Do Capuchin Monkeys (*Cebus apella*) Deal with Tokens as They Do with Real Food?

**Elsa Addessi**<sup>a</sup>, Alessandra Mancini<sup>a,b</sup>, Lara Crescimbene<sup>a,b</sup>, Elisabetta Visalberghi<sup>a</sup>

<sup>a</sup>Unit of Cognitive Primatology and Primate Centre, Institute of Cognitive Sciences and Technologies, CNR, Rome, <sup>b</sup>Università La Sapienza, Rome, Italy

E-Mail: elsa.addessi@istc.cnr.it

**Key Words:** Transitivity · *Cebus apella* · Tokens

Recent studies on the use of tokens (i.e., inherently non-valuable objects that acquire an associated value upon exchange for food with an experimenter) in non-human primates did not investigate whether individuals use tokens as symbols. Therefore, we evaluated this topic in capuchin monkeys. We trained 10 capuchins to associate two types of tokens (A and B) with different amounts of food. Then, we assessed performance in relative numerosness judgment tasks with food (Experiment 1) and with tokens A (Experiment 2). In both experiments, all capuchins chose the highest quantity regardless of the type of item presented. Then, in Experiment 3 one token B was presented against 1–5 tokens A. Four capuchins used a flexible strategy, maximizing their payoff. Experiment 4 required the capuchins to choose between 1 and 2 tokens B, and 3 and 6 tokens A. Only one subject always maximized his payoff in this task. Finally, Experiment 5 aimed to assess whether the value assigned to three tokens combined according to transitivity (i.e. if an individual prefers A to B and B to C, then she should prefer A to C). We selected three foods (such as A > B, B > C, and A > C) and capuchins learned to associate a different token with each food. Then, in the experimental phase, they received paired comparisons (2A vs. 1B, 1A vs. 1–5B; 2B vs. 1C, 1B vs. 1–5C; 2A vs. 1C, 1A vs. 1–5C) between different quantities of food (phase 1) and tokens (phase 2). Results indicate that monkeys assign a relative value to food and tokens, satisfying transitivity both in a weak sense (order of preference) and in a strong (quantitative) sense. This study suggests that capuchins can reason with tokens as they do with real foods, thereby suggesting that they understand the symbolic nature of tokens.

Inhibition of a Prepotent Response in Mangabeys (Cercocebus torquatus lunulatus)

A. Albiach-Serrano, F. Guillén-Salazar, J. Call

Max Planck Institut für Evolutionäre Anthropologie, Leipzig, Germany; Universidad Cardenal Herrera (Unidad de Etología y Bienestar Animal), Valencia, Spain
E-Mail: anna_serrano@eva.mpg.de

Key Words: Inhibitory control • Reverse contingency task • Quantity discrimination • Cercocebus torquatus lunulatus

Inhibitory control of certain responses and the ability to generate new ones are two important features of flexible problem solving. A paradigm that has been used to study inhibitory skills is the reverse contingency task, in which two different quantities of food are offered to a subject who receives the array he did not choose. Despite their initial tendency, several non-human primates can learn to select the smaller of the two food amounts to obtain the larger one. Nevertheless, with the exception of two studies on great apes and rhesus monkeys (Macaca mulatta), most studies required correction procedures and substitution of actual food quantities by symbolic stimuli. Here we show the results of applying a reverse contingency task to four mangabeys (Cercocebus torquatus lunulatus) in the absence of any procedural modification. We presented subjects with two sets of stimuli: 1:4 raisins and 0:4 raisins. Three mangabeys succeeded with both pairs of stimuli. Mastery of the 0:4 pair was harder to acquire than the 1:4 pair. Retesting the animals, after a period of 7–10 months without testing, evidenced good retention of the original task and successful transfer to two novel pairs: 4:7 and 2:8.

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Inter-Specific Kin Recognition: Are Humans Able to Identify Family Relatives among Other Primate Species?

A. Alvergne, D. Caillaud, M. Charpentier, E. Huchard, L. Martinez, M. Raymond

Institute of Evolutionary Sciences, University of Montpellier II – CC065, Montpellier, France; Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; Duke University, Department of Biology, and Department of Biological Anthropology and Anatomy, Durham, NC, USA; Language and Intelligence Section, Primate Research Institute, Kyoto University, Inuyama, Japan
E-Mail: alvergne@isem.univ-montp2.fr

Key Words: Kin recognition • Facial resemblance • Chacma baboons • Chimpanzees • Lowland gorillas • Mandrills

Evidence that kinship influences the social behaviour of individuals has been found in most primate species and significant advances have been made in understanding kin recognition in nepotism and mate choice situations. However, how individuals discriminate conspecifics on the basis of genetic relatedness remains unclear. Due to both the observed variability of faces within most primate species and the evidence for specialized brain areas involved in facial recognition, facial traits represent a unique opportunity to examine kin recognition in primates. Recognition of related individuals based on facial similarities has been demonstrated in chimpanzees, in intra-specific (chimpanzee judges) as well as in inter-specific (human judges) contexts (Vokey et al., 2004). This interesting situation raises questions about the importance
of facial resemblance for kin recognition in primates, and the evolution of this trait (i.e. ancestral or derived character). Here, we assess parent-offspring resemblance on facial traits for various primate species (chacma baboons, chimpanzees, lowland gorillas and mandrills) with human judges. Resemblance is evaluated by having judges identify the true parent (either the mother or the father), choosing between three adults of the same sex on the basis of photographs of faces. For each offspring, the resemblance to the father and to the mother is measured independently with the same judges. Preliminary results on gorillas and mandrills suggest that the use of facial resemblance to assess relatedness is likely to be an ancestral trait in primates. For all studied species, patterns of parent-offspring resemblance as assessed by human judges are related to the social system characteristics of the species. In particular, do individuals resemble more those with whom they are more likely to interact with during their life? Results will be discussed within an evolutionary context.

Response Facilitation in the Great Apes
F. Amici¹, ², J. Call³

¹Research Centre in Evolutionary Anthropology and Paleoenecology, School of Biological and Earth Sciences, John Moores University, Liverpool, UK; ²Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; ³Ethologie Station, University of Utrecht, Utrecht, The Netherlands
E-Mail: f.amici@eva.mpg.de

Key Words: Response facilitation · Great apes · Novel behaviour · Imitation

There has been much controversy about whether non-human animals can learn novel behaviours by imitation. The ability to imitate has, indeed, important implications for the biological and phylogenetic foundations of cognitive complexity, and imitation has often been considered the most cognitively complex form of social learning. In this study, we tested the four great ape species on two response facilitation tasks. Response facilitation, like imitation, involves copying the behaviour of others, but unlike imitation, it does not involve learning new behaviours. In the first task, the experimenter sat in front of the subject and repeatedly performed only one out of five actions (yawning, nose-wiping, scratching, wrist-shaking or hand-closing), all belonging to the individuals’ repertoire. In the second task, the subject was shown a 3-minute video of several conspecifics repeatedly performing only one out of three actions (yawning, nose-wiping or scratching). In both tasks, we measured the subjects’ propensity spontaneously to copy the models’ actions. When the model was a human, we could not find evidence for response facilitation in any of the great apes. When the model was a conspecific, only chimpanzees showed some evidence for response facilitation, but only for yawning. However, there were important individual differences with only about 30% of the subjects showing the effect. Since contagious yawning has been linked with empathy, we can speculate that some chimpanzees may possess more advanced empathic abilities than other species.
Inhibitory Skills Are Associated with High Levels of Fission-Fusion Dynamics

F. Amici, F. Aureli, J. Call

Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Earth Sciences, John Moores University, Liverpool, UK; Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; Ethologie Station, University of Utrecht, Utrecht, The Netherlands

E-Mail: f.amici@eva.mpg.de

Key Words: Fission-fusion dynamics · Behavioural inhibition · Monkeys · Apes

Social complexity has been suggested as a main selective pressure for enhanced cognitive skills. High levels of fission-fusion dynamics may add further complexity because group members are rarely all together and they need to deal with the challenges of splitting and merging in subgroups of variable compositions. Such fission-fusion sociality has been proposed as a possible reason for differences in cognitive abilities between monkeys and apes. Key species for testing this hypothesis are spider monkeys, the monkey species with a level of fission-fusion dynamics similar to that of three of the great apes, and gorillas, which live in relatively cohesive groups. One of the possible enhanced cognitive skills linked to high levels of fission-fusion dynamics is behavioural inhibition, as being able to control responses could be critical when the appropriate response differs depending on group composition. To investigate whether the level of fission-fusion dynamics affects behavioural inhibition, we compared apes and monkeys with high levels of fission-fusion dynamics (chimpanzees, bonobos, orangutans and spider monkeys) with those living in more cohesive groups (gorillas, capuchin monkeys and long-tailed macaques) on two different tasks requiring inhibition in the physical domain. In the Middle Cup Task, in which subjects had to inhibit the intermediate action of selecting the middle cup, spider monkeys outperformed all the species living in more cohesive groups in most sets of trials. In the Delay of Gratification Task, spider monkeys were able to retrieve the larger food quantity after a delay which was comparable to that of chimpanzees and bonobos, and significantly longer than that of capuchin monkeys and long-tailed macaques. These results support our hypothesis that inhibitory skills are enhanced in species with a high level of fission-fusion dynamics, and suggest that the enhancement might be more strongly related to socio-ecological pressures than to common evolutionary history.

Chimpanzee Relationships in Captivity: An All-Male Group and a Mixed-Sex Group

Mara Andreoli, Caterina Spiezio, Donata Grassi

Biology Department, University of Parma, Parma; Research Department, Parco Natura Viva – Garda Zoological Park, Bussolengo, Verona, Italy

E-Mail: altamarea23@libero.it

Key Words: Chimpanzees · Affiliation · Social interaction · Grooming · Social behaviour

Chimpanzees live in communities whose members associate in temporary parties that vary in size and composition. The formation of strong social bonds between male chimpanzees is well documented in the wild. These bonds are reflected through high levels of affiliation and cooperation. Affiliation manifests itself through association, grooming and proximity, whereas cooperation consists of participating in territorial boundary patrols and agonistic support. This study was conducted with two groups of chimpanzees held at Parco Natura Viva – Garda Zoological Park, Italy: an all-male group with five adult males confiscated by the Government...
in 1992 and a mixed-sex group composed of ten subjects, seven females and three males. The aim of this research was to analyze the social interactions among individuals belonging to the two different groups in order to verify whether these chimpanzees show different social behaviour potentially due to sex-ratio differences. Our results highlight that the two groups did not show different patterns of social behaviour even though there were significant differences in individual behaviours between the two groups. These results seem to indicate that the sex ratio factor does not influence the social alliances and strategies within the group. Thus, our findings seem to indicate that the all-male group of chimpanzees can be considered a helpful option for chimpanzee captive management.

**Aggressive and Affinitive Behaviours around the Mating Period in Berenty Sifakas (Propithecus verreauxi): Preliminary Results**

Daniela Antonacci, Ivan Norscia, Elisabetta Palagi

*Centro Interdipartimentale, Museo di Storia Naturale e del Territorio, Università di Pisa, Calci (Pisa), Dipartimento di Biologia, Università di Pisa, Pisa, Italy*

E-Mail: antonacci_daniela@yahoo.it

**Key Words:** Sifaka · Social behaviour · Hierarchy · Mating · *Propithecus verreauxi*

Sifakas live in multimale-multifemale groups characterized by female philopatry and dominance. Females have a tightly delimited mating season usually embracing two months (starting January) and breeding is concentrated in a few days. Although widely investigated in terms of demography, ecology, and socio-biology at different sites in Madagascar (e.g. Kirindy CFFP and Beza-Mahafaly), sifaka social behaviour has not been investigated in any depth at Berenty Forest. In order to fill this gap, we observed two groups of sifakas (group A and B, of 8 and 6 individuals, respectively) in the northern part of Berenty Reserve (Ankoba; S 24.99°; E 46.29°). Data were collected during the wet season (pre-mating period: November–December 2006 and mating period: January–February 2007), via focal and all occurrences sampling methods. We determined the kind of hierarchy (using the Matman test) in the two groups and analysed the differences in aggressive and affinitive patterns both within and between periods, according to sex and context (resting, feeding, or sexual behaviour). Our results suggest that sifakas can modulate their behavioural patterns, showing a social flexibility possibly related to mate choice by females and/or female access by males.

