristics, Relationship Quality and Post-Conflict Behaviour in Wild Male Assamese Macaques**

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*Key Words:* Social behaviour • Post-conflict behaviour • Social stress • Male bonds

Reconciliation and consolation are mechanisms integrating cooperation and conflict in groups of animals. Increased rates of affiliative interaction among former opponents in aggressive encounters or among opponents and third parties are thought to reduce post-conflict anx-



ity. According to Aureli's 1997 Integrated Hypothesis, the disruptive effect of conflicts is most significant in valuable relationships and hence (1) both post-conflict anxiety and conciliatory tendency should be positively related to relationship quality, and (2) the positive relationship between conciliatory tendency and level of conflict escalation increases in strength with relationship quality. This study aims at testing these predictions as well as the existence of third party post-conflict affiliation in male Assamese macaques (*Macaca assamensis*) where male bonding and agonistic alliances form an integral part of the competitive regime. All adult and large subadult males of a large, wild, multimale-multifemale group living in Phu Khieo Wildlife Sanctuary in Thailand were observed. Focal animal sampling was used to collect data on affiliative, affiliative, agonistic, and comfort behaviour between October 2006 and April 2008. Behavioural data were supplemented with collection of weekly faecal samples of all males, which were analyzed for glucocorticoid concentration as a measure of physiological stress. Post-conflict behaviour was compared to baseline levels of affiliation as well as to matched controls. The results are discussed in light of current theory on the ultimate causes of post-conflict behaviour and the role of post-conflict behaviour in mitigating the physiological costs of a given social status.

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### **Tool Use and Terrestriality in Wild Bearded Capuchin Monkey (*Cebus libidinosus*)**

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*Key Words:* *Cebus libidinosus* • Time budget • Terrestriality • Nut cracking

The abilities of capuchin monkeys (*Cebus* spp.) to use tools and to solve problems in captivity are remarkable, while reports of tool use in the wild were, until very recently, rare and anecdotal. It has been suggested that their arboreal habit limits their chances of encountering and using tools. In this study, we report the activity budget and the use of tools by two wild sympatric groups of *Cebus libidinosus* living at Fazenda Boa Vista (Piauí, Brazil). Results show that capuchins at FBV perform many activities on the ground (foraging, sleeping, playing, as well as nut cracking); the percent of time spent on the ground is higher than reported for other populations living in forest habitat and similar to that reported for the *caatinga* capuchins which also use tools. The monkeys routinely use hammers and anvils to crack open palm nuts and other encased fruits. Food is relatively abundant all year long and frequency of tool use does not vary in relation to monthly food availability or rainfall, but reflects the availability of the most exploited nut species. Overall these results suggest that tool use in capuchins is not a response to food shortage and that its emergence might have been favoured by terrestrial habits.

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## Signals during Grooming Interactions in Wild Vervet Monkeys

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*Key Words:* Grooming signals · Cooperation · Vervets

Mutual grooming plays a central role for the establishment and maintenance of social relationships in primates. Allogrooming has a hygienic function through removal of ectoparasites and a strategic function through the bonding with coalition partners. Many studies have measured the duration of grooming bouts to address detailed functional aspects; however, we currently lack information about the signals that primates employ to inform others about their intentions and needs concerning grooming interactions. These proximate aspects are essential to properly understand cooperative interactions like allogrooming. Here, we studied three behaviours shown in grooming interactions among adult females of two free-ranging vervet monkey groups – approach, change of body position of the groomed individual, and lip smacking – and asked what signalling functions they might have. We found that approach does not reliably predict which individual will receive grooming first, though individuals gave more grooming during the interaction when they approached than when they were approached. This latter result supports the idea that approach may signal the willingness to form a bond. Presentation of a new body part appeared to be the main signal to negotiate a prolongation of the partner grooming. Finally, lip smacking was used in potentially stressful circumstances like using the mouth to remove ectoparasites or trying to access a mother's infant. We hope that our exploratory study will inspire colleagues to start looking at the role of communication in cooperative interactions in their study animals for a better appreciation of how animals achieve cooperation and bargain exchange rates.

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## Monkeys Can Calculate Pay-Offs before Gambling in an Exchange Task

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*Key Words:* Calculation · Economics · Cognition · Primates

Economists assume that gambling is based on cognitive computation. We asked whether monkeys maximize pay-offs in situations necessitating the comparison of costs and benefits. Monkeys were tested in an exchange task requiring the return of given food amounts to experimenters in order to obtain larger amounts. Subjects were 8 tufted capuchin monkeys (*Cebus apella*), 7 long-tailed macaques (*Macaca fascicularis*) and 6 Tonkean macaques (*Macaca tonkeana*), all maintained at the Strasbourg Primatology Centre. In a first experiment, subjects had to adjust their return to the amounts given back by two different human partners. The first partner was calculating, meaning that she gave a number of raisins proportional to the subject's amount. The second was non-calculating, meaning that she gave a constant number. Subjects should return a maximal amount to the first and a minimal amount to the second to maximize pay-offs. Results showed that most subjects could not differentiate between partners. Only one

Tonkean macaque was able to maximize pay-offs by returning different amounts to human partners. In a second experiment, subjects had to exchange with the non-calculating partner only. One third of subjects learned to diminish the returned amount, reducing it to 1–2 raisins. In a third experiment, we resumed the procedure of the first experiment. Once again, subjects were unable to return different amounts to partners, although one of them did stop gambling with the calculating partner. We conclude that monkeys can maximize pay-offs by calculating benefits, although this is a challenging task for them.

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## The More the Merrier: Cooperative Breeding and Cognitive Ability in Common Marmosets (*Callithrix jacchus*)

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**Key Words:** Transfer Index · Reversal learning · Inhibitory control · Cooperative breeding · Cognition · Social intelligence · Callitrichids · Primates

The Cooperative Breeding Hypothesis proposes that many of the processes required for shared care and provisioning can also foster cognitive performance, particularly in the social domain. Supporting this prediction, it has been shown that cooperatively breeding callitrichids systematically outperform their more independently breeding sister taxon, the cebines (i.e. *Cebus* and *Saimiri*), in the social domain but score lower in non-social cognitive tasks. However, the comparison of callitrichids and cebines is highly conservative because cebines have larger brains and absolute brain size is positively related to non-social cognition in primates. To assess whether cooperative breeding is associated not only with socio-cognitive performance, but also with cognitive ability in the non-social domain, this study investigated whether callitrichids perform better than would be expected given their brain size, rather than compared to their sister taxon. The Transfer Index (TI) is a measure of the reversal-learning paradigm, which is a reliable and comparable method for measuring mental flexibility, particularly in terms of inhibitory control of prepotent responses, in the non-social domain. In a first part, we show that across primates the TI is consistently correlated with absolute brain size. In the second part, we measured the TI in 14 common marmosets (*Callithrix jacchus*) and found them to show significantly higher performance relative to their brain size than a comparable group of *Cebus*. The results suggest that cooperative breeding might not only enhance socio-cognitive abilities, but also support the efficiency of brain tissue in non-social cognitive tasks. We discuss how this link might come about.

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## The Use of Gesture-Sequences in Orang-Utans

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**Key Words:** Orang-utans · Gesture-sequences · Intentional communication · Premeditation · Persistence · Evolution of language

A growing body of research shows that great apes' gestures are used flexibly across different contexts with a considerable degree of individual variability [Call and Tomasello, 2007]. The comparative, cross-species investigation of gestural communication contributes to the question

of how human language may have evolved and the role gestures might have played in this context. Compared to isolated gestures, the use of gesture-sequences provides the opportunity to manipulate the communicative situation more effectively and to adapt to the corresponding behaviour of the recipient. Thus, gesture-sequences facilitate (i) immediate adaptation to the recipient's reaction to a preceding single gesture, reflecting the sender's persistence in trying to achieve a communicative goal, or even (ii) strategies reflecting some kind of premeditation, such as the intentional use of specific gesture-sequences to manipulate the recipient's attention. We provide a systematic investigation, based on observations of the interactions of captive orang-utans with other group members. A total of 16 individuals in two different groups was observed, resulting in 160 h of video footage. The gesture-sequences observed were mainly repetitions of one and the same gesture. The majority of gesture-sequences consisted of tactile gestures and was directed to an attending recipient. Although there are some instances indicating a strategic use in terms of persistence and/or premeditation, the majority of gesture-sequences seem to derive from a context-dependent individual arousal. To discuss socio-ecological and evolutionary impacts on the development of intentional communication systems in general, the present data are compared with existing data on the use of gesture-sequences in chimpanzees [Liebal et al., 2004].

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## Experiments on Inter-Specific Food Competition in Two Coexisting Mouse Lemur Species in North-Western Madagascar

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*Key Words:* Feeding · Agonistic conflict · Niche · Interspecific dominance · Ankarafantsika · Mouse lemur

The grey mouse lemur (*Microcebus murinus*) and the golden-brown mouse lemur (*M. ravelobensis*) are found in areas of sympatry in north-western Madagascar. The two morphologically similar sister species have overlapping feeding niches of partly monopolizable food resources, with the main part of the diet consisting of the same food items. In this study, we investigate whether the two species possess a stable interspecific dominance pattern that would indicate a predictable bias in resource monopolization potential. Systematic cage observations with pairs of captured female mouse lemurs of both species were carried out. Twenty experimental dyads were tested in a two-cage arrangement, separated from each other outside experiments. Two days of habituation and four subsequent days of 1-hour confrontation experiments were conducted before releasing the animals again. In twelve of twenty pairs, enough conflicts were observed to decide on dominance relationships. *M. murinus* was dominant over *M. ravelobensis* in 75% of these dyads. Dominance did not depend systematically on body mass and was positively correlated with time spent feeding ( $p < 0.05$ ). The ability to monopolize stationary food resources by means of inter-specific dominance could entail a considerable advantage during resource acquisition. The potential ecological and evolutionary implications of the findings for the coexistence of the two mouse lemur species in zones of sympatry will be discussed.