**Genetic Identification of Confiscated Orangutans for Their Release in the Wild**

Natasha Arora, Dyah Perwitasari-Farajallah, Joko Pamungkas, Michael Krützen

Anthropological Institute and Museum, Zürich, Switzerland

E-Mail: n.arora@aim.uzh.ch

**Key Words:** Orangutans · Conservation · Borneo · Sumatra · Mitochondrial DNA

Orangutans, critically endangered Asian great apes found on the islands of Borneo and Sumatra, have been subject to a drastic decline in number due to habitat loss and fragmentation, and poaching for the illegal pet trade. Rehabilitation centres form part of the conservation efforts to care for orphaned and confiscated individuals before their release into the wild. Molecular identification of the subspecies and population of origin of such individuals would be highly advantageous for their proper reintroduction into the wild. Mitochondrial DNA (mtDNA) data from previous studies indicate significant differences between Bornean and Su-
matran populations for the hypervariable region of the D-loop and some protein-coding genes. We have carried out population genetic analyses for a group of 36 orangutans confiscated in Thailand and returned to Indonesia last year. Preliminary sequence analyses of the hypervariable region of mtDNA have so far revealed low nucleotide diversity among the samples. Alignments displayed 10 different haplotypes, one of which was particularly common and possibly characteristic of the Bornean subspecies. Further and more detailed analyses are currently being performed. This study highlights the need for thorough and large-scale haplotyping of wild populations on the verge of extinction.

Ranging Costs in Wild Spider Monkeys
Norberto Asensio\textsuperscript{a}, Amanda H. Korstjens\textsuperscript{b, c}, Filippo Aureli\textsuperscript{a}
\textsuperscript{a}Research Centre in Evolutionary Anthropology and Palaeoecology, School of Biological and Earth Sciences, Liverpool John Moores University, \textsuperscript{b}School of Biological Sciences, University of Liverpool, Liverpool, \textsuperscript{c}School of Conservation Sciences, Bournemouth University, Bournemouth, UK
E-Mail: n.asensio@ljmu.ac.uk

Key Words: Spider monkeys \cdot Competition \cdot Costa Rica \cdot Fission-fusion dynamic

Intragroup feeding competition is one of the most significant costs of group living. One important aspect of such a cost is a component of scramble competition, often reflected in a positive relationship between travel distance and group size. This is especially so for frugivorous animals living in habitats with seasonal variation in fruit availability. In species with high levels of fission-fusion dynamics, community members can adjust group size to local food availability by fissioning into small subgroups. This adjustment is viewed as a way to deal with scramble competition and thus reduce ranging costs. We studied the effect of subgroup size and seasonality on four components of ranging costs (travel distance, time spent travelling, speed and travel effort) focusing on the movements between food patches of the members of a community of spider monkeys in Santa Rosa National Park, Costa Rica. We did not find an effect of the two variables on any of the ranging cost components, suggesting that costs are kept to a similar level across seasons and subgroup size categories. Smaller subgroups could visit larger patches as well as smaller ones, but larger subgroups did not visit small patches. Compared to the food patch previously visited, spider monkeys visited larger patches just after fusions (and smaller patches just after fissions). However, there was a cost associated with such an adjustment as they covered a greater distance between patches after fusions. This rapid adjustment, even if it came at a short-term cost, is evidence of the effectiveness of fission-fusion dynamics, especially because the cost was not long-lasting, as larger subgroups did not, on average, experience greater ranging costs than smaller ones.
Rank-Dependent Differences in Loud Call Frequency and Structure in Sulawesi Crested Black Macaques (*Macaca nigra*)

Gholib Assahad\(^a,b\), Christof Neumann\(^b,c\), Kurt Hammerschmidt\(^d\), Dyah Perwitasari-Farajallah\(^a\), Antje Engelhardt\(^a,b\)

\(^a\)Primate Research Centre, Bogor Agricultural University, Bogor, Indonesia; \(^b\)Department of Reproductive Biology, German Primate Centre, Göttingen; \(^c\)Institute for Biology II, University of Leipzig; \(^d\)Research Group Cognitive Ethology, German Primate Centre, Göttingen, Germany

E-Mail: ghalib_asd@yahoo.co.id

Key Words: *Macaca nigra* · Loud calls · Sexual selection · Male dominance rank

In *Macaca nigra*, in contrast to other macaques, all adult males of a group utter loud calls, which suggests that these calls play an important role in inter- and/or intra-sexual selection. To test assumptions deriving from this hypothesis, we investigated the relationship between the frequency and acoustic structure of calls and male dominance rank. We studied 17 adult males from two groups of *Macaca nigra* living in the Tangkoko-Batuangus Nature Reserve, North Sulawesi, Indonesia. Behavioural data collection (focal animal sampling) was combined with ad libitum sound recording and detailed acoustic analysis. During the period July to December 2006, we were able to gather a mean of 66.8 h (range: 31.5–80.1 h) of behavioural data per male and to record a total of 690 loud calls. 253 high-quality calls from 16 males were used for acoustic analysis. The number of elements per call and 35 further call parameters were measured: 9 in the time domain and 26 in the frequency domain. We found a clear correlation between the number of calls given by a male per day and his dominance rank (Spearman’s rank correlation: \(rs = -0.547, n = 17, p = 0.023\)). Concerning call structure, we found a significant correlation between male dominance rank and 13 parameters: high-ranking males uttered calls with more and longer elements, a lower second dominant frequency band and more energy in higher frequencies than low-ranking males. Thus, our results show that male loud calls encode male dominance rank. Future playback experiments will help to clarify whether this information is salient to conspecifics and whether females are more attracted by calls from dominant than from low-ranking males. Furthermore, we will compare our results with data on male body weight, physiological status and aggressive behaviour to investigate the role of loud calls in male-male competition.

Home Range Use by the Red Slender Loris (*Loris tardigradus tardigradus*) in Masmullah Proposed Forest Reserve, Sri Lanka

Lilia Bernede, A.S. Beresford, K.A.I. Nekaris, A. Gunawardene

Nocturnal Primate Research Group, Department of Anthropology, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK

E-Mail: lilia_bernede@yahoo.co.uk

Key Words: Red slender loris · Home range · Social interaction · Movement patterns

The red slender loris, *Loris tardigradus tardigradus*, is an insectivorous, nocturnal and arboreal primate endemic to the diminishing rainforests of southern Sri Lanka. Very little is known of the social organisation and behaviour of this strepsirrhine. This study is the first to present data on home range and spatial patterns of *L. t. tardigradus*. Behavioural, morphometric and locational data were obtained by capture and radio-telemetry of 22 individuals between August 2005 and August 2006. The study was conducted in Masmullah Proposed Forest Re-
serve, a 296-ha fragmented moist monsoon forest in southern Sri Lanka. Over 700 hours of continuous radio-tracking data were analysed using MCP (95%) and Kernel analysis (95%) methods. The average female home range was larger than the average male home range, and home range overlap was higher inter-sexually than intra-sexually. Generally, inter-sexual overlap occurred between one male and one female. In some cases, the home range of one male would overlap that of another female who was not part of his sleeping group. Based on home range overlap, social interactions and sleeping sites, two types of males were found; males that were settled and paired with a female, and unsettled males. No difference in home range size was found between these two types of males. Females showed variation in home range size and spatial movement patterns, which may have been related to age and reproductive status. We also present data on average nightly path length, in relation to sex, moon phase and season. These results are discussed in the context of the social system of other slender loris species and strepsirrhines.

Competitive Ability as a Predictor of Coalition Success in Barbary Macaques

Annie Bissonnette, Carel van Schaik

Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: a.bissonnette@aim.unizh.ch

Key Words: Coalition • Competitive ability • Barbary macaques • Dyads

Coalitions are coordinated attacks directed by two or more animals against the same target. Quantitative models on coalition formation attempt to explain the variability documented in non-human primates, focusing on the feasibility and/or profitability component of coalitions. These models use ad hoc measures of competitive ability (CA) and generally assume that coalitions are strong enough to beat their target when the sum of the CAs of the coalition members is greater than the CA of the target. For the first time, we intended to test the validity of this assumption by deriving a field-based estimate of individual CA. The study was conducted during the mating season 2006/07 in a large semi-free ranging group of Barbary macaques (Macaca sylvanus), where male-male coalitions are common. The CA of males was estimated using a semi-experimental protocol, where two males had to compete over access to a prized food resource (i.e. a nut). According to their outcomes, the tests were classified as either ‘decided’ when one rival ate the nut or ‘undecided’ when a third party snatched the nut away. Based on a subset of 151 nut tests (i.e. 50% of all possible male-male dyads were tested at least once), a CA value was attributed to each male using a modified version of the David score (David, 1987, Biometrika 74:432). The results indicate a 75–80% fit between the behavioural outcomes (i.e. target defeated or not) of 83 coalitions and the predicted outcomes based on the CAs of males, which suggests that the assumption used by previous models is mostly correct. Additional factors influencing the success of coalitions, as well as the theoretical implications of these results, are discussed.
Preliminary Results on Activity Budget, Feeding Ecology and Ranging Behaviour of Wild Pig-Tailed Macaques (*Macaca nemestrina leonina*) in Khao Yai National Park, Thailand

Gilles Bottin*, Marie Claude Huynen*, Tommaso Savini*,b

*a University of Liège, Faculty of Science, Department of Environmental Science and Management, Biology of Behaviour Unit, Liège, Belgium; b King Mongkut’s University of Technology Thonburi, School of Bioresources and Technology, Conservation Ecology Group, Bangkok, Thailand

E-Mail: gilleeeees@gmail.com

Key Words: Pigtail macaques · Feeding · Socio-ecology · Home range · Activity budget

Pig-tailed macaque ecology and behaviour is still largely unknown, as studies on this species in the wild are rare and based on fragmentary observations. In 2006, we started a long-term project investigating the socio-ecological profile of two semi-habituated troops in Khao Yai National Park, Thailand. We present here the preliminary results on activity budget, feeding ecology and home range obtained on a semi-habituated troop (HQ) living in close contact with park staff and visitors, as well as data on ranging and habituation progress of a second troop (CAM) living in more pristine forest, far from human activity. Data were recorded using 10-min scan sampling from sleeping-tree to sleeping-tree, and included information on habitat type, individual identification, age/sex class, canopy height used, attention status, behaviour (activity and social interactions, with specified donors/receivers). Food items (species, part consumed) were also recorded; with more than 50 species identified to date. During contacts with the macaques, we recorded GPS coordinates every 30 min. The home range of the HQ troop is about 1 km², with a daily travel distance of 2600 m (+/– 250 m) and an average speed of 236 m/hour. The home range of the other troop (CAM) is about 3.2 km², with a daily travel distance of about 4500 meters (+/– 250 m) and an average speed of 370 m/hour. Preliminary analysis of habitat use shows that macaques tend to spend most of the early morning and late afternoon in close proximity to human settlements, while they spend the middle of the day mainly in the pristine forest.

Male Reproductive Success in Free-Ranging Barbary Macaques: Influence of Male Rank and Female Direct Mate Choice

Katrina Brauch*,b, Michael Historian*, Antje Engelhard*, J. Keith Hodges*

*Department of Reproductive Biology, German Primate Centre, Göttingen, b Department of Behavioural Biology, University of Muenster, Muenster, Germany

E-Mail: kbrauch@dpz.eu

Key Words: Barbary macaques · Male rank · Paternity · Hormone · Mate choice

Studies of multi-male primate groups have often shown that rank is an important determinant of male reproductive success, although the mechanisms leading to rank-related reproductive skew in primates remain unclear. In the present study, we examined the relationship between male rank and paternity outcome by investigating the relative importance of male monopolisation, direct female mate choice and post-copulatory mechanisms in a group of free-ranging Barbary macaques (*Macaca sylvanus*) in Gibraltar. Behavioural observations were combined with faecal hormone analysis in order to determine timing of the female fertile phase (13 cycles, 8 females), and genetic analysis was performed for assessment of paternity (n = 12). Rank had a significant effect on paternity, with the majority of infants (n = 9) being sired by high-ranking (rank 1–3) males, although this was not the result of differential male monopolis-
ination ability since females copulated with almost all group males during their fertile phase. High-ranking males, however, consorted females significantly more often and for a longer duration compared to low-ranking males and also showed significantly higher rates of copulation and ejaculation. In addition, there was a rank-related difference in female solicitation frequencies, with a strong bias towards high-ranking males. The frequencies/duration of behaviours shown by or towards the likely fathers, however, did not differ significantly from those shown by or towards non-fathers. The data indicate that rank is an important determinant of male reproductive success in free-ranging Barbary macaques. More importantly they suggest that, in contrast to other macaque species (e.g. long-tailed macaques), the observed reproductive skew is related more to mechanisms of direct female mate choice than to male monopolisation of fertile females. However, since females mate with many males and fathers are not preferred over non-fathers, paternity among high-ranking individuals seems to be determined by mechanisms operating at the post-copulatory level, such as sperm competition or cryptic female choice.

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**Inequity Aversion in Great Apes?**

*Juliane Bräuer, Josep Call, Michael Tomasello*

Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

E-Mail: jbraeuer@eva.mpg.de

**Key Words:** Chimpanzee · Competition · Inequity aversion

Brosnan et al. (2005) found that chimpanzees showed increased levels of rejection of less-preferred food when competitors received better food than themselves and postulated as an explanation inequity aversion. In the current study, we extended these findings by adding important control conditions, and we investigated whether inequity aversion could also be found in the other great ape species. In our study, subjects showed exactly the opposite pattern of food rejection to the subjects of Brosnan et al. (2005). Our apes ignored fewer food pieces and waited longer when a conspecific received better food than themselves. Moreover, chimpanzees begged more vigorously when the conspecific gotfavoured food. The most plausible explanation for these results is the food expectation hypothesis – seeing another individual receive high-quality food creates the expectation of receiving the same food oneself – and not inequity aversion.