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## Orang-Utan Locomotion on Flexible Branches

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**Key Words:** Orang-utan · Locomotion · Support flexibility · Compliance · Biomechanics

Predictions suggest that the flexibility (compliance) of branches and their long elastic recoil time means that arboreal mammals will lose energy to branches during locomotion. Locomotion on peripheral branches that are particularly small in diameter compared to the mass of an animal will therefore be particularly expensive. Since the Sumatran orang-utan (*Pongo abelii*) is the largest habitually arboreal primate and since it has one of the broadest repertoires of positional behaviour of all the primates (consisting of over 100 biomechanically distinct postural and locomotor behaviours), we hypothesize that this species possesses unique locomotor strategies for controlling the flexibility of supports during arboreal travel. We tested these hypotheses during a year-long field study of 10 wild Sumatran orang-utan in the Ketambe Research Station, Gunung Leuser National Park, Indonesia. We obtained 2,811 observations of orang-utan locomotion and the supports on which they moved. We found that Sumatran orang-utans exhibit unique strategies to control support compliance that differ both from those predicted and from those observed in other arboreal primates. These results have implications for our understanding of locomotor diversity in fossil and extant apes.

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## Do Tufted Capuchin Monkeys (*Cebus apella nigrinus*) Trade Grooming for Infant Handling?

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**Key Words:** Biological market · Infant handling · Female-female interactions · Affiliative behaviours · Neotropical primates

The biological market theory has been applied to the study of the influence of newborn infants on social interactions among females, suggesting the existence of an 'infant market' in which grooming is traded for infant handling. In such a market, females are divided into two trader classes: mothers (controlling access to infants), and other females (i.e., handlers), which offer grooming to mothers in exchange for access to their infants. In this context, variations in the number of available infants per handler alter the supply/demand ratio and generate the market effect. Thus, when fewer infants are available, the price (i.e., grooming) paid to gain access to them is supposed to increase. We examined whether tufted capuchin females (*Cebus apella nigrinus*) interchanged grooming for infant handling by addressing three questions: Does the birth of an infant cause an increase in the grooming and approaches received by its mother? Does grooming given by handlers to mothers facilitate infant handling? Does the price (grooming) paid by handlers vary according to the supply of infants available? Data were collected over 15 months on 10 mothers belonging to three wild groups of tufted capuchin monkeys living in Iguazú National Park, Argentina. Our results show that females were interested in newborn infants and that grooming by handlers increased their likelihood of gaining access to infants. However, grooming by handlers did not vary in relation to the number of infants available, suggesting that market models may not completely describe the pattern of grooming interchange among females in this species.

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## Personality Research: Theoretical and Methodological Foundations for Studying the Behaviour and Mind of the Individual

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*Key Words:* Personality · Temperament · Individual differences · Measurement · Species comparisons

Many primate species exhibit pronounced variations in individual-specific patterns of behaviour and mind that are commonly construed as personality or temperament differences. Their relevance to primatology, in particular to ecological and evolutionary research questions, is increasingly recognised yet theoretical and methodological foundations are still not well established. Using empirical examples, I present three meta-theoretical core issues of personality research, and explore commonalities and differences to behavioural biology. First, I explain the theoretical and methodological foundations needed to quantify the individuals' behavioural characteristics. I emphasise that sufficient aggregation across occasions and empirical evidence of temporal reliability is essential in order to extract individual-specific patterns from behavioural data that always contain random and error variation within and between individuals as well. I show how variable- and individual-centred analyses allow the quantification of individual uniqueness based on empirical comparability with other individuals. I also explain why cross-situational consistency is often only moderate in primates. Second, I present various methodological approaches to select personality constructs for empirical studies, and contrast advantages and limitations of top-down approaches, such as from the human Five Factor Model, with those of systematic bottom-up approaches, such as the Behavioural Repertoire Approach [Uher, 2008a, b]. Third, I show that personality constructs can be measured reliably with various methods ranging from ethological behaviour observations to intuitive ratings of human observers using behaviour-descriptive verb inventories and trait adjective inventories. Finally, I explain theoretical concepts and methodologies to compare personality variation among species, and highlight the potential of cross-species personality research for evolutionary research questions.

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## Female Orang-Utan Social, Genetic and Spatial Relationships

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*Key Words:* Social organization · Relatedness · Association pattern · Range overlap

Female Bornean orang-utans (*Pongo pygmaeus wurmbii*) tend to range in the company of only their youngest offspring, and spend only short periods of time in association with conspecifics. In Tuanan, central Kalimantan, more than 15,000 h of focal observation on adult females were collected which were analyzed in combination with their ranging data and genetic relatedness. Kernel density estimation was employed to assess detailed patterns of range use by 5 adult females; for an additional 4 females the home range borders inside the study area could be determined in a biologically meaningful way. Non-invasively collected faecal samples were used to determine genetic relatedness among all females encountered in the study area, using genotypes from 26 microsatellite loci and mtDNA control region haplotypes. Females from the same matriline were found to have a higher degree of overlap of their home ranges and of their core areas. In addition, they had more frequent encounters, longer associations and more positive social interactions with each other than with females of different matriline. In particular, there

was also more social play among their dependent offspring. These results show a tolerance of females towards their maternal kin to establish ranges close to and overlapping with their own, and, possibly, social benefits for the offspring of large matrilineal groups who get more opportunity for social interactions with peers. Relationships between non-related females, in contrast, are more antagonistic and result mostly in avoidance and low overlap of ranges. Thus, just as in Sumatran orang-utans, the more solitary Bornean orang-utan females appear to form social and spatial clusters, which are based on matrilineal relatedness.

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## Seasonality Restricts Brain Size in Lemurs and Lorises

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*Key Words:* Expensive Brain hypothesis · Comparative analysis · Costs · Brain size · Prosimians

Larger brains bring about benefits, such as enhanced food acquisition, spatial orientation and social skills, but they also have costs. The costs have received little attention, even though brain tissue is energetically extremely expensive and needs a constant energy supply. The Expensive Brain hypothesis predicts that ecological factors may limit the energy available to brains, and therefore that animals living in highly seasonal habitats, facing periods of energy scarcity, should have a reduced brain size. To test whether these highly seasonal habitats affect brain size in prosimians, we conducted a comparative analysis to assess the influence of seasonality on brain size of lorises and lemurs ( $n = 49$  species). Our results show a significant negative correlation between rainfall seasonality and brain size for lorises and a significant negative correlation between dietary seasonality and brain size (controlling for both body mass and phylogenetic relatedness), indicating that seasonality has a constraining effect on brain size in the prosimians.

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## Faecal Glucocorticoid Levels of Zoo and Wild Bornean Orang-Utans: How Stressed Are Orang-Utans in Captivity?

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*Key Words:* Animal welfare · Stress · *Pongo pygmaeus* · Orang-utan · Faecal glucocorticoids

Glucocorticoid levels are commonly used as an indicator of stress in vertebrates and are increasingly becoming important for animal welfare and conservation. For example, transport of animals, illnesses and diseases, and changes in group composition and housing conditions have been associated with increased glucocorticoid levels. While these events clearly cause stress, basal glucocorticoid levels of captive animals may also serve as a useful indicator of welfare status. However, in order to evaluate if basal stress levels of captive animals are maladaptive, we need to compare them with levels from wild populations. To our knowledge, this has not yet been accomplished in any primate species. In this study, we assessed the range of glucocorticoid concentrations experienced by wild Bornean orang-utans and compared these levels with those measured in zoo orang-utans. Faecal samples were collected at the Tuanan field site



in Central Kalimantan from 11 males and 10 females (368 samples) and from 6 males and 11 females living in 9 zoos (197 samples). All samples were stored frozen after collection and analyzed using a cortisol metabolite assay previously validated for the species. Preliminary results indicate that wild animals have lower baseline glucocorticoid levels and show less inter-individual variation than their zoo-living counterparts. Although the reason for this is not yet clear, we suggest that the more unnatural housing of zoo orang-utans in permanent groups may represent a social stressor leading to consistently elevated glucocorticoid levels and that this may be one factor involved in the relatively poor reproductive performance of orang-utans in captivity compared to the other great ape species.

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## **The Ontogeny of Snake Recognition in Wild Tufted Capuchin Monkeys (*Cebus apella nigrinus*)**

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*Key Words:* Anti-predator · Alarm calls · Age difference · Snakes · Field experiments · *Cebus apella nigrinus*

Infants and juveniles of many species face a higher risk of predation due to their smaller body size. As such, immature individuals would appear to be at somewhat less risk if they possessed adult-like abilities to recognize threats and respond appropriately. Previous research on the ontogeny of predator recognition has shown contradictory results, with studies of wild and captive subjects often offering different conclusions. Among Neotropical primates, such studies have thus far been conducted only in captivity. This study examines the ontogeny of threat recognition among wild tufted capuchin monkeys (*Cebus apella nigrinus*) in Iguazú National Park, Argentina, by examining age differences in propensity to alarm call in response to both threatening and non-threatening snakes. Data were collected using continuous focal sampling in experimental contexts wherein decoys of venomous or non-venomous/non-predatory snakes were placed in an area in which the monkeys were expected to pass. Results show that infants alarm called to venomous snakes less often than adults did, while juveniles did not differ from adults in this regard. Among infants and juveniles, there were no differences in their alarm responses to threatening and non-threatening snakes, while adults alarm called more often in response to threatening than to non-threatening snakes. The observed trends indicate that the recognition of snakes as dangerous is not fully developed until the juvenile stage, and that the ability to differentiate between threatening and non-threatening snakes does not develop until after the juvenile period.

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## Environmental Causes of Geographic Variation between Populations of Wild Orang-Utans (*Pongo* sp.)