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**Male Life History Patterns and Reproductive Success in Western Gorillas – Insights from Mbeli Bai, Republic of Congo**

*Thomas Breuer*, *Emma J. Stokes*, *Richard Parnell*, *Andrew Robbins*, *Martha M. Robbins*

*Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; Mbeli Bai Study, Wildlife Conservation Society – Congo Program, Brazzaville, Republic of Congo; Wildlife Conservation Society, Bronx, NY, USA*

E-Mail: breuer@eva.mpg.de

**Key Words:** Gorilla · Reproduction · Life history · Group formation

Studying life history patterns and reproductive strategies of individuals is important for our understanding of the evolution of diversity among primate social systems. Our current knowledge about these traits in the genus *Gorilla* predominantly comes from one folivorous mountain gorilla population. However, there are large ecological differences between mountain gorillas and western gorillas, with the latter having a seasonally frugivorous diet potentially...
causing differences in life history patterns. While a large proportion of mountain gorilla groups are multi-male, western gorilla groups are nearly exclusively one-male groups. These differences in social structure are likely due to differences in male life history strategies and may result in higher variance in male reproductive success. We here provide for the first time a thorough description of western male gorilla life history stages, patterns of male dispersal, group formation and group disintegration and estimates of male reproductive success. In the study population at Mbeli Bai in the Nouabalé-Ndoki National Park, Republic of Congo, we have monitored more than 250 western gorillas for up to 12 years. In western gorillas, young silverbacks almost exclusively leave their (presumed) natal group to become solitary for several years before being able to acquire females and form new social groups. However, immature males also frequently transfer into other groups or join solitary males due to the high rate of group disintegrations. These target groups are often well established groups with potentially older harem holders or non-reproductive groups without fertile females. Due to the one-male harem structure of western gorillas, up to one third of the population's silverbacks remain without adult females and male reproductive success is highly skewed towards a few silverbacks, demonstrating that male-male competition for access to fertile females is an important mechanism forming the social structure of this highly sexually dimorphic great ape.

Preliminary Results on the Behavioural Ecology of a Long-Tailed Macaque (Macaca fascicularis) Population in Disturbed Urban Habitats, Bangkok (Thailand)

Fany Brotcorne\textsuperscript{a}, Marie Claude Huynen\textsuperscript{a}, Tommaso Savini\textsuperscript{b}

\textsuperscript{a}University of Liège, Faculty of Science, Department of Environmental Science and Management, Biology of Behaviour Unit, Liège, Belgium; \textsuperscript{b}King Mongkut’s University of Technology Thonburi, School of Bioresources and Technology, Conservation Ecology Group, Bangkok, Thailand

E-Mail: fbrotcorne@student.ulg.ac.be

Key Words: Habitats · Demography · Behaviour · Ecology · Long-tailed macaques

In many tropical regions of the world, humans and non-human primates share habitats, and their interactions are increasingly common. As a result, human presence has an important impact on the demography, behaviour and overall ecology of non-human primate populations. More specifically, the increasing human pressure represents a critical danger for the survival of most other primate species, often leading to the local extinction of entire populations. However, some primate species show a high degree of plasticity when facing human disturbance, and even adapt their ecological behaviour to heavily modified urban areas. Our research project, in collaboration with the City of Bangkok, focuses on long-tailed macaques (Macaca fascicularis), a species distributed throughout Southeast Asia, and one that has a great ability to adapt to urban habitats. The goal of our study is to define the impact of urbanized habitat fragments on the social interaction and reproductive patterns of the macaques, in order to design sustainable management plans and reduce conflicts with local human populations. We present preliminary results from a 4-month study period (May to August 2007) on a large semi-provisioned troop living in the south of Bangkok in a suburban area. Data were collected via instantaneous scan sampling for activity budget, and focal sampling for diet, while aggressive and sexual interactions within the group were noted ad libitum. The study group, 128 animals (10 adult males, 6 subadults, 48 adult females (39 had an infant) and 64 juveniles), uses an area of 1 ha, where there is considerable human activity. In the coming year, we plan to extend our observations to a second troop inhabiting an estimated area of 5 km\textsuperscript{2} of pristine mangrove with an ongoing forest regeneration project.
Playful Expressions and Their Contexts in One-Year-Old Chimpanzees

Kirsty M. Brown, Kim A. Bard
Centre for the Study of Emotion, Department of Psychology, University of Portsmouth, Portsmouth, UK
E-Mail: kirsty.brown@port.ac.uk

Key Words: Chimpanzee · Emotion · Laughter · Socialisation · Play

The evolutionary origin of human smiles and laughter and their function in everyday life are topics of increasing interest to emotion researchers. The chimpanzee play face expression shares some aspects of form and function with human smiles and laughter, and comparisons highlight our shared evolutionary heritage and species-specific adaptations. The present study contributes to this field by describing the socialisation of play faces and playful motor expressions in chimpanzee infants. Four chimpanzee infants, living with their mothers in a large colony at Chester Zoo, were observed at 9, 12 and 15 months of age. Analysis focused on playful activities: context, play partners, presence of playful expressions and others’ responsiveness to these expressions. Preliminary results indicate that playful expressions are most likely to occur during rough and tumble social play. Age-related changes appear to occur with older infants becoming increasingly adept at using play faces to communicate during social play. Solitary play contexts – object play and acrobatic play – also feature in a sizeable proportion of infants’ playful expressions. Responsiveness to playful expressions seems to be greatest amongst other chimpanzee infants, rather than among mothers or older play partners, and peer interactions have the highest rate of play face matching. Concurrent studies with human infants, conducted by the same authors, help to understand the different roles of peers and mothers in the socialisation of playful expressions. Overall, this study considers the effects of socialisation on the emotional, communicative and signal value of playful expressions in infant chimpanzees.

Are Common Marmosets Prosocial? Eliminating Alternative Hypotheses

Judith Maria Burkart, Carel van Schaik
Anthropological Institute, University of Zürich, Zürich, Switzerland
E-Mail: judith.burkart@aim.uzh.ch

Key Words: Common marmoset · Social facilitation · Partner

Recent results suggest that common marmosets, unlike chimpanzees, show other-regarding preferences (ORPs, i.e. a concern for the well-being of their group members): When they have the opportunity to provide food for a conspecific at low cost, they do so systematically. However, there are several alternative explanations that potentially might account for this outcome in the absence of true prosociality, such as social facilitation by the presence of a partner, stimulus enhancement, food obsession, the expectation of reciprocation, or a lack of causal understanding of the experimental set-up. We addressed these alternative explanations on the basis of additional data, both from a detailed re-analysis of the marmosets’ behaviour during the original ORP study and from supplementary control experiments. In light of these data, we conclude that the most parsimonious explanation of the marmosets’ behaviour in the ORP study is that it is underlain by a truly prosocial motivational predisposition. This finding is corroborated by the fact that in bonded pairs of common marmosets, the extent of expressed prosociality is positively correlated with the duration of the pair bond as well.
as with the number of offspring produced together. Our findings have several implications: (i) ORPs are not unique to humans; (ii) their evolution does not require any advanced cognitive abilities; (iii) rather, their emergence seems to be linked to cooperative breeding, which is exhibited both by marmosets and humans, but not chimpanzees.

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**The Primate Mind in the Wild**

*Richard W. Byrne*

Scottish Primate Research Group and Centre for Social Learning & Cognitive Evolution, School of Psychology, University of St Andrews, St Andrews, UK

E-Mail: rwb@st-andrews.ac.uk

**Key Words:** Great apes · Deceptive tactics · Cognition · Neocortex

This lecture uses two topics in primate cognition to show that observational field data can provide crucial information for understanding the primate mind. Learning to deceive familiar conspecifics (tactical deception) is a good indicator of cognitive ability, for which a unique corpus of data exists spanning all major primate taxa. To learn deceptive tactics, individuals must distinguish their companions as individuals, keep track of who is currently in view, and learn from a single trial. The frequency of deception varies dramatically across species and depends on the size of the neocortex: both absolute volume and neocortex ratio are good predictors of the rate of use. The animals may not understand the deceptions they practice; however, tactics may be learnt without comprehension of their mechanism. Evidence that primates deceive in an ‘intentional’ way is much more sparse and is limited to the great apes, where there are cases in all species. This monkey/ape difference is consistent with other lines of evidence suggesting that great apes have greater cognitive understanding than monkeys – in particular, understanding of the intentions of other individuals. The evolutionary origin of this cognitive advance remains controversial, and will form the background to the second part of the lecture. Great apes do not live in systematically more complex groups than those of monkeys. However, all great apes feed in complex ways, apparently giving them access to foods that monkeys cannot exploit. In the programmes of manual action apes use for these tasks, several different stages of processing are reliably sequenced; the hands are used in complementary roles, co-ordinated together to achieve a single goal; and the overall plan is hierarchical, with modules repeated or omitted according to task demands. The overall programme seems to be learnt by imitation (but not by slavish copying of details), which suggests that great apes are able to interpret the skilled actions of others: discerning the results to which particular actions are normally aimed and the steps necessary to achieve them. The ability to use regularities in skilled behaviour to work out the underlying correlational structure of intentional action, behaviour parsing, is a crucial first step in understanding mental states. Plausibly, the ability to interpret intelligent action by behaviour parsing derived in evolution from the need for great apes to compete effectively with (smaller, more agile) monkeys for similar foods, allowing the later development of an ability to ‘read’ intentions of others.
Spatial Position of Individuals within Western Lowland Gorilla Groups: What Can We Learn about Social Relationships?

Damien Caillaud\(^a\), Julio Benavides\(^b\), Nelly Ménard\(^b\), Michel Raymond\(^b\)

\(^a\)Institut des Sciences de l’Evolution, Université de Montpellier 2, Montpellier, France
\(^b\)Station Biologique de l’Université de Rennes 1, Paimpont, France
E-Mail: caillaud@univ-montp2.fr

Key Words: Spatial position • Lowland gorilla • Social relationships • Associations

In group-living species, the spatial position of individuals has important effects on their fitness. For example, intensity of feeding competition, predation risk and the probability of getting support from other individuals in cases of conflict are likely to vary with respect to spatial position. Individuals are expected to move within their group in order to balance these costs and benefits. Western lowland gorilla group size ranges from 2 to more than 20 individuals. Breeding groups are composed of a unique mature male – the silverback – and one to eleven females. Within-group female social relationships are still largely unknown in this species. Females of the same group are rarely related and thus are not expected to form strong coalitions within the group. Preferential spatial association of females is, therefore, not expected to occur. However, as the silverback of each group provides each female with protection against predators and possibly against infanticidal males, his position is expected to explain part of the variability in the position of the females. Lastly, if the benefit of being close to the silverback varies among females, e.g., if they have dependant infants, or if a hierarchy exists among females, their relative positioning around the silverback is expected to be constant with time. A total of 280 complete inter-individual distance matrices concerning 28 different groups were collected using a photogrammetric method in Lokoué Bai, Odzala-Kokoua National Park, Congo. The rules governing the positioning of individuals within their group were investigated in order to infer within-group social relationships. The concordance between the results obtained and predictions from the socio-ecological model is discussed.

A Preliminary Study of the Primate Community in the Protected Area of Oglán Alto, Arajuno-Pastaza, Ecuador

G.A. Carrillo-Bilbao, J.J. Bravo, S. Martin, M.-C. Huynen

Project Primates Oglán, Amazonian Scientific Station Juri Juri Kawsay of the Central University of Ecuador, Quito, Ecuador
E-Mail: sarahmartinsolano@gmail.com

Key Words: Neotropical primates • Ecology • Oglán Alto • Ecuador • Census • Group composition

Primate communities play a very important role in the dynamics of tropical forests. Nevertheless, there is a lack of research on primates in the Amazonian site of Oglán Alto. Project Primates Oglán involves a long-term study of primate community ecology, centred in a 3,344 ha area of the Oglán Alto Protected Forest, Arajuno, Ecuador. We have identified two types of forest: lowland rain forest and piedmont forest. Initially, four exploratory trips were made between June 2006 and January 2007 and the intensive phase of field research began in March 2007. The primate census was based on direct and indirect observations such as auditory records, faeces and food consumption traces. In addition, for each encounter, we recorded the location, total number of individuals and group composition. For monitoring, four transects of 4 km each and one global trail system have been established; these are mapped and marked at 25-m intervals. We have identified four groups of *Alouatta seniculus*, four groups of *Saguinus*
fuscicollis and one group of Lagothrix lagotricha. So far, a 10,000-m system of trails and transects has been established across 200 ha. Our next steps include completing the phenology transects and habituating the study animals in order to gather ecological and ethological data on the primate groups to gain insights into the ecological dynamics of the Oglán Protected Forest.

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**The Nut-Cracker: Bridging Archaeology and Primatology – Chimpanzee Stone Tool Use in Bossou and Diecké, Guinea**

*Susana Carvalho*, **Cláudia Sousa**, **Tetsuro Matsuzawa**

* Department of Anthropology, Faculty of Sciences and Technology, University of Coimbra, Coimbra, **Department of Anthropology, Faculty of Social and Human Sciences, New University of Lisbon, Lisbon, Portugal; Primate Research Institute, Kyoto University, Inuyama, Japan*

E-Mail: arqscarvalho@gmail.com

**Key Words:** Chimpanzee · Tool use · Nut-cracking · Stone tools · Oldowan

Recent studies bridging natural and social sciences have brought innovative insights into the field of human evolution. These include the evolutionary origins of technology and the variables that may explain the genesis of tool use by human and non-human primates. Through a new scientific perspective combining ethological and archaeological methods, including direct and indirect records of tool use in several nut-cracking sites used by chimpanzees (*Pan troglodytes verus*) in Guinea, Western Africa, new data were collected based on the analysis of lithic assemblages currently used by the chimpanzees. Data indicate that chimpanzees are not only attributing functions to their stone tools, but also reusing, discarding or changing tool function after fracture, according to identified stone features. A complex operational sequence of repeated, though flexible, behaviours was recorded during the nut-cracking process, demanding the capacity to mentally anticipate a certain number of tasks. Additionally, there was evidence of regional diversity within different nut-cracking assemblages, and this can be tentatively related to an adaptation capacity to variables such as the consumption of different nut species, the type of raw materials available or tool mobility. These results suggest that chimpanzees select and adjust their tools according to particular attributes of stones, maintaining patterned dimensions that differ between regions. This can be linked with cultural causality, thus allowing associations between chimpanzee groups and tool typologies. Moreover, this typological and technological regional variability, reflected in the analysed stone tools, can be interpreted as a response to particular ecological conditions, suggesting that external factors could have also influenced the origins of diversity and complexity of lithic industries for human and non-human primates. A pattern of three different types of resource exploitation strategies inside activity areas of nut-cracking sites revealed similarities with some of the characteristics documented for Oldowan contexts, suggesting that these strategies could date back to the last common ancestor between *Pan* and hominins.
Artistic Expression in Primates

N. Casiraghi\textsuperscript{a,b}, M. Zizzo\textsuperscript{a}

\textsuperscript{a}Centro Tutela e Ricerca Fauna Esotica e Selvatica di Monte Adone, Sassu Marconi,  
\textsuperscript{b}Università degli Studi di Milano, Milano, Italy  
E-Mail: noemi.casiraghi@gmail.com

Key Words: Chimpanzee \cdot Expression \cdot Lateralization

The purpose of our research was to analyse the artistic creation of a group of twelve chimpanzees. Our investigation chiefly focused on parameters that could highlight the use and choice of colours, the preference for right or left hand, the use of space and the sense of balance on the paper. The study was conducted at the ‘Centro Tutela e Ricerca Fauna Esotica e Selvatica di Monte Adone’ in Italy. The observations took place over a period of six months, during which we had one drawing session per week. The chimpanzees we evaluated were housed in two groups of six individuals; therefore, we considered the two groups separately. We opted to use the same materials for all the drawings: black and white paper and wax crayons of ten different colours. The results show general patterns in the choice of colours (most favoured red) and in lateralization (mostly using the right hand) but also individual differences in the use of space and in the method of drawing. This work is the first step in more extended study to compare the artistic creations of chimpanzees with those of children and ‘enfants sauvages’, thereby making a scientific contribution to the study of the origin of aesthetics and art.

Gibbon Feeding Ecology and Diet Characteristics

Susan M. Cheyne

Wildlife Conservation Research Unit, Department of Zoology, Oxford University,  
Tubney, UK  
E-Mail: susan.cheyne@zoo.ox.ac.uk

Key Words: Gibbon \cdot Ecology \cdot Diet \cdot Nutrition \cdot Central Kalimantan

The Sebangau National Park (SNP) in Central Kalimantan, Indonesia, is home to the world’s largest orangutan population and, probably, to one of the largest populations of Bornean agile gibbon, \textit{Hylobates albibarbis}. Seven groups of gibbons were habituated and followed daily for 24 months from June 2005 to June 2007. Data were collected on behaviour, food species eaten, distance travelled, singing behaviour and feeding-tree revisitation frequency. Forest productivity was measured monthly using established plots. Knowledge of those food-trees most important to the gibbons’ continued survival in the Sebangau is essential for their conservation. Data will be presented on the nutritional characteristics of food, with analysis of the food eaten and of the same food species at different times of year when the gibbons did not feed on them. Basic behavioural data from the habituated groups and phenology data will also be presented and the implications for conservation of the Sebangau gibbons discussed. SNP encompasses one of the largest peat-swamp forests in the world and is recognized as a low-productivity habitat, thus gibbons would be expected to rely on fallback foods. During the dry season, gibbons ate flowers in far greater quantities than previously noted (for either Sebangau or other sites): 21% flowers in the dry season compared to 3% in the wet season and leaf consumption also increased, from 17 to 21%. Feeding-bout length increased during times of food scarcity (27 min dry vs. 12 min wet), as did daily distance travelled (dry average 1800 m, wet average 1300 m), because the gibbons were searching more widely for food in the dry season. There was no significant difference in singing behaviour during times of low food availability. This study indicates that gibbons are very adaptable in both diet and behaviour and that they can exploit low-productivity forest well. It also sheds light on possible fallback food species exploited in times of food scarcity.
The Effect of Inbreeding on Infant Mortality in Captive Bonobos (Pan paniscus), Determined from DNA Analysis of Hair Samples

Sara Van Coillie\textsuperscript{a,b}, Peter Galbusera\textsuperscript{a}, Amy Roeder\textsuperscript{d}, Werner Schempp\textsuperscript{c}, Jeroen Stevens\textsuperscript{a}, Mike Bruford\textsuperscript{d}, Kristin Leus\textsuperscript{a}

\textsuperscript{a}Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp,\textsuperscript{b}Department of Biology, University of Antwerp, Antwerp (Wilrijk), Belgium;\textsuperscript{c}Institute of Human Genetics, University of Freiburg, Freiburg, Germany;\textsuperscript{d}Cardiff School of Biosciences, Cardiff University, Cardiff, UK

E-Mail: sara.vancoillie@kmda.org

Key Words: Inbreeding · Bonobo · Nuclear DNA · Paternity

Inbreeding and the loss of genetic diversity may lower fitness and reduce the potential for a population to adapt to changing environments. We investigated the effects of inbreeding on infant mortality in the captive population of bonobos (Pan paniscus). Using Great Ape Kit and PowerPlex\textsuperscript{®} 16 System (Promega), nuclear DNA was amplified from hair samples. Fifty-four bonobos were genotyped at 8 tetranucleotide repeat microsatellite loci. In addition, high-quality pedigree data from other genotyped individuals were used, so that, in total, 140 captive born individuals were included in this study. Inbreeding coefficients were calculated for each individual with confirmed paternity. Individuals with an inbreeding coefficient of zero were classified as ‘non-inbred’, while individuals with an inbreeding coefficient greater than zero were classified as ‘inbred’. Infant mortality was defined as all deaths prior to the age of 12 months. We found that infant mortality of inbred young was higher, though not significantly so, than that of non-inbred young (31.25 vs. 12.1%; Fisher exact test; \( p = 0.0548 \)). However, the total cost of inbreeding for bonobos is probably underestimated. Firstly, inbred individuals that survive to adulthood may still suffer reduced fitness via reduced adult survival, poor performance in mating competition, reduced fecundity and less proficiency in parental care. In addition, the breeding programme for captive bonobos aims to avoid inbreeding as much as possible and, as a result, there is a lower statistical power to detect inbreeding depression. We can conclude that inbreeding reduces infant survival, but that the total magnitude of inbreeding depression is probably underestimated.

The Question of Play: A Comparison between Chimpanzees (Pan troglodytes) and Lowland Gorillas (Gorilla gorilla gorilla)

Giada Cordoni, Daniela Antonacci, Elisabetta Palagi

Centro Interdipartimentale, Museo di Storia Naturale e del Territorio, Università di Pisa, Calci, Pisa, Italy

E-Mail: giada.cordoni@tiscali.it

Key Words: Chimpanzee · Lowland gorilla · Play · Social organization

Play appears to be a multi-functional behaviour and it seems to have different roles in different species. Within a given species, playful interactions can be influenced by variables such as social structure, age, sex and context. Previous literature lacks cross-species studies on play dynamics. In order to fill this gap, we investigated possible differences in playful activity between two primate species characterized by different social organizations: chimpanzees (Pan troglodytes), living in fission-fusion societies, and lowland gorillas (Gorilla gorilla gorilla), living in one-dominant male groups. The observations were carried out on two groups of chimpanzees, one at Zoo Parc de Beauval (France) and the other at Dierenpark Amersfoort (The Netherlands), and on a colony of lowland gorillas housed in Apenheul Primate Park (The Nether-
lands). We found that the overall level of playful interactions did not differ between chimpanzees and gorillas. Nevertheless, dissimilarities were found depending on sex, age and kinship of playmates. The results will be discussed in relation to the social skill and motor training hypotheses.

Using the Two-Action Method to Test for Social Transmission in Despotic Ring-Tailed Lemurs

D. Custance\textsuperscript{a}, N. Rakotomalala\textsuperscript{b}, H. Rasamimanana\textsuperscript{b}
\textsuperscript{a}Goldsmiths College, Department of Psychology, London, UK; \textsuperscript{b}C/O Ecole Normale Superieure, University of Antananarivo, Antananarivo, Madagascar
E-Mail: d.custance@gold.ac.uk

Key Words: Ring-tailed lemur • Aggression • Tolerance • Rank

The two-action method was used to test for the effect of social dynamics upon social transmission in wild ring-tailed lemurs from Berenty Reserve, Madagascar. 42 lemurs were presented with puzzle objects that could be opened in different ways. A latch was swivelled or flipped on a feeding tube, while a lid was pulled open by a strap or handle on a puzzle box. Members of a control group were presented with test objects that could be opened either way for 20–30-min sessions over ten consecutive days. Top-ranking females from the two experimental groups were presented with test objects that could be opened in only one of the two contrasting ways. After five days of 15-min demonstration sessions, five boxes that could be opened either way were presented for 20 to 30 min over 10 consecutive days to each of the two experimental groups. There was no evidence that the lemurs preferentially learned the particular demonstrated variant. Focal proximity and social data indicated that ring-tailed lemurs live in a ‘despotic’ society with rigid hierarchies, high levels of aggression and low tolerance for proximity. Hence, most lemurs were unable to approach sufficiently closely during demonstrations to learn from high-ranking demonstrators. This pattern of results is consistent with Coussi-Korbel and Fragaszy’s model of social dynamics and social learning.

Planning in the Wild? A Study of the Cognitive Abilities of Wild Orangutans (Pongo pygmaeus) at South Aceh, Sumatra, Indonesia

Laura A. Damerius, Carel P. van Schaik
Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: damerius@gmail.com

Key Words: Orangutans • Travel direction • Cognition • Call

Future planning is a very demanding feature, and there is no doubt that humans are able to exhibit it when considering future needs. Even though, for a long time, it was thought that animals were not capable of prospective cognition, recent studies have shown that animals can mentally time travel into the past and future. The question then arises, what does the evidence for future planning by great apes in captivity tells us about their cognitive abilities in the wild? The goal of this study was to address this question by examining if wild orangutans are capable of planning for future travel direction. This study looked at the future travel direction of flanged Sumatran males in respect to their long call to investigate whether they announced their future travel direction hours in advance by long calling in the direction of travel. The study was conducted using basic methods, which involved comparing the difference in the angle of calling to
the future travel direction with an expected pattern of random movement. Flanged male orang-utans clearly move in the direction of calling for at least 2.5 h after the call and remain closer to the area of the call for a period of about 5 h post-call. The function of this behaviour may be to attract and to inform females about the males’ future location. In summary, there is evidence that flanged male orangutans have prospective cognition for future travel direction. These results indicate that future planning is not only found among captive orangutans, but also in the wild.