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**Key Words:** Geographic variation · Orang-utan · *Pongo* · Behavioural ecology · Social organisation · Cultural repertoire

The often remarkable degree of geographic variation between populations of a single taxon provides an exciting opportunity to investigate some of the mechanisms that lie at the heart of modern-day evolutionary theory. Of particular interest to behavioural primatologists, geographic variation allows investigations into the relative importance of local adaptation and phylogeny in shaping animal social systems. Here, we present a multivariate analysis of the behavioural ecology and social organisation of 10 populations of wild orang-utan (*Pongo* sp.) from both Sumatra and Borneo. Distinct differences between the two islands, as well as between the currently recognised taxonomic units, were apparent. We subsequently used these findings to distinguish between three hypotheses and tested whether the observed pattern of variation could be related to: (i) overall habitat productivity, (ii) temporal fluctuations in habitat productivity, and (iii) random genetic drift caused by geographic separation. We also examined whether these hypotheses could explain the geographic variation in the cultural repertoires of the different populations.

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## Hybridization in African Papionins – Processes and Phylogeographic Implications

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**Key Words:** Phylogeography · Reticulation · Introgression · Speciation · Papionini · Africa

Hybridization as a mechanism of speciation has been long recognized by botanists. Among animals, however, successful hybridization was regarded a rare phenomenon. Due to the application of molecular techniques this view has radically changed within the last decade. Hints of hybridization were found in almost all examined radiations, including primates. In this respect papionins constitute an interesting taxon. We have studied the phylogeny of several African members of this taxon (*Papio*, *Rungwecebus*, *Theropithecus*, *Lophocebus*) mainly on the basis of their mitochondrial genome. As a general picture, discordance between our phylogenetic reconstruction and morphology-based taxonomy became apparent. Such discordance between taxonomy and phylogenies is often the first hint and an evidential footprint of past reticulate events that led to mosaic genomes. Our results suggest that male introgression might have played a predominant role in shaping the contemporary phylogeographic pattern of African papionins. Here we will present new data on African papionin phylogeny which suggest that hybridization events, such as introgression with nuclear swamping or mitochondrial capture, may have impacted their evolution and speciation processes.

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## Poster Presentations

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### **Cortisol and Cortisone Measurement in Great Apes' (*Gorilla gorilla*, *Pan panicus* and Sumatran Orang-Utan) Saliva – One Hydrogen Atom Makes a Big Difference!**

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*Key Words:* Great apes · Cortisol · Cortisone · Saliva

Cortisol and cortisone are glucocorticoids. Cortisone is known as the inactive form of cortisol, which can be reactivated easily. In human saliva, the concentration of cortisone is higher than that of cortisol. In great apes, only a few studies are available of cortisol concentrations in saliva and none concerning cortisone concentration. In this study, the levels of cortisol and cortisone in apes' saliva were analyzed to compare the results with those of humans. Saliva samples of three captive great ape species (western lowland gorillas, Sumatran orang-utans and bonobos) were collected at Frankfurt Zoo, Germany. Immunoreactive cortisol and cortisone concentrations were measured using enzyme immunoassays. Saliva of all three studied species contained both steroids. In general, in all three species the concentration of cortisone was higher than the level of cortisol. Moreover, the cortisone concentrations differed highly significantly among the species ( $p < 0.001$ ). The highest cortisol and cortisone concentrations were measured in bonobos' saliva. In comparison, we found the lowest concentrations for both steroids in the saliva of Sumatran orang-utans. Furthermore, a highly significant correlation was seen between cortisol and cortisone concentrations in all three species. We found that, as in human saliva, the cortisone concentration in the saliva of all three great ape species is higher than the cortisol concentration. The higher amount of cortisone in apes' saliva may be caused by  $11\beta$ -hydroxysteroid dehydrogenase type 2 in the salivary glands or a lack of binding protein for this steroid.

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### **Are Dominant Males More Successful Reproductively?**

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*Key Words:* Mating strategy · *Procolobus tephrosceles* · Priority access model · Mating frequency · Copulatory pattern · Sexual swelling

It is considered that a high ranking position in group-living animals confers certain advantages over other individuals. Red colobus (*Procolobus tephrosceles*) live in multimale mating systems in which males are ranked in a dominance hierarchy that determines access to receptive females. Females develop extended conspicuous ovulatory and post-conception swellings, which arouse sexual interest in males and, consequently, promote male-male competition. Since females copulate with several males during their cycle, sperm competition may be another form of male-male competition in this species. Moreover, red colobus are considered to be multiple

mounters; therefore, sexual selection may have favoured morphological or copulatory patterns that increase reproductive success. In this study, we linked male social rank and sexual behaviour with data on female swelling morphology and reproductive states in a population of 39 wild red colobus. We found that priority of access to receptive females, as measured by monopolisation and mating frequency, was correlated with the male's status in the hierarchy. However, we found that subordinate males ejaculated more frequently after mounting a female than did dominant males; thus, subordinate males make good use of the few opportunities available.

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### **Testing a Model of Coalition Formation in Two Macaque Species, *Macaca sylvanus* and *Macaca assamensis***

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*Key Words:* *Macaca sylvanus* · *Macaca assamensis* · Coalition model · Sexual competition · Male-male coalitions

Coalitions among males are limited in their taxonomic distribution and even in primates where they are relatively common not all species display them. Recently, van Schaik and colleagues [2004] proposed a cost-benefit model to explain the variability in male-male coalitions in primates. This model states that the occurrence and type of coalitions observed within multimale groups is determined by the level of sexual contest competition that males experience. At present, the model is largely untested. The aim of this study is to evaluate the heuristic value of the coalition model, using data on coalitions in one semi-free ranging group of Barbary macaques (*Macaca sylvanus*) and one wild group of Assamese macaques (*Macaca assamensis*). These two species are seasonal breeders and have a promiscuous mating system, which should translate into a relatively low contest potential for males. These are the very conditions under which the model predicts the occurrence of all-up, non-rank changing coalitions. Coalitions among males were frequent during the mating season in both species. As expected, all-up, non-rank changing coalitions were most commonly observed in Barbary macaques. However, this coalition type was rare in Assamese macaques. The theoretical implications of these findings as well as possible reasons for the difference in coalition patterns between Assamese and Barbary macaque males are discussed in the light of other studies on primates.

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### **Role of the H.E.L.P Congo Project in Protecting the Biodiversity of the Conkouati-Douli National Park (CDNP) in Congo, Brazzaville**

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*Key Words:* Biodiversity · Mammals · Protection · Conservation · Densities

The H.E.L.P (Habitats, Ecologie et Liberté des Primates) Congo project has, since 1996, successfully released 41 chimpanzees within 'the Triangle', an area within Conkouati-Douli National Park (CDNP). The rich biodiversity of CDNP makes it the most ecologically diverse

protected area in Congo, but increased human population growth, hunting and deforestation threaten protected mammal populations living within and around the park. Continued monitoring of the released chimpanzees by the H.E.L.P Congo project staff and researchers has meant, though, that 'the Triangle' zone has been closely surveyed. It is therefore anticipated that the wildlife within this area are protected from anthropogenic processes which threaten their survival through the presence of H.E.L.P Congo project staff. The present study aimed to: (1) calculate densities for the following species: *Gorilla gorilla*; *Pan troglodytes*; *Cercopithecus cephus*; *Cercocebus torquatus*; *Lophocebus albigena*; *Mandrillus sphinx*; *Cercopithecus pogonias* and 11 other mammal species; (2) identify whether there has been an increase in the abundance of wildlife since 1998; (3) show whether the H.E.L.P Congo project played a significant role in the protection of the ecosystems within the CDNP. Using line transect surveys, distance sampling and indirect counts of ape nests, it was found that there had been an overall increase from 1998 to 2009. It was, therefore, concluded that the H.E.L.P Congo project does play an important role in protecting the wildlife within 'the Triangle' in the CDNP. The aspects which contributed to the protection of the species studied are discussed.

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### **Female Behaviour and Stress Levels in Response to Interactions with Males in Bornean Orang-Utans (*Pongo pygmaeus wurmbii*)**

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*Key Words:* Orang-utan · Female harassment · Faecal glucocorticoid

A striking feature in orang-utans is the occurrence of two different male morphs. In Sumatra, females prefer to mate with fully developed flanged males, whereas unflanged males are often observed to force copulations with females. Data from Borneo suggest that both flanged and unflanged males frequently force copulations with females. This study examines male-female relationships in Bornean orang-utans (*Pongo pygmaeus wurmbii*), in particular the response of females towards the two different morphs of male orang-utans. We collected detailed behavioural data and applied non-invasive methods to determine stress hormone levels of females. Fieldwork took place in Tuanan, Central Kalimantan. During a period of one and a half year, about 5,000 hours of behavioural focal observations on females and 240 faecal samples of 10 adult females in different reproductive states were collected. For 125 days, females were observed with a male, with 57 days spent with flanged males and 68 with unflanged males. We observed 23 copulations, of which 15 involved unflanged males and 8 involved flanged males. The proportion of cooperative matings was similar in both male morphs with 50% in flanged and 40% in unflanged males. We compare faecal glucocorticoid-metabolite concentrations of females during encounters with males with basal values of these females. We expect elevated stress hormone levels during encounters with males compared to times spent alone or with other females, and that forced copulations induce a higher stress response compared to cooperative ones. Furthermore, we examine whether the stress response differs between encounters with unflanged and flanged males. Behavioural data provide additional information about who initiates and maintains female-male relationships.

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## **A Parasitological Survey of Semi-Captive Drills (*Mandrillus leucophaeus*): Implications for Reintroduction to the Wild**

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*Key Words:* *Mandrillus leucophaeus* · Gastrointestinal parasites · Semi-captive · Reintroduction · Non-invasive

Found only in fragments of rainforest in Cameroon, Nigeria and Bioko Island, the drill (*Mandrillus leucophaeus*) is a large, terrestrial monkey that occupies the most restricted geographical range of any African primate. Due to hunting and habitat loss, the drill is also one of the most highly endangered primates in Africa. In 2000, in response to these threats, the Drill Rehabilitation and Breeding Centre (DRBC) was established in Eastern Nigeria with the main aim of establishing a semi-captive breeding group of drills with a view to their eventual reintroduction to the wild. Indeed, a reintroduction of 100 animals is planned for the near future. Previous studies on orang-utan (*Pongo* spp.), red ruffed lemur (*Varecia variegata*) and golden lion tamarin (*Leontopithecus rosalia*) reintroductions demonstrate the capacity for parasitic disease to seriously undermine the achievements of conservation initiatives. Over a three-month period, 100 faecal samples from the drill group at the DRBC which is to be reintroduced were non-invasively collected and examined for the presence of gastrointestinal parasites. The results provided previously non-existent, baseline parasitological data on the gastrointestinal parasites that infect semi-captive drills, data that will be used to develop protocols for their reintroduction to the wild. Gastrointestinal infection is common in semi-captive drills and can have significant implications for their welfare and prospects for reintroduction to the wild.