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**Proximate Cues and Ultimate Determinants of Brown Lemur Cathemerality in a Humid Littoral and in a Dry Gallery Forest in Southern Madagascar**

Giuseppe Donati\(^a\), Nicoletta Baldi\(^b\), Valentina Morelli\(^b\), Joerg U. Ganzhorn\(^c\), Silvana M. Borgognini-Tarli\(^b\)

\(^a\)Nocturnal Primate Research Group, Department of Anthropology and Geography, Oxford Brookes University, Oxford, UK; \(^b\)Department of Biology, Unit of Anthropology, University of Pisa, Pisa, Italy; \(^c\)Biozentrum Grindel, Department of Animal Ecology and Conservation, Hamburg, Germany

E-Mail: gdonati@brookes.ac.uk

**Key Words:** Lemurs · Activity · Photoperiodic changes · Luminosity · Cathemerality

So far, two lemur genera, *Eulemur* and *Hapalemur*, and a platyrrhine species, *Aotus azarae*, have been shown to routinely exhibit a mixture of daytime and nighttime activity, i.e. cathemerality. Given the rarity of this phenomenon in primates, its proximate and ultimate factors are still debated. Until now, the adaptive reasons for this apparently odd lifestyle are based mainly on four non-mutually exclusive hypotheses: metabolic dietary-related needs, antipredator strategy, competition avoidance and thermoregulatory benefits. However, different methodologies used at different study sites complicate comparative analyses which might shed light on potential common determinants. Also, little effort has been made to tease apart proximate cues from potential ultimate factors in the multivariate context of activity correlates. In order to overcome some of these problems, we compared the cathemeral activity of two brown lemur populations living in two different habitats. Two groups of *Eulemur collaris* and one group of hybrids *E. collaris* × *E. fulvus rufus* were followed year-round in a humid littoral and in a dry gallery forest in southern Madagascar. Data were collected using a 5-min instantaneous method, with sampling equally distributed between day and night. Photoperiodic changes, nocturnal luminosity and temperatures were recorded or derived at the two sites. Exposure to birds of prey and aggressive interactions with individuals of the same species or other lemur species were evaluated. Biochemical analyses of all food items were also carried out. We weighted the different effects of proximate and ultimate factors via the ANCOVA analysis using as the dependent variable the ratio between diurnal and nocturnal activity. Photoperiodic changes and nocturnal luminosity were the two proximate factors which accounted for most of the variability at the two sites. Diet quality had also a significant effect on the diurnality index, suggesting a role of metabolic dietary-related needs in determining cathemerality.
Bonobo (Pan paniscus) Conflict Management and Reconciliation during Potentially Stressful Situations

Margot Van Dongen\textsuperscript{a,b}, Birgen Meuleman\textsuperscript{a}, Sonja E. Koski\textsuperscript{c,d}, Jef Pereboom\textsuperscript{a}, Elisabeth H.M. Sterck\textsuperscript{e}

\textsuperscript{a}Centre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, \textsuperscript{b}Department of Biology, University of Antwerp, Antwerp (Wilrijk), Belgium; \textsuperscript{c}Leverhulme Centre for Human Evolutionary Studies, Department of Biological Anthropology, University of Cambridge, Cambridge, UK; \textsuperscript{d}Centre of Excellence in Evolutionary Studies, Department of Biological and Environmental Studies, University of Jyväskylä, Jyväskylä, Finland; \textsuperscript{e}Behavioural Biology, Utrecht University, Utrecht, The Netherlands

E-Mail: margot.vandongen@student.ua.ac.be

Key Words: Bonobo · Conflict · Sexual behaviour · Tension

Social association inevitably leads to conflicts. Since aggression carries a risk of injury, increases the risk of further aggression and damages social relationships, mechanisms of conflict prevention and resolution are a critical component of the social life of any group-living species. Bonobos (Pan paniscus) reputedly are a peaceful species, for which sexual behaviours have been convincingly described as a mechanism to reduce tension. In tense situations, such as at feeding time, rates of sexual behaviour are higher compared to control situations. Moreover, conflicts are often reconciled by sexual behaviour, and high rates of sexual behaviour have been linked to the establishment of new relationships. Our main goal in this study was to examine the effect of potentially tense situations, i.e., spatial crowding (seasonally changing housing conditions) and social disruption (the introduction of a new female to an established social group), on baseline cortisol levels in urine to establish whether these are stressful situations for captive bonobos. Subsequently, we examined whether sexual behaviours are indeed, as suggested, a general mechanism used by bonobos to prevent and resolve conflicts during such situations. Spatial crowding caused higher cortisol levels and this effect was even more pronounced after the introduction of a new group member. Sexual behaviours seemed to function as conflict prevention mechanism during social disruption but not spatial crowding, during which only the rate of non-sexual social behaviours was increased. Conflicts were reconciled more often when individuals had to cope with both spatial crowding and social disruption. In conclusion, sexual behaviour certainly is an important aspect of the bonobo’s social life, though it seems not to be the only mechanism to reduce tension.

Microhabitat Variables Influencing Abundance and Distribution of Diurnal Primates (Trachypithecus vetulus vetulus and Macaca sinica aurifrons) in a Fragmented Rainforest Network in Southern Sri Lanka

P.H. Douglas\textsuperscript{a}, R.S. Moore\textsuperscript{a}, S. Wimalasuriya\textsuperscript{b}, A. Gunawardene\textsuperscript{c}, K.A.I. Nekaris\textsuperscript{a}

\textsuperscript{a}Oxford Brookes University, Anthropology Centre for Conservation Environment and Development, School of Social Sciences and Law, Oxford, UK; \textsuperscript{b}LORRIS, Bangamukand Estate, Pitigala, \textsuperscript{c}University of Ruhuna, Department of Animal Science, Mapalana, Sri Lanka

E-Mail: highland_chimp@yahoo.ca

Key Words: Trachypithecus · Macaca · Sri Lanka · Abundance · Microhabitat variable · Isolation · Protection · Conservation

Sri Lanka’s Wet Zone is a region that boasts incredible diversity of endemic fauna and flora. The combined deleterious effects of forest fragmentation and anthropogenic distur-
bance currently threaten two endemic species of primate, the purple-faced leaf monkey (*Trachypithecus vetulus*) and the toque macaque (*Macaca sinica*). The aims of this study were to address the paucity of information available on these species. Surveys were carried out in 2004 and 2006 on the subspecies *T.v. vetulus* and *M.s. aurifrons* to assess their abundance and distribution across 19 forest fragments ranging in size from 2 ha to 1360 ha. Forest fragments were surveyed floristically using plotless sampling. Line transect sampling and auditory sampling methods were used to determine presence/absence and/or relative abundance of each subspecies in the fragments. Microhabitat variables were then assessed to investigate habitat parameters that were positively correlated with the presence of primates, and thus might serve as future indicators of primate presence. The results reveal that several habitat variables are heavily associated with primate presence, including larger DBH and basal area, greater canopy continuity, and greater distance from human habitation. Forest patches in close proximity to monasteries also had greater densities of primates. Habitat isolation and anthropogenic disturbance, including farming, trap guns and selective logging, were associated with absence of primates. With only 26 rainforest patches protected (averaging 1300 ha in size with 13 of them less than 500 ha) in the provinces where this study took place, our study shows that improved protection of the few large remaining forest patches is vital for the conservation and preservation of Sri Lanka’s rainforest primates.

### Post-Conception Mating in Wild Long-Tailed Macaques (*Macaca fascicularis*)

*Antje Engelhardt, J. Keith Hodges, Michael Heistermann*

Department of Reproductive Biology, German Primate Centre, Göttingen, Germany

E-Mail: aengelhardt@dpz.eu

**Key Words:** Long-tailed macaques • Conception • Hormone analysis • Reproductive strategy • *Macaca fascicularis*

In many anthropoid primates, mating activity is not restricted to the ovarian cycle but also occurs during pregnancy. Although it has been suggested that the main function of this post-conception mating is to confuse paternity, it is not clear whether male primates can distinguish between the fertile phase of the conception cycle (FPCC) and the period of peak post-conception mating (peak PCM). We examined whether the pattern of specific female sexual traits (sexual behaviours, swellings) and female attractiveness to males differ between these two periods. The study was carried out on 6 wild female long-tailed macaques in Ketambe, the Gunung Leuser National Park, North Sumatra, Indonesia using faecal hormone analysis to generate female sex hormone profiles during conception cycles and early pregnancy. All females exhibited a distinct period of heightened mating activity around days 45–60 of gestation. During peak PCM, swelling size and frequency of female solicitations were significantly correlated with changes in the oestrogen to progesterone ratio (rswell = 0.614, n = 21, p = 0.003; rssoli = 0.473, n = 21, p = 0.030). Swelling size, frequency of female sexual behaviours and copulations and proportion of male-initiated copulations and ejaculations were not significantly different between FPCC and peak PCM. Although males spent significantly less time consort ing females during peak PCM (Z = –2.2, p = 0.028), they invested heavily in terms of reproductive costs associated with mate-guarding and mating during pregnancy. This was particularly evident for low-ranking and non-resident males. We conclude that post-conception mating in wild long-tailed macaques is not merely a by-product of endocrine changes, but that it may form part of a female reproductive strategy to confuse paternity, which appears to apply particularly to low-ranking and extra-group males.
Reproductive Biology of Sulawesi Crested Black Macaques
(Macaca nigra)

Antje Engelhardt\textsuperscript{a,b}, Dyah Perwitasari Farajallah\textsuperscript{b}

\textsuperscript{a}Department of Reproductive Biology, German Primate Centre, Göttingen, Germany; 
\textsuperscript{b}Primate Research Centre, Bogor Agricultural University, Indonesia

E-Mail: aengelhardt@dpz.eu

Key Words: Sulawesi macaque • Reproduction • Ovarian cycle • Seasonality

Although the Sulawesi macaque is of considerable importance for the understanding of primate evolution, almost nothing is known about its reproductive biology in the wild. Knowledge of reproductive parameters is, however, important for evolutionary studies and for the management of small, separated wild populations in which many Sulawesi macaques are found nowadays. The aim of our study was, therefore, to investigate basic reproductive parameters in wild \textit{Macaca nigra}. We observed two habituated groups (64 and 57 individuals) in the Tangkoko–Batuangus Nature Reserve, North Sulawesi on a daily basis for 13 months starting in April 2006. So far, we have observed 70 ovarian cycles in adult females, using sexual swellings as indication of ovarian activity. Females had a mean of 2.4 cycles (range: 1–4) from lactational amenorhoea until conception, but had significantly fewer cycles after abortion or loss of infant ($U = –2.4, p = 0.02, n_1 = 6, n_2 = 18$). The average ovarian cycle (measured from swelling detumescence to detumescence) lasted 35.4 days (range: 27–57) with females having significantly shorter third than second cycles ($Z = –2.8, p = 0.005, n = 10$). Swellings showed a similar pattern: females had a mean of 19.4 cycle days (range: 8–63) with swellings, but swelling duration became significantly shorter from the first to the second and from the second to the third cycle ($Z_{1–2} = –2.1, p_{1–2} = 0.035, n_{1–2} = 15, Z_{2–3} = –2.8, p_{2–3} = 0.005, n_{2–3} = 10$). Though Sulawesi macaques are thought to have no reproductive seasonality, in both groups the number of females with ovarian activity was highest during August to January (mean: 9 and 5 females per month) and 83% of infants were born from January to May. The infant sex ratio was almost equal (1.07, $n = 31$). Taking into account that there are no felid predators on Sulawesi, infant mortality was relatively high: 19.4% of infants died/disappeared during the first year. Our continuing studies will expand to include data on sex hormones and reproductive strategies.

A Comparison of Calling Patterns of Purple-Faced Leaf Monkeys (Trachypithecus vetulus vetulus and T.v. nestor) in Sri Lanka’s Wet Zone

C. Eschmann\textsuperscript{a}, K.A.I. Nekaris\textsuperscript{b}, P.H. Douglas\textsuperscript{a}, L.P. Birkett\textsuperscript{a}, A. Gunawardene\textsuperscript{b}

\textsuperscript{a}Oxford Brookes University, Anthropology Centre for Conservation Environment and Development, School of Social Sciences and Law, Oxford, UK; 
\textsuperscript{b}University of Ruhuna, Department of Animal Science, Mapalana, Sri Lanka

E-Mail: caitesch@gmail.com

Key Words: \textit{Trachypithecus vetulus} • Biodiversity • Loud call • Bioacoustic

A paucity of studies document Sri Lankan primates from the Wet Zone, a biodiversity hotspot, where 3% of rainforest remains in isolated and disturbed patches. Two threatened taxa of purple-faced leaf monkey are endemic to Sri Lanka’s lowland rainforests: \textit{Trachypithecus vetulus vetulus} (Endangered) and \textit{T.v. nestor} (Critically Endangered). These subspecies are both severely impacted by forest fragmentation, and most remaining populations live in either small forest fragments, or in the case of the latter subspecies, almost completely in home gardens. Due to their shy nature, very little is known about the behaviour and ecology of these taxa. How-
ever, the regular loud calls emitted by these leaf monkeys allow for cross subspecies comparisons. From 2005–2007, we recorded the calling patterns of *T.v. vetulus* at Masmullah Proposed Forest Reserve and Bangamukande Estate and *T.v. nestor* at Talangama Wetland. Time, duration, weather conditions and stimulant of call (dawn call, induced by other monkeys, induced by human disturbance or weather) were noted. Type of call was also noted and recorded with a Sony Professional tape recorder and a Sennheisser unidirectional microphone. The bioacoustic structures of the calls were analysed with AvisoftPro, and compared for subspecific differences. In this paper, we compare these factors between the two sites and quantitatively describe the calls of the two subspecies for the first time. If significant differences in calling behaviour in areas more disturbed by humans are noted, this can prove to be a valuable tool for assessing the impact of fragmentation on the well-being of these endangered colobines.