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## **Social Learning in Marmosets: Evidence for Conformity?**

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*Key Words:* Social learning · Conformity · Cultural transmission · *Callithrix jacchus*

Conformity can be defined as a disproportionate tendency to follow the majority, which in turn increases the homogeneity of behaviour within the group and the heterogeneity between groups. While for humans it has been shown that they not only copy the majority, but do so disproportionately and thus show a conformity bias, so far there is no evidence for conformity in non-human primates. The aim of this project is to investigate whether common marmosets (*Callithrix jacchus*) conform disproportionately to the behaviour shown by the majority in a social learning task in a foraging context. The first step of this experiment was to determine whether the subjects could learn the task, obtaining a food reward from a puzzle box, by watching a virtual demonstrator (subjects  $n = 17$ ). Preliminary analyses revealed that the subjects use social information to solve this foraging task. Specifically, they paid attention to and frequently chose and explored the same side of the apparatus as the virtual demonstrator. In the next step, demonstrators show two alternative solutions at different frequencies. Thus, subjects, for example, see one solution performed by 25% of demonstrators, but the second solution by 75%. According to the above definition, marmosets would show a conformity bias if they disproportionately chose the more frequently presented alternative, i.e. in more than 75%. If this prediction is met, this would be the first evidence of true conformity in a non-human primate.

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## Bird-of-Prey Turns Prey: Do Chimpanzees Hunt for Sport?

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*Key Words:* Chimpanzee · Hunt · Play · Evolution

Hunting and meat-eating are well-known behavioural patterns in many chimpanzee communities. However, bird hunting seems to be only an occasional behaviour, done mainly by juveniles and young adolescents. Among the chimpanzees of Bossou, in Guinea, predatory behaviours show such low frequencies that they have been described as incidental. Only two hunting events, in which a mammalian prey was not consumed, but rather was turned into a toy for chasing play, had been seen until now. Here, we report the first record of bird hunting (West African wood-owl, *Ciccaba woodfordi*) at Bossou, which was not followed by prey consumption. The episode lasted 4 h, during which one adolescent male always carried the bird's carcass. The hunter made four tree-nests and one ground-nest during this period, and played with the prey item in the nests. Ecological availability and distribution of prey may explain some differences between hunting frequencies across sites, although it probably does not directly influence the emergence of pursuit-hunting. The present report sustains the hypothesis that social traditions may explain better the lack of horizontal diffusion of hunting in some chimpanzee communities. Inventive play (innovation) and object manipulation (motor skill enhancement), which improve during the infant and juvenile periods, may be seen as key-behaviours linked to the evolutionary origins of hunting.

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## First Diurnal Primate Survey in Samkos Wildlife Sanctuary, Cardamom Mountains, Southwest Cambodia, during the Wet Season

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*Key Words:* Cambodia · Cardamom Mountains · Samkos Wildlife Sanctuary · Survey · Diurnal mammal · Gemaine's langur · *Trachypithecus germaini*

During two months, we conducted a diurnal mammal survey focusing on primates in Samkos Wildlife Sanctuary (3,338 km<sup>2</sup>) in the Cardamom Mountains (10,000 km<sup>2</sup>), southwest Cambodia. The natural sanctuary is characterized by forest types ranging from dry deciduous forest to hill evergreen forest. Only one previous diurnal mammal survey has been conducted in the area. This was carried out in 2000 during the dry season by Flora & Fauna International (FFI). The present survey represents the first conducted during the wet season (May and July). We used both distance sampling and occupancy modelling along 15 transects 2 kilometres in length. Transects were walked three times each to estimate the density of the endangered Indo-chinese silvered langur (*Trachypithecus germaini*) using distance sampling and conventional transect methods. Occupancy points (n = 45) were visited five times each, to record abundance of other large diurnal mammals, including *Hylobates pileatus*, *Macaca fascicularis*, and *Macaca nemestrina*. All four species of diurnal primate were present in the Samkos Wildlife Sanctuary, confirming the 2000 FFI survey results. Among these, three are classified as threatened by IUCN (2008). We present the abundance estimation of each species, and compare current



densities to those reported in 2000. We correlate these findings to available habitat, quantified in  $2 \times 20$  m plots ( $n = 45$ ), in order to make conservation recommendations for primates in this reserve.

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## **Comparison of Urinary PdG and Salivary Progesterone Levels for the Assessment of Ovarian Functioning: A Study of Nomadic Mongolian Herders**

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*Key Words:* Progestogens · Humans · Urine · Saliva · Ovarian function

Anthropological studies of ovarian hormones in community-dwelling women usually rely on assays of non-invasively collected samples of saliva or urine. Enzyme immunoassay (EIA) of saliva directly measures the biologically active hormone, progesterone, but its low concentration in saliva requires additional extraction and concentration steps in the assay procedure. EIA of urine samples measures the principal urinary progesterone metabolite, pregnanediol glucuronide (PdG). The high concentration of PdG in urine eliminates the need for extraction and concentration steps. But the measurement must be corrected, using either urinary creatinine concentration or specific gravity, for intra- and inter-individual variation in the water content of sampled voids. The choice of which bodily fluid to use in a specific study is guided by several factors, including the logistics of collection and storage. Less attention has been given to the possibility that inter-individual variability in salivary progesterone might not parallel that in urinary PdG. A direct comparison of measured levels of salivary progesterone and urinary PdG is needed to determine if both methods yield comparable results. This study evaluates and compares the salivary and urinary hormonal profiles of 25 ovarian cycles from pre-menopausal Mongolian nomadic herders (self-collection of daily samples for one complete menstrual cycle). We verify the agreement of the estimated days of ovulation, and the distributions across individuals of hormonal indices. We also ascertain the correlation between age and anthropometrics, and several indices of either salivary progesterone or urinary PdG, and consider the implications of these analyses for testing hypotheses in reproductive ecology and women's health.

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## **Social Housing of Surplus Males of Captive Javan Langurs (*Trachypithecus auratus*): Implication of Castration as a Management Tool**

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*Key Words:* Surplus males · Population management · Bachelor groups · Aggression · Castration

Javan langurs (*Trachypithecus auratus*) live naturally in social groups containing primarily only one adult male. Due to a sex ratio of approximately 1:1 zoos are confronted with a sur-

plus of males. This study examined if surplus males can gain socially by being kept in bachelor and multimale-multifemale groups and assessed if castration can be used as a managerial tool in terms of controlling aggression levels among male group members. Behavioural data were collected during a 6-week study for a total of 180 h in Howletts and Port Lympne Wild Animal Parks (UK). Agonistic behaviours (divided into with and without physical contact) and affiliative behaviours (such as allogrooming) of male group members as well as behavioural indicators of stress (such as scratching) were recorded using the focal continuous animal sampling method. Furthermore, instantaneous scan sampling was carried out to record the spatial relationship among male individuals. Males in three bachelor groups (containing both castrated and non-castrated individuals) consisting of two to three individuals, as well as males in two mixed-sex groups (one group containing only castrated males, the other group containing castrated and non-castrated males) were observed. The results of comparing rates of agonistic and affiliative behaviours, of spatial proximity and of stress indicators between non-castrated and castrated males, will be discussed. The study assessed the welfare implications of various group formations and the results also have implications for the feasibility of using castration as a behavioural management tool in the maintenance of surplus male Javan langurs in bachelor or breeding groups.

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## Social Interactions between Females in Wild Crested Macaques, *Macaca nigra*

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**Key Words:** Social behaviour · *Macaca nigra* · Female social relationships · Primate social systems

Macaque species show strong unity in their basic social structure. At the same time they display a great diversity in their social styles, ranging from despotic to tolerant, and are, therefore, a good model for the study of factors influencing such variation. However, data on tolerant species, such as *Macaca nigra*, mostly come from studies on captive groups. Thus, knowledge about their social behaviour in the wild remains very limited. This study aims at characterizing the social relationships between female crested macaques. For this purpose, two habituated wild groups, composed of 75 (21 adult females, 13 adult males) and 55 (16 adult females, 6 adult males) individuals, have been studied in the Tangkoko Nature Reserve, North Sulawesi, Indonesia, since June 2008. More than 900 hours of behavioural data on activity budget, nearest neighbours, aggressive and affiliative interactions have been collected on the 37 females. A number of questions concerning social interactions between females are being addressed: What are the affiliation and aggression rates? What is the nature of the hierarchy females establish? How does dominance rank influence affiliative interactions and spatial proximity? How are grooming interactions characterized? This study is the first to investigate extensively such questions in a species described as tolerant and ultimately aims at achieving a better understanding of what factors might drive the evolution of social systems in macaques as well as in primates in general.

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## The Evolution of Social Behaviour: A Case Study

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*Key Words:* Chimpanzee · Independence · Social network · Mother-infant relationship · Social skills

Independence from mothers is crucial for the establishment and maintenance of social relationships with group members in animals with complex social organization such as chimpanzees (*Pan troglodytes*). We investigated the achievement of locomotor, foraging and social independence and social network size in captive infant and juvenile (n = 6) chimpanzees housed at Chester Zoo, UK. We predicted a decrease in the frequency of being carried, suckling and sitting in contact and an increase in proximity and other social interactions as immatures achieve independence. We also hypothesized an increase in social interactions with social partners, other than their mothers, and an increase in the number of social partners. Our results were consistent with our predictions. Firstly, we found a decrease in the frequency of being carried and suckling. Secondly, as infants grew older, time spent in sitting in contact decreased whereas time spent in proximity increased. In addition, duration of grooming received from mothers and other group members decreased, whereas the duration of high intensity play increased as infants achieved independence. Furthermore, the frequency of sitting in contact with social partners, other than their mothers, decreased, while the frequency of proximity increased with more social independence. The total number (and the percentage of social partners that were different) was higher for infants and juveniles than their mothers. These findings suggest that as infant and juvenile chimpanzees achieve independence from their mothers, they form strong social bonds with other social partners and increase the size of their social networks.

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## Population Structure and Hunting of Guinea Baboons in Guinea-Bissau

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*Key Words:* Guinea baboons · Population structure · Hunting · Guinea-Bissau · Warfare

Cantanhez Forest Park (Guinea-Bissau) was one of the most important battlefields during the war of independence against Portuguese colonization (1963–1974) and during this time and subsequently, demographic declines have been recorded in Guinea baboons (*Papio hamadryas papio*) due to hunting. Our aims were: (i) to clarify the historic poaching pressure towards this primate and (ii) to establish the present population structure of Guinea baboons within the park. Information regarding the historic hunting pressure was obtained by interviews with ex-Portuguese military hunters (n = 6) and by ex-Portuguese military testimonies (n = 21). The current distribution was determined using scats and/or vocalizations. Qualitative information obtained from interviews and testimonies revealed that baboons were constantly present in the Cantanhez Peninsula during the period but have decreased since the late 1980s. Key reasons were: (i) an increase in hunting by militia and (ii) baboon meat commercialization in the capital. During the war, baboon meat was frequently consumed by Guinean-Bissau troops but not by Portuguese military personnel, who instead bought and kept individuals as pets. The present

distribution, an estimated area of 188 to 273 km<sup>2</sup>, includes the east of the Peninsula, although this is interrupted by agricultural areas. Further work will evaluate the effect of hunting pressure on the genetic population structure and diversity. This project is funded by Fundação para a Ciência e Tecnologia (SFRH/BD/37417/2007).

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## **Behavioural Stereotypies and Behavioural Change Rates in Ex-Pet and Zoo-Reared Capuchins: Implications for Cognitive Damage**

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*Key Words:* Ex-pet primates · Stereotypy · Welfare · Striatum dysfunction · Physiological development

There has been research suggesting a link between behavioural stereotypies and behaviour change rates with striatum dysfunction in bank voles and songbirds. Research has also shown a strong correlation with abnormal rearing and social deprivation with the aetiology of abnormal stereotypic behaviour in primates. The purpose of this project was to look at the cognitive impacts of being reared as a pet through a scientific investigation of behavioural change rates and observed stereotypies, and the possible link these results may have to support the prevalence of striatum dysfunction in ex-pet monkeys. The subjects of this experiment were a group of 8 ex-pet capuchins (*Cebus apella*) from the Monkey Sanctuary Trust, Cornwall, and 8 mother-reared capuchins serving as a control group from Port Lympne Zoo, Kent. Capuchins were chosen as a study subject because they are legal pets in many countries including the UK and USA and have the largest brains of the New World primates. Through continuous focal sampling, behavioural observations were recorded at the same time daily over a 15-minute session per individual with a total of 112 h of behavioural observation data for the ex-pet and mother-reared groups. Stereotypic frequencies and the mean behavioural change rate per minute were calculated to compare the ex-pet and mother-reared groups' data. We will discuss the implications of keeping primates as pets and the potential harm it can have on the physiological development and welfare of pet primates.

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## **Peer Conflict Resolution and Dominance in Portuguese Preschool Children**

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*Key Words:* Conflict resolution · Preschool children · Reconciliation · Social dominance · Social competence

Preschoolers, like non-human primates, develop conflict resolution strategies, such as reconciliation, in order to minimize the costs of competing for limited resources. Our main objective was assessing the relation between reconciliation and social dominance within a preschool peer group. The participants were 25 four-year-old Portuguese children attending the same preschool group in the metropolitan area of Lisbon. Data on conflict and reconciliation were collected using PC-MC method [de Waal and Yoshihara, 1983]. A corrected conciliatory tendency [Veenema et al., 1994] of 55% was obtained at the group level of analysis. David's Score

[Gammell et al., 2003] was used to quantify dominance relationships. Overall dominant children showed higher levels of conciliatory tendency in conflict resolution, independently of the dyadic gender composition. Thus, dominant children when resolving conflicts in this group used prosocial strategies beyond the coercive ones. Moreover, further dyadic analysis revealed that the smaller the status difference between the opponents, the greater was their conciliatory tendency. A plausible interpretation of the above results may be stated in terms of attraction to adjacent rank [Seyfarth, 1977], implying greater positive interaction and alliance formation between children of similar status.

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## Facial Rating: The Influence of Symmetry and Beauty Products on Mate Choice

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*Key Words:* Mate choice · Facial symmetry · Beauty products · Human · Attractiveness

Many studies suggest that facial symmetry, as an indicator of stability in the development and health of an individual, influences the evaluation of the characteristics of a partner. Our hypothesis is that in addition to symmetry, other factors like the use of beauty products can be artificial phenotypic stimuli that influence mate choice. Our study was carried out in diverse public institutions in Santiago, Chile, with 262 men and 456 women. They had to evaluate three images of the faces of people of the opposite sex with different levels of facial symmetry. In the girls' pictures, the one with the smallest facial symmetry had the lips (almost imperceptibly) painted. In the men's pictures, the one with intermediate facial symmetry had glossy hair. Most of the women considered the man with the highest facial symmetry to be the most attractive, healthier, more desirable for casual sexual relationships, and of higher social dominance. However, the man with the least facial symmetry was considered by most women to be more intelligent and better at caring for children. Most of the men considered the woman with the least symmetrical face (but with the slightly painted lips) as healthier and of higher social dominance. Most men considered women with both higher and lower facial symmetry as the most attractive. We concluded that facial symmetry influences the evaluation of the partner's characteristics, but other factors, such as the use of beauty products, can be more important phenotypic signals than facial symmetry.

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## Seasonal and Social Influences on Faecal Androgen and Glucocorticoid Excretion in Wild Male Long-Tailed Macaques (*Macaca fascicularis*)

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**Key Words:** Long-tailed macaque · Males · Reproductive seasonality · Androgens · Glucocorticoids

Whereas it is well known that in strictly seasonal breeding primates, males show pronounced changes in testicular and adrenal hormone levels concurrent with reproductive activity, endocrine patterns in males of non-strictly seasonal breeding primate species and their relation to seasonal and social correlates remain largely unknown. Here, we examined the annual pattern of faecal androgen and glucocorticoid excretion and its relationship to environmental (rainfall, temperature) and social factors (rank, number of receptive females) in a group of wild long-tailed macaques (*Macaca fascicularis*), a species with a moderate degree of reproductive seasonality. The study was carried out in the Gunung Leuser National Park, northern Sumatra, Indonesia, over a period of ten months encompassing the conception and birth season. Our results show that male long-tailed macaques exhibit a distinct annual variation in both androgen and glucocorticoid levels. Androgen (but not glucocorticoid) levels were significantly elevated during the conception period in association with elevated rates of male-male aggression and copulatory activity and both were strongly related to the number of receptive females. Neither glucocorticoid nor androgen levels were related to male dominance rank or to the environmental parameters investigated. Interestingly, levels of both hormones started to increase in the late birth season 1–2 months prior to the upcoming mating season, suggesting that male long-tailed macaques undergo hormonal changes in preparation for the challenges associated with breeding. Our data provide evidence that males of a non-strictly seasonal breeding species show endocrine patterns generally similar to those found in strictly seasonal breeders.

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## The Accuracy of Sexual Swellings as Indicators for the Reproductive Status of Female Red Colobus (*Ptilocolobus tephrosceles*)

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**Key Words:** Mating strategies · Sexual signals · Colobines · Female mating competition · Sexual swellings

Females of some primates exhibit exaggerated swellings of the perineal skin, particularly around the middle of the ovarian cycle. It seems inevitable that swellings are very costly for the females. However, sexual swellings have evolved independently at least three times in primates, suggesting a very strong selective advantage. Although there is consensus that sexual swellings have evolved in the context of sexual selection, their functional significance remains unsolved. The present study (at Kibale National Park, Uganda) is the first detailed study on mating strategies in *Procolobus tephrosceles*. The aim is to investigate how accurate sexual swellings are as indicators of female receptivity, and how female behaviour and receptivity differ in *P. tephrosceles* and *P. badius*. Sexual swellings in *P. tephrosceles* are a lot smaller than those in *P. badius*. We showed that, in contrast to *P. badius*, female *P. tephrosceles* do not emit copulation calls.

Possibly, female *P. tephrosceles* have more control over mating partners than *P. badius* due to a lower degree of male aggressiveness and less reproductive overlap among females. In addition, females can be receptive for a month (or more) in both species and pregnant females develop swellings too. Our first analyses suggest that, although males are interested in both, they prefer females with conception cycles over those with post-conception swellings. Our preliminary results support the hypothesis that swellings evolved as a female counter-strategy to male coercion/monopolisation that maximises paternity confusion and female promiscuity.

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## About Being Nice: Further Evidence for Prosociality in Common Marmosets

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*Key Words:* Prosociality · Cooperative breeding · Common marmosets · Helping

Humans are known to be highly cooperative and care about the welfare of others, whether related or not. Recent evidence suggests that this prosociality is not unique to humans, but also present in non-human primates, particularly in those engaging in allomaternal care and provisioning. In order to evaluate the hypothesis that cooperative breeders have the preconditions to show prosociality, we (i) have to replicate the finding that cooperative breeders do show spontaneous prosociality and (ii) test additional species that engage in shared care and provisioning to different degrees. Here, we present data replicating the finding that common marmosets show spontaneous prosociality, using an experimental setting suitable to test for spontaneous prosociality in a group context and therefore without having to separate individuals. We tested two family groups of common marmosets (*Callithrix jacchus*, n = 15) in their home cages with all group members present. Subjects had previously participated in experiments of prosociality in a different paradigm. Preliminary results are in agreement with the data previously obtained from the same individuals and confirm the presence of spontaneous prosociality in this species. Additionally, this experimental setting is suitable to test for spontaneous prosociality across different species in an easy and comparable way. Such directly comparable data from various species may contribute to a better understanding of the distribution of spontaneous prosociality in non-human primates.