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**Influences of Environmental Factors on Vocal Communication in Baboons**

*Elodie Ey, Kurt Hammerschmidt, Dietmar Zinner, Julia Fischer*

Research Group Cognitive Ethology, German Primate Centre, Göttingen, Germany

E-Mail: elodie.ey@dpz.gwdg.de

**Key Words:** Baboons · Vocal communication · Contact calls · Gashaka Gumti

The vocal communication of non-human primates may be shaped by different factors, for instance phylogenetic relatedness, social structure and habitat. These factors may affect both the usage of signals in different contexts, as well as their acoustic structure. Here, we focus on the importance of the environmental factor and study how the habitat influences the usage and structure of contact calls of two groups of wild olive baboons (*Papio hamadryas anubis*), frequenting both forest and woodland savannah in Gashaka Gumti National Park, Nigeria. We assume that the usage and structure of vocal signals are adapted to the acoustic properties of the habitat in which they are uttered, in order to cope with ambient noise and sound distortion during propagation. We expect calls uttered in forest to be given at a higher rate, be longer, of lower frequency, and with energy concentrated in lower frequencies than those given in open habitat. To test these hypotheses, we characterize the environment in which calls are given and we record contact calls. We compare their contexts of emission and their acoustic parameters between the different habitat types. Preliminary analyses show a greater influence of the habitat on call usage than on call structure.

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**The Behaviour of Galago senegalensis under Semi-Natural Conditions: Factors Affecting Activity and Social Behaviour**

*Gloria Fernández Lázaro, F.J. De Miguel Águeda, A. López Goya*

Zoology Department, Autónoma University, Cantoblanco, Spain

E-Mail: galaglory@gmail.com

**Key Words:** Nocturnal primates · *Galago senegalensis* · Social behaviour · Reproduction

The information available today on the behaviour of nocturnal primates is similar to that in the middle of the 1970s on diurnal primates. For galagos, the influence of visitors in zoos has not been studied and this work aims to correct that. The study analysed the influence of the public and other factors (sex, age, months of the year and food) on the behaviour of *Galago senegalensis*. The subjects (4 males, 1 female and 1 infant) lived on a reversed light cycle. Data were collected for 7 months. Four 15-min focal samples were taken each month for each subject during the most active hours of the waking cycle (night). Statistical differences were analyzed...
with non-parametric tests using SPSS 13.0 and Statgraphics Plus 4.1 computer programs.

There were no age and food differences in the behaviour. Males were more often out of sight than the female, increasing from December to May. Males are likely the dispersing sex in galagos. The number of occasions when the animals were not seen changed according to the reproductive pattern and when infants were around. The public can affect the alertness of the animals, although it was noted that if there were more than five people, any increase in numbers seemed not to affect the animals. In April there was a steep rise in agonistic behaviour, probably related to oestrus of the female. The female urinated more than the males. Sex differences in urine washing suggest that this behaviour serves to communicate reproductive condition. The lack of stereotypic behaviour and reproduction under semi-natural conditions suggest the good health of the animals. Nevertheless, we recommend the introduction of young females, which would ensure the future well-being of the group.

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**Homeobox Genes and Their Role in the Development and Evolution of the Human Brain**

M. Fiore, B. Chiarelli

Dipartimento di Biologia Animale e Genetica, Laboratori di Antropologia, Gruppo di Ricerca in Scienze Cognitive, Università di Firenze, Firenze, Italy

E-Mail: mariagiulia.fiore@unifi.it

**Key Words:** Homeobox genes · Morphogenesis · Human genome

Increasing knowledge of the eukaryotic genome and the development of experimental embryology has provided new tools for the study of morphogenesis. Homeobox genes regulate many aspects of development in animals. The term refers to specific very conservative sequences of about 180 base pairs. These DNA sequences contain about 180 pairs of identical bases, and are indispensable for the identification of particular nervous system structures in vertebrates, including humans. Their function is to direct cellular and tissue development, and hence morphogenesis. In vertebrates, these genes are organized in very similar units of repetitive groups, distributed in four clusters. They are situated in chromosomes 2, 7, 12 and 17 in humans and in chromosomes 2, 6, 11 and 15 in the mouse. Neurons of different shape and function are organized with respect to each other to form particular connections, which in turn create a dense web of interactions. So the study of Hox genes is of fundamental importance not only for physical anthropology, but also for an understanding of human cognition. We propose a project to characterize the sequences of these genes in the human genome and in those of Pan and Macaca. The comparison could yield important information about the evolution of human encephalisation and could thus elucidate brain evolution in humans and non-human primates.

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**The Influence of Music on Behaviour: A Comparative Study of Two Species of Non-Human Primates in Captivity**

Lara Fistarol

Donata Grassi

Caterina Spiezio

a Biology Department, University of Padua, Padova; b Research Department, Parco Natura Viva – Garda Zoological Park, Bussolengo, Verona, Italy

E-Mail: larafistarol@libero.it

**Key Words:** Lemurs · Macaques · Music · Enrichment

Many studies have shown that music may have positive effects on human behaviour and mood. Recent work has focused on questions about the adaptative value of music by looking at
whether non-human animals could have any perception of ‘musicality’. The influence of music on animal behaviour has been studied in a variety of species, including birds, cows, horses, dogs and primates. The authors of these studies report changes in the behaviour of the animals exposed to music. In this study we investigated the effects of music on the behaviour of two species of non-human primates (Lemur catta and Macaca nemestrina) housed in a zoological park. Lemurs and macaques were exposed to different types of music. Our results show that individuals of both species show changes in behaviour under the influence of music. Moreover, different types of music seem to have a different effect on behaviour, suggesting that lemurs and macaques may recognise different music. Therefore, it seems possible to use music as enrichment for zoo-housed primates.

Record of the Gapeworm Mammomonogamus laryngeus (Raillet, 1899) (Syngamidae: Nematoda) in a Semi-Wild Population of Sumatran Orangutans (Pongo pygmaeus abelii Lesson, 1827) in Indonesia

I. Foitová, B. Koubková, V. Baruš, W. Nurcahyo

4Institute of Botany and Zoology, Masaryk University, Brno, 5Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic; 6Department of Parasitology, Faculty of Veterinary Medicine, Gadjah Mada University, Yogyakarta, Indonesia
E-Mail: foitova@sci.muni.cz

Key Words: Orangutans · Nematodes · Parasite · Conservation · Reintroduction

One adult syngamid nematode parasite was found during routine clinical observation from sputum of Pongo pygmaeus abelli and determined to be Mammomonogamus laryngeus (Raillet, 1899). This finding confirmed previous records of syngamid nematodes, identified only as Mammomonogamus sp. by Collet et al. (1986), in the faeces of orangutans kept at the Bohorok Orangutan Rehabilitation Centre in Northern Sumatra, Indonesia. The nematodes presented a serious health hazard to rehabilitants in this locality. Detailed surveys on present and potential pathogens affecting health and survival of wild orangutans are necessary to ensure species conservation and enable successful reintroduction.

A Multidimensional Approach to Investigations of Primate Communication

Gillian Sebestyen Forrester

Department of Psychology, School of Life Sciences, University of Sussex, Falmer, UK
E-Mail: g.sebestyen@gmail.com

Key Words: Great Apes · Language · Communication

Many of the walls we have erected to separate human behaviour from that of other animals are disintegrating as comparative studies reveal that apes are capable of performing many of the cognitive skills once believed to be evolutionary adaptations unique to the human species (e.g. tool use, cooperative hunting). However, the semantic and syntactic structure underlying human language still sets us apart from our closest living relatives. Research suggests that the ability to acquire and use human language is linked to the evolution of specific increased neocortical volume (Barton & Dunbar, 1997). Although comparative research suggests
that primates share much of the machinery underlying speech perception, and some of the mechanisms humans use to learn language (Weiss & Newport, 2006), we have not been successful in revealing a comparable level of complexity in great ape communication. Does this mean that a structured form of communication does not exist in our closest living relatives? Or, is it possible that we have not previously employed an observational method that has the potential to reveal the complexity of ape behaviour? This presentation focuses on a multidimensional framework for capturing, coding and analyzing behavioural signals in great apes. The term ‘multidimensional’ is used to illustrate that communication and other cognitively driven behaviours are multicomponent, dynamic, distributed and context dependant. I present a tool for objectively and quantitatively assessing the signals produced during great ape behaviour without preconceived notions of signal meaning, animal emotion or intention. A data-rich coding scheme quantifies physical and contextual elements of behavioural signals captured on synchronized digital video cameras. The main goals of this approach are: to assess a comprehensive range of sensory signals within context, to reveal latent structure in synchronous and sequential signals, and to make inferences between the behavioural patterns and their underlying neural processes.

Effects of Food Presentation and Diet on Species-Typical Foraging and Tool Use Behaviours in Five Captive Orangutan Groups

Sarah Fowkes
Oxford Brookes University, Anthropology Centre for Conservation Environment and Development, School of Social Sciences and Law, Oxford, UK
E-Mail: sarah_fowkes@hotmail.co.uk

Key Words: Orangutan · Captivity · Zoo · Diet · Reintroduction

The conservation efforts of zoos are principally to house and to breed populations of endangered species in captivity. The status of Pongo abelii as Critically Endangered and of Pongo pygmaeus as Endangered suggests that ex-situ orangutan populations are vital as, despite efforts to conserve orangutans in their natural environment, ensuring their survival is becoming impossible (IUCN, 2006). An important factor in ex-situ captive breeding is to reintroduce endangered species into their natural habitats; therefore, the primary goal of zoos should be to maintain species-typical behaviours to ensure the survival of viable populations (Stanley-Price, 1991). The most prevalent environmental modification for orangutans in captivity is that of diet and methods of food procurement. Therefore, the aim of the current study was to determine what species-typical foraging behaviours are affected by a captive environment. Data were collected using continuous focal animal sampling from captive Pongo abelii and Pongo pygmaeus groups housed at five UK zoos. All instances of food manipulation, processing and tool use in the groups were recorded in accordance with ethograms of orangutan species-typical foraging and tool use behaviours developed by Parker & Gibson (1977), Lethmate (1982) and Russon (2001). Food items consumed and the presentation of the food items were recorded to determine whether the subject’s diet affects foraging behaviours. It was predicted that if captive animals display food acquisition strategies similar to their wild counterparts, then this would provide evidence that the animals were in an adequate captive environment (Bloomsmith, 1989). Current results suggest that adequate captive environments are those which provide whole food items presented on enclosure roofs or concealed, thereby promoting the highest rate of species-typical foraging behaviours.
Reconciliation, Consolation and Relationship Quality in Chimpanzees

Orlaith N. Fraser, Filippo Aureli

Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Liverpool, UK
E-Mail: o.fraser@2004.ljmu.ac.uk

Key Words: Chimpanzee · Aggression · Reconciliation · Consolation

One of the costs of aggressive conflicts in gregarious animals is damage to the relationship between the opponents. This can lead to loss of benefits afforded by that relationship and increased stress. Reconciliation (the post-conflict affiliative reunion between former opponents) can repair the relationship between former opponents and reduce stress but also carries risks of renewed aggression. Thus, reconciliation rates vary across dyads according to relationship quality, and more valuable relationships are expected to have a higher rate of reconciliation. This study used a multivariate approach to measuring relationship quality in captive chimpanzees, using principle component analysis to extract three components of relationship quality (value, compatibility and security) from nine behavioural variables. Whilst kin and individuals of a similar age were found to be more valuable, no effect of sex combination was found on relationship value. Kin and female-female dyads were found to be more compatible than non-kin and dyads including males. The effect of multiple factors, including the components of relationship quality, on the occurrence of reconciliation and consolation (an affiliative interaction directed from a third party to the conflict victim) was analysed using a generalised linear mixed model. The best predictor of reconciliation was the absence of consolation and the best predictor of consolation was the absence of reconciliation, indicating that consolation may substitute for reconciliation. In support of this, consolation was found to function as a post-conflict stress-alleviation mechanism, reducing a behavioural indicator of stress in victims of aggressive conflict.