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## Phylogeny of Baboons in Southern Africa

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*Key Words:* Phylogeny · *Papio* · Cytochrome b · Nuclear swamping

Recently identified haplogroups based on mtDNA suggest great genetic variation within the genus *Papio*. The deepest split was found between northern and southern baboon lineages. The border between these lineages is supposed to be in Tanzania, but the exact location requires further investigation. We focused on the southern lineage of the genus *Papio* where two distinct morphotypes (species) can be identified, yellow and chacma baboons. Based on complete cytochrome b sequences, we identified six haplogroups, three each for yellow and chacma baboons, indicating discordance between mtDNA phylogeny and taxonomy. We further collected faecal



samples at 51 sites in central and southern Tanzania. Our analysis revealed haplotypes belonging to the northern lineage in central Tanzania, while haplotypes belonging to the southern lineage were found only in the southern part of the country. The now confirmed border between the lineages cuts through the range of yellow baboons causing the mitochondria of yellow baboons from southern Tanzania to be more closely related to those of chacma baboons than to the mitochondria of their conspecifics from central Tanzania. Discordances between mtDNA phylogeny and taxonomy are common in baboons and can be explained by nuclear swamping events.

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## Mosquito Avoidance Drives Selection of Nest Tree Species in Bornean Orang-Utans

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*Key Words:* Mosquito avoidance strategies · Night nests · Climatic factors · Anacardiaceae · Ecology

Nest tree species selection by orang-utans is thought to be driven by habitat, climatic conditions and predator avoidance. Based on a previous study on a wild population of Bornean orang-utans (*Pongo pygmaeus wurmbii*) at Tuanan in Central Kalimantan, Indonesia, a comparison was made with Sungai Lading, another field site in Central Kalimantan. Over 3,000 nests were described at Tuanan and 345 for Sungai Lading in terms of architectural, structural and protective features. Age-sex class differences were found in tree species selection and structural features of the nests as a possible response to elevated mosquito density. Some live intact plants are known to repel mosquitoes, mainly based on secondary compounds in their leaves and barks. Furthermore, a previous in situ mosquito assay revealed that leaves and branches of *Camposperma coriaceum* trees significantly repel nocturnal mosquitoes, whereas some other tree species tend to attract them. New results show that orang-utans at both sites preferentially use trees with anti-mosquito properties during periods with a higher mosquito density ('mosquito season'). The same tree species are used by orang-utans from Tuanan and Sungai Lading for leaf carrying (carrying branches of this particular species to use as covers of nests built in other trees), which was also reported as a possible cultural variant. Thus we suggest that parasite avoidance is of great importance in the selection of nest tree species.

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## The Multi-Group Diversity in Primate Communities: Studying Interaction and the Evolution of Social Strategies with Agent-Based Models

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*Key Words:* Social strategies · Diversity · Social interaction · Agent-based model · Social diversity

To understand the structure of a large-scale biological, social or technological system, it can be helpful to deconstruct the system into smaller subunits or modules. We propose to develop an information-theoretic approach to identify the modules of which the system is composed by finding an approximation to its interconnectedness. We will explain the advantages of this approach and illustrate them by partitioning a number of real-world and model networks.

The methods available for studying biological systems have widened our ability to gather comprehensive system (community)-level information on a huge number of interactions from diverse individuals. These approaches show that these systems are connected through a dense network of non-linear interactions among its components, and that this interconnectedness is responsible for their efficiency and adaptability. This interconnectedness, however, poses significant challenges to researchers trying to interpret these data and to extract the principles that will enable us to build new theories and to make new predictions. A central idea in biology is that life processes are hierarchically organized. Additionally, it seems plausible that this hierarchical structure plays an important role in the systems' dynamics. However, given a set of individuals, and their interactions, we still do not have an objective method to assess whether such hierarchical organization does indeed exist or to identify the different levels in the hierarchy.

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## The Flexible Use of the Gesture 'Touch' in Chimpanzees

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*Key Words:* Chimpanzees · Gestures · Touch · Flexibility · Function

Recently, chimpanzees have been shown to use some gestures flexibly, that is, the meaning is context-dependent. Data were collected in a longitudinal study documenting gesture use across contexts for infant, 1 to 5 years of age, and adult chimpanzees. Here we report on (1) the extent to which the gesture 'touch' is used flexibly and (2) whether there is a difference in the use of the gesture by adult versus infant chimpanzees. Videotaped observations were collected for 11 adults (3 male) and 3 infants (1 male) housed in a semi-natural social group at the Kyoto University Primate Research Institute (KUPRI) in Japan (total of 43 hours of video). All contexts in which the gestures occurred were recorded, along with the initiator and the receiver of each gesture. Touch was the most flexible gesture observed: We found that touch occurred in 20 different single contexts and 6 blended contexts. The most frequent contexts for touch, for both the adults and infants, were contact, greet, groom and play. The findings from this study show the extent of versatility in the gesture touch. Numerous gestures were used flexibly (17 of 36 gestures), but (1) were limited to a few contexts or (2) the different contexts tended to be closely related in function (such as appeasement and providing comfort). This study illustrates the importance of contextualized meaning in understanding flexibility in the gesture use of great apes.

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## The Impact of Browse and Fruit Consumption on Regurgitation and Reingestion in Captive Western Lowland Gorillas (*Gorilla gorilla gorilla*)

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*Key Words:* *Gorilla gorilla gorilla* · Diet · Abnormal behaviour · Captive management · Browse

Regurgitation and reingestion (R/R) is an abnormal behaviour that regularly occurs in captive western lowland gorillas (*Gorilla gorilla gorilla*; WLG), and has been linked to differences in the diets of captive and wild populations. Captive WLG receive excess dietary sugar,

and not sufficient fibre. Past evidence has shown links between increasing fibre and browse and subsequent reduction of R/R. We conducted an experimental study which assessed the individual and combined effects of fibre and sugar on R/R behaviours in two gorilla groups at Port Lympne Wildlife Park in England. Behavioural observations of R/R were carried out across the following phases of our study: Phase 1: baseline data collection with regular diet; Phase 2: regular diet plus browse supplementation; Phase 3: regular diet with high-sugar fruit excluded; Phase 4: regular diet plus browse supplementation and high-sugar fruit excluded; Phase 5: return to baseline with the regular diet. Each study phase lasted ten days and continuous focal sampling techniques were employed. The results from this study will provide information pertaining to the captive gorilla dietary regimens and their effect on behaviour. The implications of these results will be discussed in terms of their relevance to captive gorilla diets and reducing R/R. They provide systematic, empirical evidence for the relationship between nutritive intake and behaviour, and this study sheds light onto dietary care in captive great apes and how this contributes to psychological and physical health and welfare.

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### **Glucocorticoid and Androgen Levels in Flanged and Unflanged Wild Bornean Orang-Utans**

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*Key Words:* Orang-utan · Male bimaturism · Faecal glucocorticoid · Faecal androgen

Adult male orang-utans can be either unflanged or flanged, coinciding with different morphology, behaviour and reproductive strategies. In wild Sumatran orang-utans it has been shown that the duration of a male's unflanged state is highly variable and can last more than 15 years. In addition, there are numerous reports from zoos that unflanged males only begin to develop secondary sexual features after isolation from other mature males. This led to the suggestion that the development of secondary features by unflanged males is suppressed by flanged males. According to this hypothesis, unflanged males are expected to have higher stress levels and concomitant low levels of androgens, which are responsible for the development of secondary sexual features in a variety of species. Recent studies have tested this hypothesis and found no significant difference in cortisol and testosterone levels between arrested and fully developed males. However, these studies were conducted with zoo animals living under unnatural conditions, which may have distorted the results. Our study investigates differences in faecal hormone levels between flanged and unflanged males from a wild population in Tuanan, Central Kalimantan. Between April 2007 and December 2008, faecal samples (n = 120) from 11 flanged and from eight unflanged males were non-invasively collected. In addition, samples were also collected from two developing males which, based on zoo studies, were expected to show the highest levels in cortisol and androgens. Previous zoo studies suggest that this transitional phase is the most stressful life phase at least for zoo orang-utans. Faecal glucocorticoid and androgen metabolite analysis is currently underway using assays previously validated for zoo orang-utans.

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## Visibility between Neighbouring Groups of Capuchin Monkeys: Influence on Intragroup Aggression and Social Relationships

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*Key Words:* Inter-group interactions · Social relationship · Reconciliation

Socio-ecological models predict how primate social organization is influenced by the nature of competitive regimes to which groups are subjected. In this study, we tested whether intra-group social relationships of capuchin monkeys (*Cebus apella*) in captivity were influenced by the interactions with a neighbouring group. According to one hypothesis based on socio-ecological theory, intra-group social relationships should be positively reinforced by the presence of another group in order to deal with the perceived external threat. Animals would thus show lower intra-group aggression rates, more affiliative interactions, and higher post-conflict reconciliation rates. An alternative hypothesis suggests that visual interactions with another group may constitute a constant source of tension and thus negatively affect intra-group social relationships. This would lead to higher intra-group aggression rates, and possibly fewer affiliative interactions, and lower post-conflict reconciliation rates. In this work, an experimental setting was created in order to modify the visual contact between the study group (n = 12) and a neighbouring group of tufted capuchin monkeys housed in the CNR Primate Centre, Rome. Observational data on affiliation, reconciliation and aggression were collected in two experimental conditions ('In view' and 'Out of view'). The results showed that when visual access was allowed rates of intra-group aggression increased significantly and the effect of rank on aggression was stronger. In contrast, experimental conditions did not affect socio-positive interactions. These results suggest that the presence of another group has a negative influence on intra-group social relationships.

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## Social Relationships among Immatures and Adult Non-Mothers of Captive *Gorilla g. gorilla*

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*Key Words:* Gorilla · Social relationships · Immatures · Social development

In the wild, gorilla immatures start their independence at 3 years of age; however, their socialization starts much earlier. Mothers can influence the socialization process by their movements/presence in proximity to certain other individuals and by tolerating others' interest in the infant. With growing independence, the infant actively seeks contact. As the silverback is the necessary protector, the infants should seek his proximity. According to the literature, other contacts are chosen following kinship and the relationships of the mother. In a captive gorilla group (Apenheul/NL), consisting of one silverback, five adult females and five offspring, we tested if the association partners of immatures were also those of their mothers. Over a period of five statistical days (46 observation days, 155 h in total), four older offspring were observed for 20 h each, the six adults for 12.5 h each. The majority of the relationships of offspring

towards adults reflected maternal social preferences. However, in some juvenile-adult dyads the association could not be explained in this way. Other factors, such as former social events, presence of newborn infants or changing maternal interests, influenced initiation of proximity or friendly interactions. The relationship towards the young adult male, who was not the father of the older offspring, included sexual interest (probably as a strategy to calm his aggression) and playful behaviour.

We gratefully acknowledge the staff at Primate Park Apenheul/NL.

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## Sex-Biased Dispersal Affecting the Social Relationships in Two Colobine Monkeys in Guinea Bissau

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**Key Words:** Colobus monkeys · Aggressive behaviour · Affiliative behaviour · Sympatry · Sex-biased dispersal

Western red colobus (*Piliocolobus badius temminckii*) and western black-and-white colobus (*Colobus polykomos*) are two African colobine monkeys. Although phylogenetically close and very often living in sympatry, the two species exhibit very different social systems. Western red colobus live in large social groups comprising several adult males and females, where dispersal is mainly female-mediated and females exhibit conspicuous sexual swellings. In contrast, western black-and-white colobus live in much smaller groups with one to three adult males, in which dispersal is mainly male-mediated and no clear sexual behaviour is displayed by ovulating females. In this project, one social group of each species is being studied in Cantanhez Forest, Guinea Bissau, in order to understand how these different social systems can affect within-group social dynamics. Ad libitum and focal data were collected for six months. In western black-and-white colobus, we expected closer social bonding between females as a result of female philopatry. In contrast, male coalition formation and weak social bonding between females were expected to occur in western red colobus as a consequence of male philopatry. Results show stronger social bonding between red than black-and-white colobus females. In black-and-white colobus, females engage in affiliative interactions more often with males than with other females and are more aggressive towards each other than are red colobus females. These preliminary findings seem to show different within social group dynamics from what was expected considering the social systems described above. More behavioural data will be collected and genetic data will be provided in order to better understand these unexpected behavioural patterns.

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## **An Investigation into the Environmental Factors Affecting Behavioural Stress in Captive Pied Tamarins, *Saguinus bicolor***

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*Key Words:* Captive management • Callitrichidae • Enclosure • Visitors • Wasting Marmoset Syndrome

The pied tamarin, *Saguinus bicolor*, a Neotropical primate from Brazil classified as endangered by IUCN, is affected by human activities and loss of habitat. In captivity, this species is extremely sensitive and often suffers from a condition similar to the fatal and possibly stress-related Wasting Marmoset Syndrome. To investigate factors influencing behavioural stress levels in captivity a study was conducted at Durrell Wildlife Conservation Trust. The study focused on the impacts of visitors, keepers and other callitrichids nearby, as previous studies have shown these factors to have a negative effect on captive primates. Sixteen adult individuals of *S. bicolor*, six females and ten males, living in eight groups, were studied. Five groups were kept in on-show exhibits and three groups were kept in off-show exhibits, i.e. no visitor access. Data collection took place over four weeks using continuous focal sampling and approximately 100 h of data were collected. Additionally, measures of visitor density, weather, temperature and humidity were recorded. A comparison was made between on-show and off-show exhibits in terms of stress levels shown. In addition, the use of the outdoor enclosures in relation to weather conditions was evaluated. This study was designed to identify stressful factors affecting *S. bicolor* in captivity in order to help zoos and sanctuaries keeping this species provide optimal living conditions and help *S. bicolor* thrive in captivity. Results of this study are discussed in the light of other studies of captive callitrichids, and a series of recommendations are developed.

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## **Post-Conflict Affiliation in Barbary Macaques Increases the Chances of Renewed Aggression**

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*Key Words:* Aggression • Barbary macaques • *Macaca sylvanus* • Post-conflict management • Reconciliation

Post-conflict affiliation is assumed to repair social relationships after disturbance and to function as reconciliation. While numerous studies have addressed the factors that determine the occurrence of post-conflict affiliation, few have tested the effects of post-conflict affiliation on subsequent interactions. We studied the post-conflict behaviour of female Barbary macaques, *Macaca sylvanus*, living in the enclosure 'La Forêt des Singes' at Rocamadour, France. Based on a sample of 914 conflicts occurring in 224 dyads, we found that 32% of all conflicts were followed by post-conflict affiliation. Female Barbary macaques invested more in post-conflict affiliation with valuable partners, and they modulated their post-conflict behaviour in relation to relationship and conflict characteristics. Remarkably though, affiliative post-conflict interactions increased the short-term probability of renewed aggression by the former aggressor to 16% compared to 9% for conflicts that were not followed by affiliative behaviour. Such renewed aggression after post-conflict affiliation occurred particularly frequently among

females and after conflicts over food, suggesting that post-conflict affiliation sometimes falsely lures the former victim to stay in the vicinity, even at the risk of receiving renewed aggression. Our data collection protocol did not allow us to examine longer-term consequences for a relationship where the former victim experienced a renewed attack; however, at least in the short term, it appears that post-conflict affiliation in Barbary macaque females does not necessarily serve to reconcile former opponents. Instead, the occurrence of renewed aggression might be an expression of the ambivalent character of the social relationships in this rather tolerant species.

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### What Is the Best Strategy to Access Females in Oestrus?

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*Key Words:* Multimale mating system • Sexual signal • *Ptilocolobus tephrosceles* • Male mating strategies • Sexual swellings

A high rank often confers advantages due to increased access to resources like nutrients or females in oestrus ('priority of access' model). Sexual swellings in females may generally help males assess the reproductive state of females and adjust their mating behaviour accordingly. However, the reliability of the signal has been found to be highly imprecise in several species. We observed red colobus monkeys (*Ptilocolobus tephrosceles*) in Kibale National Park to investigate the role of swellings for male and female mating strategies in this species. Red colobus live in multimale-multifemale groups with male philopatry, where females copulate with several males during each cycle. Using a variety of data collection techniques during a six-month study on a group of 37 individuals, we found that young males, in particular, tried to monopolise females with swellings. We documented several cases where pregnant females continued to display sexual swellings. It has been suggested that pregnant females exhibit sexual swellings in order to confuse paternity and thereby reduce the risk of male harassment or even infanticide. While males still copulated with these females, we found a clear reduction in sexual activities compared to females in oestrus. This result suggests that pregnant females are less attractive and that males may be able to partly assess the reproductive state of females.

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### Preliminary Study of the Bengal Slow Loris at Phnom Samkos Wildlife Sanctuary, Cambodia

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*Key Words:* Survey • Density • Population decline • Exudate feeding • Conservation • *Nycticebus bengalensis*

The Bengal slow loris (*Nycticebus bengalensis*) is a little studied primate endemic to Bangladesh, Cambodia, China, India, Laos PDR, Myanmar, Thailand and Vietnam. Classified as vulnerable, based on habitat loss, data from wild populations are scanty. Over three months in 2009, we calculated encounter rates of *N. bengalensis* along 15 transects in Phnom Samkos in



the Cardamon Mountains, and collected preliminary data on their behaviour and ecology. These data were supplemented with interviews from indigenous people, who traditionally collect slow lorises for medicinal purposes. As in previous studies of Bengal slow lorises, encounter rates were low, averaging 0.15 animals/km. Local people reported a dramatic decline in lorises, and noted that in order to find lorises, they had to walk further into the forest than they did 5 and 10 years previously. Lorises are ranked as highly important in Khmer traditional medicine, supposedly curing more than 100 ailments. We were able to radio collar two individuals, who were followed for approximately 40 h. Although visibility was poor, behavioural data revealed that *N. bengalensis* relies heavily on exudates, but also supplements its diet with fruits and insects. Animals were observed to travel more than 800 m per night; travel was continuous. When resting did occur, it was in bouts of up to two hours. Animals occurred at low abundance, and numbers are still declining. A longer-term study currently underway at Phnom Samkos will further address these conservation issues.

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## Hand-Rearing of a Crowned Sifaka

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*Key Words:* Crowned sifaka · *Propithecus coronatus* · Hand-rearing · Training

There are few crowned sifaka (*Propithecus coronatus*) in captivity: only 17 individuals (April 2009) can be found in 6 European zoos. Holly is a wild born female imported from Madagascar in 1993. She has bred several times but has not managed to raise her young; they have all died several days after birth. She is a very good mother but since her nipples are abnormal, she can not feed her infants. However, it is very important that she has infants to provide new blood in the captive population. We decided, therefore, to hand-rear her next infant. Since we assumed that her only problem was that she was not able to feed her offspring and bearing in mind that we thought that she would be a good mother, we decided that the next infant should stay with her as much as possible. We thought that this would help future offspring develop successfully. In consequence, we started a training programme to facilitate access to the offspring. We needed to have access to the infant without capturing the mother, and so needed to teach Holly to let us take her infant from her to feed it. The aim of the training was to block Holly into a small space – ‘the training cage’ – and to be able to touch her within this space on very specific areas of her body where the infant was likely to be attached, that is to say, the groin, the belly, etc. During the first weeks of its life, Holly and her infant were together for several hours a day in the training cage. For the rest of the time, the infant was always in visual contact with its parents because we rearranged the lemurs’ enclosure to allow access to all the equipment required for hand-rearing the infant and we fed it in the enclosure. The contact between the infant and its parents, especially its mother, was not broken and the youngster has been a full member of the group since its birth. Several infants have now been hand-reared and the training programme has worked for 2 other females.