Food Choice Strategies of Mountain Gorilla Groups in Bwindi Impenetrable National Park, Uganda

Jessica Ganas*, Sylvia Ortmannb, Martha M. Robbinsa

aMax Planck Institute for Evolutionary Anthropology, Leipzig, bLeibniz Institute for Zoo and Wildlife Research, Berlin, Germany
E-Mail: ganas@eva.mpg.de

Key Words: Mountain gorilla · Food choice · Nutrition · Biomass · Bwindi

Determining the factors that influence food choice is important to understand how they may influence an animal’s survival and reproduction and population growth. Between September 2004 and August 2005, we studied the food choice of four mountain gorilla groups that consume herbs and fruit at two separate locations (Buhoma and Ruhija) differing in food availability in Bwindi Impenetrable National Park, Uganda. We tested three food choice hypotheses, considering both the nutritional and secondary metabolite content of food and food availability. Regardless of changes in herb availability, the herb diet was positively influenced by herb biomass and sugar content while negatively influenced by fibres/condensed tannin and protein content. Regardless of changes in fruit availability, fruit consumption was influenced by those species that had relatively high availability and low condensed tannin content. Additionally, the gorillas did not increase their consumption of herbs high in fibre and sugar during periods of low fruit availability to compensate for the lack of fruit (easily digested energy). Finally, gorillas at the location with higher fruit availability (Buhoma) avoided fibres/condensed tannins in their herb diets significantly more than gorillas at the other location (Ruhija). This suggests that Ruhija gorillas compensated for the low amount of energy available from fruit by obtaining...
their energy needs from herbs. Our results demonstrate that Bwindi gorillas use a food choice strategy of avoiding anti-feedants (fibres and phenols), consuming species that are more abundant, and that nutrient content is less important in food choice. Our results also suggest that both locations in Bwindi have a good food supply, the gorillas can seek alternative foods even at times of low fruit availability, and that it is likely sufficient for survival and perhaps growth of this endangered gorilla population.

Impact of Social Context on Female Reproductive Function in a Group of Captive Olive Baboons (Papio anubis)
C. Garciaa, P.C. Leeb, L. Rosettaa

Section of Ecology, Primate Research Institute, Kyoto University, Inuyama, Japan; Behaviour and Evolution Research Group, Department of Psychology, University of Stirling, Stirling, UK; Laboratoire de Dynamique de l’Evolution Humaine, CNRS UPR 2147, Paris, France
E-Mail: cecile@pri.kyoto-u.ac.jp

Key Words: Papio anubis · Reproduction · Fertility · Social status

In primates, the energetic and social environment of females is thought to have a profound influence on reproductive function and fertility. In addition to individual health and energetic influences on menstrual cycles and fertility, social constraints could act to impair reproductive function. This impairment could range from a moderate diminution of reproductive hormone secretion to a complete suppression of fertility. This study uses two years of data on female fertility in 23 semi-free ranging olive baboons (Papio anubis) to investigate possible effects of social status, expressed via dominance rank, age and local environment on the duration of post-partum amenorrhea, the number of cycles before conception, the menstrual cycle length and interbirth intervals. We found that social dominance rank was a significant factor affecting female fertility. Short post-partum amenorrhea was associated with being of mid or high rank. Low-ranking females experienced more cycles prior to conception, longer cycles (once cycling was well established) and had smaller sexual swellings than did high-ranking females. Low-ranking females also had longer intervals between successive births. As female energy intake was unrelated to dominance, we suggest that social stresses are important suppressors of the hormonal and lactational competence of low-ranking females. Both acute and chronic stresses may play important roles in fertility outcomes for these baboons and further research is needed to understand the role of stress and subtle menstrual cycle abnormalities in female mammal fertility.

Savanna Chimpanzees (Pan troglodytes verus) and Baobab Fruits (Adansonia digitata): Investigation of Percussive Technology among Three Chimpanzee Communities in Southeastern Senegal
Maja Gašperšiča, Jill D. Pruettb

Department of Social Anthropology, Institutum Studiorum Humanitäris, Ljubljana, Slovenija; Department of Anthropology, Iowa State University, Ames, IA, USA
E-Mail: majolita@yahoo.com

Key Words: Pan troglodytes verus · Baobab fruits · Tool use · Percussive technology

Percussion activities must have been important in human evolution, as they are probably a precursor technology for cracking, stone knapping and pounding. Morphological and dietary resemblances suggest that similar selective forces affected early hominins and modern chimpan-
Chimpanzees in arid and open habitats. Research on percussive technology used by chimpanzees to open baobab fruits at three Senegalese sites (Fongoli, Bandafassi and Mt. Bagnomba) might thus provide relevant clues to the evolutionary origins of tool use. We focused on techniques used in relation to microhabitat and on fruit transport from trees to feeding sites. Limited observations, the distribution of baobab remains and experiments all confirmed the predominance of arboreal cracking on large branches. Use of a trunk as an anvil was not observed and no hammer use was seen or detected through monitoring portable objects. The arboreal technique was more prominent at Fongoli (81%), while chimpanzees at Bandafassi and Mt. Bagnomba more often cracked baobab fruits terrestrially (12.9 and 20.6%, respectively). Rocks were used as anvils with the same frequency at these two sites (39.5%), while at Fongoli they were used in only 4.3% instances. Fongoli chimpanzees didn’t crack baobab fruits on platforms, while only they incorporated termite mounds. Roots were used at a similar frequency at all sites, while earth was used only at ‘mountainous’ sites. Fongoli chimpanzees were observed to transport fruits up to 1 km, although the remains were rarely found more than 500 m from the trees. Here only 9.3% of baobab remains were found beyond the fruit-fall zone, while at Bandafassi and Bagnomba they were found beyond this zone at a frequency of 32.4 and 35.6%, respectively. Baobab remains at Mt. Bagnomba were frequently distributed up to 35 m, with the maximum distance of 50 m. Cracked fruits were sometimes found in large trunk cavities, while at Bandafassi chimpanzees also carried baobab fruits into large caves among rocks.

Looking for Chimps – A Social Anthropologist’s Point of View

N. Govoroff
Laboratoire d’Anthropologie Sociale (LAS), Collège de France, Paris, France
E-Mail: nicolas.govoroff@college-de-france.fr

Key Words: Chimpanzee · Anthropomorphism · Ethno-primatology

Ethnographic fieldwork on human/unhabituated chimpanzee relations in both Ivory Coast (Koulango region) and in Ghana (Ashanti and Ewe regions) has, unsurprisingly, shown the importance of anthropomorphism in cultural representation systems. However, this is not without consequences for ethno-primatologic enquiry. Informants’ discourse is shaped by this turn of mind and generates items which may coincide with what is scientifically known about these animals but which is, in fact, of a different nature. The elements gathered during interviews can be misleading because if they sometimes result from observation they are also the product of anthropomorphic logic itself. This communication will focus on the analysis and on the methodological implications of the anthropomorphism paradigm in terms of choice of informants for research in field primatology as well as of the selection of local indigenous managers of conservation policies.

Home Range Analysis of Snub-Nosed Monkeys (Rhinopithecus bieti) at South Baima Snow Mountain Nature Reserve, China

Cyril C. Grueter
Anthropological Institute, University of Zürich-Irchel, Zürich, Switzerland
E-Mail: ccgrueter@aim.unizh.ch

Key Words: Rhinopithecus bieti · Home range · Seasonality

Home range patterns of a group of black-and-white snub-nosed monkeys (Rhinopithecus bieti) in the mountain forests of South Baima Snow Mountain Nature Reserve were examined over 14.5 months by means of direct observations. The habitat used by the focal group extends
from 2,600 to 3,900 m asl and is made up of various forest types, of which the temperate mixed deciduous broadleaf/conifer forest is the predominant one. Home range size is at least 32 km² with some disjunct core zones of relatively heavy utilization. The combined effects of large group size (n > 200) and forest heterogeneity seems to account for one of the largest home ranges of any primate. The group followed a pattern of ‘sweeps and concentrations’, using particular forest blocks intensively for a few days and interspersing these periods with long-distance movements. Winter, spring and summer home ranges were equally large, i.e. roughly 18 km². The group exhibited a more concentrated ranging pattern when fruits were readily available, resulting in a comparatively small autumn home range (9.3 km²). Neither climate nor anthropogenic perturbations were significantly correlated with monthly or seasonal home range sizes. Temporal and spatial availability of food (leaf flushing in spring, patchy occurrence of fruits in winter, abundance of fruits in autumn) are likely key determinants of range use. No support was found for the theoretical prediction of an inverse relationship between habitat quality and home range size of different subpopulations.

Ecodevelopment: An Effective Tool for Primate Conservation

A.K. Gupta
Chief Conservator of Forests, Government of Tripura, Department of Forests and Wildlife, Aranya Bhawan, Gorkha Basti, Agartala, India
E-Mail: akphayre@yahoo.com

Key Words: Macaques · Langurs · Conservation · Eco-development · Sepahijala · Wildlife Sanctuary

The main conservation threats to non-human primates are due to local people sharing habitats and other resources with them. Therefore, it is necessary to undertake such measures as would ultimately lead to the reduction and/or the complete removal of peoples’ dependency on key primate habitats and resources. Setting up of protected areas for the exclusive use of wildlife species (by keeping local people out altogether) has proved to be unsuccessful. A change in Indian Forest Policy in 1988 led to the initiation of an eco-development programme in 1991 with the main aim of generating non-forestry- and non-land-based livelihood options for the sustenance of dependent local people. An assessment was made of the population status and habitat quality of Phayre’s langurs (Trachypithecus phayre), capped langurs (T. pilatus), pigtailed macaques (Macaca nemestrina) and rhesus macaques (M. mulatta) in Sepahijala Wildlife Sanctuary (SWLS), Tripura. In addition, the local peoples’ awareness of these 4 primate species was studied. Data collection was done in two phases, before (1993–94) and after (January to May 2007) the eco-development initiatives, which were started in SWLS in 1998. The results indicate marked improvements in the primates’ habitat quality and population status, and the level of awareness among the people towards conservation of the 4 primate species as well as that of other endangered species, such as clouded leopards (Neofelis nebulosa), binturongs (Arctitis binturong) and slow lorises (Nycticebus coucang). The study further suggests that the bottom-up approach of eco-development, relying mainly on non-forestry- and non-land-based measures, has proved an effective tool for overall management of the sanctuary and to delineate limited natural resources amongst key stakeholders in space and time.


Responses to Decreasing Fruit Availability and Dietary Differences in White-Bearded Gibbons (Hylobates albibarbis) and Bornean Orangutans (Pongo pygmaeus wurmbii)

Livia Haag

Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: livia.haag@gmx.ch

Key Words: Gibbon · Orangutan · El Niño · Survival strategy

Orangutans and gibbons are sympatric apes that face similar environmental constraints. Fluctuations in food abundance can seriously affect survival strategies and these happen, in particular, during increased drought periods in El Niño years and in habitats disturbed by human activities. To reveal differences in the survival strategies of gibbons and orangutans, data were collected on both species during two wet and two dry months in the 2006 El Niño year at Tuanan, a heavily logged peat swamp forest in Central Kalimantan, Indonesia. In times of fruit abundance, gibbons and orangutans are strongly frugivorous (both species have up to 78% fruits in their monthly diet). When fruit availability is reduced, both apes have less fruit in their diet and flowers constitute the primary fallback foods, followed by vegetative matter. However, in times of low fruit abundance, gibbons are able to maintain a higher level of fruit consumption than orangutans (gibbons 51%, orangutans 40%) by feeding on small fruits in small and scattered food patches. This strategy is unprofitable for orangutans since intake rates are low and travel costs high. Because of their superior strength, orangutans eat very hard fallback foods such as the inner bark of stems or the seeds of unripe fruits, which are not accessible to gibbons. Differences in body size and strength explain the different responses to decreasing fruit availability in orangutans and gibbons and allow coexistence of these two apes.

Group Structure and Physical Characteristics of Simakobu Monkeys (Simias concolor) on the Mentawai Island of Siberut, Indonesia

Susilo Hadi, Thomas Ziegler, J. Keith Hodges

German Primate Centre, Department of Reproductive Biology, Göttingen, Germany
E-Mail: Susilohadi2004@yahoo.com

Key Words: Simakobu monkeys · Group size · Siberut · Simias concolor

This study presents data on group composition and individual physical characteristics obtained for the first time from two free-ranging groups of Simakobu monkeys (Simias concolor). The entire set of data was collected during a rare traditional hunting session of local people in North Siberut, to which the first author was invited to attend passively and gather measurements under restricted conditions. The two groups of Simakobu monkeys, all members of which were hunted down, consisted of eight and ten individuals, the latter including a pregnant female. Individuals were sexed and allocated to four age categories: infant, juvenile, subadult and adult on the basis of their physical characteristics. Additionally, measurements of the head-body length (tape measure) and body weight (digital balance) were taken and a species specific correlation between head-body length and body weight was analysed using linear regression. Mean group size was 9 individuals with an adult male-female sex ratio of 1:2.5. In each group, only one adult male was present, indicating the prevalence of single male groups and male dispersal in this species. Within age categories (sexes combined) head-body lengths ranged from 19.6–25 cm, 34–39 cm, 41–44 cm and 44–53 cm. Corresponding body weights ranged from 0.5–0.9 kg, 2.35–3.75 kg, 4.25–5.2 kg and 5.55–7.85 kg, respectively. The species specific correlation between head-body length and body weight was re-
vealed by the equation \( Y = 0.24X - 4.98 \). These measurements provide important data for comparative analysis within the subfamily Colobinae. Furthermore, the data indicate that group size of *Simias concolor* in a primary rainforest habitat in North Siberut is considerably larger than that reported from other sites on the Mentawai Islands, thus emphasising the conservation importance of this region for this rare and endemic species.