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## **A Post-Translocation Study Examining the Cause of the Population Decline of *Eulemur collaris* in Mandena Littoral Forests, South-Eastern Madagascar**

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*Key Words:* Translocation · Littoral forest · fossa · *Eulemur collaris*

Though potentially important as a conservation tool, most animal translocations, including those of primates, do not follow a long-term monitoring agenda. The absence of these data is particularly serious for prosimians. In 2000, 28 collared lemurs, *Eulemur collaris*, a flagship species for the threatened Malagasy littoral forest, were relocated from a forest fragment destroyed by human activities into a protected area. After the translocation, the population initially increased, but it has been decreasing since 2004. There are three possible hypotheses explaining the decline of the population: predation by the fossa (*Cryptoprocta ferox*), low habitat carrying capacity, or a combination of both predation and food scarcity. In order to investigate this, three groups of lemurs, totalling 10 individuals, were studied to examine the feeding ecology and health of the existing population. Phenology patterns and demographic dynamics of the population were examined through analysis of data collected by local assistants. The results of this analysis are used to reject or support the hypotheses suggested to explain the population decline and to discuss the benefits and pitfalls of lemur relocation into forest fragments.

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## **Prosocial Behaviour in Human Infants**

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*Key Words:* Prosociality · Human infants · Helping · Dictator game · Socio-cognitive abilities

Acts of helping, sharing, comforting and cooperation are common in humans and appear at the group level and towards unrelated strangers in contrast to what can be observed in other animals. Prosocial behaviour can first be observed in human infants at the age of about 18 months, in the form of helping and comforting; some studies, however, report the onset of prosocial behaviours only later, at 4 or 7 years of age. During the same time span, children develop important socio-cognitive capacities pertaining to self-other differentiation. It is still unclear whether there is a causal relationship between prosocial behaviours and socio-cognitive abilities like a theory of mind. We investigated this question by running a prosocial and a socio-cognitive task with 1.5–4-year-old children in nursery schools in Zurich, Switzerland. In the prosocial task, a focal child had the opportunity to provide another child with food. This non-verbal, behavioural, dictator game-like setting corresponds to one used for other primates, which allows for interspecies comparison. To assess socio-cognitive skills, we used five tasks, as originally designed by Wellman and Lu [2004]. We were interested in discovering if and when children behave prosocially in the dictator game task and if this is correlated with socio-cognitive developmental steps. Initial results show that some of the children behaved prosocially and a fully developed theory of mind seems not to be necessary for them to behave prosocially in this task.

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## Conservation Genetics and Phylogeography of Chimpanzees in Guinea-Bissau

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*Key Words:* Chimpanzees · Guinea-Bissau · Phylogeography · Illegal trade · Conservation genetics

The western chimpanzee, *Pan troglodytes verus*, is considered one of the most endangered chimpanzee subspecies of the African continent. Guinea-Bissau (GB) represents an important population since GB chimpanzees are found at the most westerly limit of the chimpanzee distribution, occupying a variety of habitats. Their survival is threatened by habitat destruction, conflicts with humans caused by crop raiding activity and illegal trade (pets and body parts). Their genetic structure has never been evaluated. By using non-invasive methods combined with molecular markers (mtDNA and microsatellites) this study aims to: (i) assess the genetic diversity and structure of the chimpanzee communities of GB; (ii) characterize social groups and their dynamics in Cantanhez National Park and (iii) survey gastrointestinal parasites in different communities. Fieldwork was conducted from September to November 2008 and preliminary results strongly suggest that chimpanzee body parts (i.e. skin, bones, teeth, etc.) are being used for animistic and medicinal practices, although chimpanzees are not generally hunted for food. We report this threat factor for GB for the first time. As a result of this research it will be possible to: (i) designate chimpanzee conservation management units using genetic data and (ii) determine the genetic origin of chimpanzees kept as pets and identify routes in a way to mitigate the impacts of illegal trade and hunting by direct educational intervention at the sources.

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## A New Approach to Long Call Function in Bornean Orang-Utans

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*Key Words:* Orang-utan · Communication · Long call · Social context

Long calls by flanged male orang-utans serve as a long-distance communication signal in this semi-solitary species. Two long call functions have traditionally been considered: repulsion of male rivals and attraction of female mates. In this study, we examined the effect of context on the acoustic properties of long calls as well as the ranging responses of females to them in Bornean orang-utans at Tuanan. The context differentiations were: (1) spontaneously given long calls without any disturbances observed by the human observer; (2) long calls given with preceding snag crash (pushing over of a dead tree), and (3) long calls given in response to disturbances from the environment (another male's long call, observer or falling tree nearby). Contexts 2 and 3 indicate high arousal. Analyses of long call acoustic structure among Bornean orang-utans in Tuanan revealed that context is encoded in long calls. Additionally, responses of females differed to long call context in that females with dependent offspring moved away from long calls given spontaneously whereas they ignored long calls given in high arousal. Sexually active females were on average attracted to long calls. These findings raise new ques-

tions about long call function. Earlier interpretations did not divide long calls according to context. Our findings in Tuanan indicate that spontaneously given long calls serve as an advertising signal of the calling male's spatial position to attract mates, whereas long calls given in high-arousal conditions serve to repel male rivals or (in orang-utan-observer interactions) potential predators.

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## **Predicting Primate Distributions in Sri Lanka's Forest Fragments: Using Ecological Niche Modelling to Set Conservation Priorities**

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*Key Words:* Gap analysis · GARP · GIS modelling · Maxent · Protected areas · Risk assessment · Sri Lanka

Sri Lanka is inhabited by five different primate species, each facing a variety of threats from increasingly fragmented habitats and growing human population pressures. In making relevant conservation recommendations, accurate data on primate distributions are of fundamental importance. We modelled the distributions of the red slender loris (*Loris tardigradus*), grey slender loris (*Loris lydekkerianus*), purple-faced langur (*Trachypithecus vetulus*), Sri Lankan grey langur (*Semnopithecus priam*), and the Toque macaque (*Macaca sinica*) using locality data collected over 7 years of fieldwork. Both Maxent and GARP ecological niche modelling software were used in conjunction with information from 20 GIS environmental layers to predict population distributions. Sample sizes varied for each species and all models were analysed for significance. For Maxent a jackknife validation method indicated highly significant models for all species, especially those with small sample sizes ( $n = 5-25$ ). GARP compared relatively well with small sample sizes, however, performed better than Maxent with large sample sizes ( $n = 50-100$ ). Predicted distributions were clipped by a current forest layer and compared with protected area networks and human population densities. Gap analysis and risk assessments were carried out to highlight high, medium, and low conservation priority areas. We make recommendations for protected area extensions and dispersal corridors, pointing out the practical difficulties of such projects in Sri Lanka's wet zone in particular, where primate endemism is highest, but high fragmentation and small fragment size may lead to many local extinctions in the near future.

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## **The Message of Ape Conservation in Europe: Cultural Differences with America?**

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*Key Words:* Apes · Conservation · Education · Zoos

In a recent study, Ross et al. [2008] showed that visitors in two American zoos judged chimpanzees less often as an endangered species compared to gorillas and orang-utans. Visitors

based their view on the fact that chimpanzees were often portrayed in commercials and movies. We repeated this study in Antwerp Zoo in Belgium. We presented visitors with the same pictures as Ross et al. [2008] and asked which apes they believed to be endangered. In the cases of incorrect answers, they were asked to explain their choice. Of the 233 visitors interviewed (all aged 18 years or older), 96 and 94% correctly judged gorillas and orang-utans respectively as endangered. Only 72% claimed that chimpanzees were endangered, which is significantly less than for gorillas or orang-utans. Only one respondent believed chimpanzees not to be endangered because 'they feature more in movies'. Twenty-seven percent of respondents said they had heard in the media that gorillas and/or orang-utans were endangered but that nothing had been said about chimpanzees. In comparison to America, chimpanzees have not often been featured in Belgian commercials or advertisements in the past decade. However, Belgian respondents did 'blame' the media for not being informative enough about chimpanzees. This study suggests that the media may play a role in conservation awareness and that the use of apes in commercials and movies may cause erroneous public views. It would be interesting to study cultural differences in public perception in relation to the portrayal of apes in the media in other European countries.

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### **Examination of Postural Influence on the Behaviour of Variegated Spider Monkeys (*Ateles belzebuth hybridus*) at Frankfurt Zoo, Germany**

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*Key Words:* Spider monkey • Enrichment • Social behaviour • Stereotypies

Keeping animals in captivity can be accompanied by a multitude of problems. Basic needs, like finding food, escaping predators and finding a partner, are provided by the zoos, so the animals frequently lose the motivation to perform natural behaviours. Quite often they show stereotypies, i.e. the repetition of behaviours without an apparent function. These days, the need for enrichment for captive animals is increasingly accepted. In this study, the influence of keeping conditions on the behaviour of a pair of variegated spider monkeys (*Ateles belzebuth hybridus*) at Frankfurt Zoo, Germany, was analysed. In particular, the use of different enrichment devices was investigated. The principle of these enrichments is to make access to the treats inside so-called puzzle-feeders difficult, so that the animals have to spend more time foraging. The data obtained were analysed with special emphasis on changes in daily activity, social behaviour and interactions with objects. The results show positive changes in the monkeys due to the enrichment devices. An increase in social interactions, e.g. social play, occurred. The enrichment devices can be seen as a positive addition to the daily routine. But to minimize aggressive behaviour it is important to supply an adequate number of enrichment devices.