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**Adaptive Strategies for the Use of Fallback Foods in Apes**

Mark E. Harrison  
Wildlife Research Group, The Anatomy School, University of Cambridge, Cambridge, UK  
E-Mail: harrison_me@hotmail.com

**Key Words:** Apes • Fallback food • Ecology

It has recently been suggested that the evolutionary importance of fallback foods (FBF) apply more to processing adaptations (e.g., gut morphology and dentition), whereas the evolutionary importance of preferred foods apply more to harvesting adaptations (i.e., increased search/travel efficiency), and that two classes of FBF exist: staple – available and eaten year-round, ≤100% of the diet – and filler – may not be eaten for long periods, never 100% of the diet. In this paper, I test this idea on apes and find that, generally, it is well supported. First, I compare the FBFs used by the different species and their level of reliance on these (gorilla > chimpanzee > orangutan > gibbon). Next, I compare 14 characteristics (covering travel, tool use, cranio-dental, digestive and life history adaptations) indicative of FBF dependence. I find that, while these characteristics generally fit the above level of reliance on FBFs (with gorillas and gibbons unambiguously adapted primarily for the exploitation of FBF and preferred foods, respectively), some unexpected discrepancies do occur. Despite chimpanzee’s proposed slightly greater reliance on FBFs than orangutans, orangutan cranio-dental and digestive morphology appears better adapted for FBF exploitation than that of chimpanzees. This is most probably due to the nature of the two species’ main FBF: figs for chimpanzees, and bark and leaves for orangutans. While the former have many of the properties normally exhibited by preferred foods (patchy distribution and easy processing), the latter are difficult to masticate and digest (due to their high toughness and fibre content) and are low in energy, leading to adaptations in orangutans more suited for processing fibrous foods. It is clear that FBF exploitation has a dramatic influence on ape ecology and, consequently, is likely to have been very important in hominoid evolution. Bearing this in mind, and considering the possible bias of dental morphology for exploiting FBFs rather than preferred foods/overall dietary composition, care should be taken when attempting to assess extinct hominoid diet through teeth.

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**Development of a Liquid Chromatography-Tandem Mass Spectrometry Method for the Quantification of Endogenous Steroids in Primate Urine**

Barbara Hauser, Tobias Deschner, Christophe Boesch  
Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany  
E-Mail: bhauser@eva.mpg.de

**Key Words:** Baboon • Oestrone • Pregnanediol • Cortisol • Testosterone • Mass spectrometry

A quantitative method using liquid chromatography-tandem mass spectrometry (LC-MS/MS) was developed for the simultaneous determination of 23 endogenous steroids in primate
urine. The introduced method includes oestrone, pregnandiol, cortisol, testosterone and several human urinary glucocorticoid and androgen metabolites. As the method is intended for the analysis of steroid hormones in behavioural studies on wild-living primates, it was adapted for a sample volume of 200 μl urine. The sample preparation consisted of an enzymatic hydrolysis of steroid glucuronides using β-glucuronidase from *E. coli* followed by a solvolytic cleavage of steroid sulphates employing sulphuric acid/ethyl acetate. The extraction of steroids from urine was optimized with respect to pH during extraction, type of ether and the amount of enzyme necessary for complete hydrolysis of glucuronides. The method was validated with respect to detection limits, recovery of extraction, intra- and inter-day precision and reproducibility of hydrolysis and solvolysis. The proportion of steroid hormone excreted as sulphate was determined for 21 steroids in chimpanzee urine, in order to evaluate the necessity of this step. The solvolysis proved to be essential for all investigated steroids except for pregnandiol, tetrahydrocortisol and tetrahydrocortisone, which were found to be less than 10% in the solvolysis fraction. As a first application, the ovarian cycle profile of oestrone and pregnandiol was investigated in three captive bonobos.

### The More Males, the More Dominant Are Female Primates

*Charlotte K. Hemelrijk, Jan Wantia, Karin Isler*

Theoretical Biology, Centre for Ecological and Evolutionary Studies, University of Groningen, Haren, The Netherlands

E-Mail: c.k.hemelrijk@rug.nl

**Key Words:** Dominance relationships · Aggression · Female dominance · Group composition

Although models and empirical data have shown that dominance relationships (also those between the sexes) are, at least in part, a consequence of the self-reinforcing effect of winning and losing fights (the so-called winner-loser effect), this phenomenon has been debated. To contribute to this discussion, we try to explain how groups may differ in their degree of female dominance over males. Since groups differ in composition, we investigated how group composition may influence female dominance over males through self-reinforcing effects. For this, we combined a modelling study with an empirical investigation on 22 species throughout the Primate order. We used an earlier model, called DomWorld, because it has shown that self-reinforcing effects in combination with a high intensity and frequency of aggression increase female dominance over males. In the model, individuals are made only to group and compete, whereby winning and losing fights are self-reinforcing. The sexes differ only in their fighting power: males start with a higher initial dominance value and a higher intensity of aggression than females. Results show that in the model female dominance increases with the number of males in the group, which is due to the higher percentage of interactions with individuals that have a higher intensity of aggression (males). Similarly, in our comparative study (using contrast methods), female dominance increases with the percentage of males in the group. This correlation is also related to the percentage of competitive interactions of both sexes with males and is not due to sexual dimorphism. Though this supports the importance of winner-loser effects for dominance relationships, we also investigated alternative explanations for this phenomenon. Similar analyses in other species are needed to prove that this is a general phenomenon.
Bipedalism – Adaptations in the Human Lumbar Back Musculature?
Bettina Hesse, Nadja Schilling, Martin S. Fischer, Rosemarie Fröber
Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Jena, Germany
E-Mail: bettina.hesse@uni-jena.de

Key Words: Homo · Locomotion · Bipedalism · Musculature · Body posture

Among primates, several modes of locomotion associated with different body postures have evolved. A particular specialisation of the ancestral quadrupedal locomotion in primates connected to a horizontal trunk is the upright body posture and bipedalism in humans. In humans, the gravitational force acts in line with the body axis rather than orthogonally as in quadrupedal mammals. Furthermore, the contribution of trunk movements to step length is much less during locomotion and it is mainly due to rotations about the longitudinal body axis rather than flexions in the horizontal or sagittal plane as in quadrupedal mammals. Therefore, the functional demands on the lumbar musculature are very different in humans. Surprisingly, the topography of human back muscles is very similar to that of other mammals. To find adaptations to the differing functional demands, we investigated intramuscular characteristics such as the three-dimensional distribution of muscle fibre types as an indicator of a muscle's function using immunohistochemistry. In the lumbar epaxial musculature of three male donated cadavers, a high proportion of slow fibres was found throughout all muscles. This is in contrast to results on quadrupedal mammals which had high percentages of slow contracting, fatigue-resistant fibres in deep, mono- or oligosegmental muscles only, whereas superficial muscles were dominated by fast contracting fibres. Our results indicate an equal stabilising function for both the deep, oligosegmental and the superficial multisegmental lumbar muscles in humans.

Reduced Reproductive Function in Wild Baboons Related to Natural Consumption of Plant Compounds
James P. Higham, Caroline Ross, Ymke Warren, Michael Heistermann, Ann MacLarnon
Centre for Research in Evolutionary Anthropology, Roehampton University, London, UK; Department of Reproductive Biology, German Primate Centre, Göttingen, Germany
E-Mail: j.higham@roehampton.ac.uk

Key Words: Baboon · Plant consumption · Reproduction · Progestogen · Pregnancy

A number of primatologists have suggested that the consumption of plant compounds may have direct effects on wild primate reproduction, but physiological evidence of such effects has been difficult to come by. We studied the reproductive biology of two troops of olive baboons (Papio hamadryas anubis) at Gashaka-Gumti National Park, Nigeria. During this study we identified an unexpected pattern of seasonal progestogen excretion, which occurred across all females in both troops, regardless of reproductive state (i.e. during pregnancy, lactation and cycling phases). We searched our detailed feeding data on the study animals, and found that only one species of plant was consumed by both troops when elevated progestogens were measured and not at any other times of the year: the African black plum Vitex doniana. A search of the literature revealed that the Mediterranean species of this genus, Vitex agnus castus, is renowned for its effects on the reproductive biology of women. Samples of V. doniana collected in the field revealed the presence of high concentrations of progestogen-like compounds not found in other plant species consumed by the study baboons. Levels of progestogen excretion by females during periods of V. doniana consumption are higher than those found during pregnancy, and prevent the expression of the sexual swelling, which is associated with ovulatory activity. As consortship and copulatory activity in baboons occur almost exclusively in the pres-
ence of a sexual swelling, *V. doniana* appears to act on cycling females as both a physiological contraceptive (simulating pregnancy in a similar way to some forms of the human contraceptive pill), and a social contraceptive (the absence of sexual swelling reducing association and copulation with males). The wide range of medicinal properties attributed to plants in the *Vitex* genus may help to explain why this feeding behaviour is still beneficial for females.

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**Network Scaling Reveals Consistent Patterns in Hierarchical Animal Societies**

*Russell Hill*, *Alex Bentley*, *Robin Dunbar*

*Evolutionary Anthropology Research Group, Durham University, Durham, Evolutionary Psychology & Behavioural Ecology Research Group, University of Liverpool, Liverpool, UK*  
E-Mail: r.a.hill@durham.ac.uk

**Key Words:** Gelada · Baboon · Hierarchical societies · Group size

Human networks are hierarchically structured and we have shown previously that these hierarchical societies are arranged in a coherent set of characteristic group sizes organized according to a geometric series with a preferred scaling ratio close to three. Humans are not the only species to live in hierarchical societies, however, and many mammalian species have social organizations with a number of identifiable network levels. A key question, therefore, is whether these hierarchical networks in other species have a similar scaling ratio to those observed in humans. Here we present an analysis based on fractal network theory to show that gelada and hamadryas baboons, as well as orca and elephants, appear to have similar network scaling ratios to those observed in humans. The implications of these consistent patterns will be discussed.

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**Conservative Choices in an Innovation-and-Transmission Experiment with Captive Chimpanzee Groups**

*Christine Hrubesch, Signe Preuschoft, Carel van Schaik*

Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland  
E-Mail: hrubesch@aim.unizh.ch

**Key Words:** Chimpanzee · Social learning · Innovation

Wild chimpanzees and orangutans show ample evidence of geographic variation in socially transmitted skills and signals, similar to human culture. Experiments have confirmed their capability in observational forms of social learning, but we know little about the rules governing the adoption of novel skills. We conducted an innovation-and-transmission experiment with 13 chimpanzees, living in two groups at hopE sanctuary, Gänserndorf, Austria. Individuals were presented with a board where food items had to be maneuvered around obstacles. Most chimpanzees used sticks to acquire the food, but five adults spontaneously invented a novel technique, rattling the board. This spread to other group members as chimpanzees watched each other’s techniques and, subsequently, almost all tested the rattling technique. But their choice of technique did not depend on whom they had observed, nor on what their friends or dominant group members did. Instead, chimpanzees who were especially proficient with sticks continued to use them almost exclusively, and were reluctant to switch to the rattle technique, despite it being objectively more efficient. When we made rattling impossible by fixing the board, exclusive rattlers kept trying to rattle and made no attempt to acquire the stick technique. We conclude that innovators serve as models stimulating experimentation with alternative solutions, but that chimpanzees are conservative in that mastery in one skill inhibits individual exploration as well as adopt-
Females of some Old World primate taxa exhibit exaggerated perineal swellings during an extended period around ovulation. The origin and maintenance of these conspicuous ornaments, which are likely to be sexually-selected, have intrigued evolutionary biologists for decades. Despite major theoretical interest and an increasing number of empirical studies, selective pressures operating on this trait are still poorly understood. Two main hypotheses are currently tested. First, the reliable-indicator hypothesis (Pagel, 1994) presents swellings as honest signals of condition in a sex-reversed version of the traditional sexual-selection models. Second, the graded-signal hypothesis (Nunn, 1999) incorporates swellings in a female strategy to alter costs and benefits of male reproductive decisions in an inter-sexual conflict context. However, the latter hypothesis is difficult to test, while field studies of the former are limited to only two cases with contradictory findings (Domb and Pagel, 2001; Deschner et al., 2004). We propose to test predictions made by the reliable indicator hypothesis in a wild population of chacma baboons (Papio ursinus) from Tsaobis Leopard Park, Namibia. Several features of the swellings are examined. Their maximal size (length, width, depth and area) is determined using digital photographs calibrated by a rangefinder. The maximal swelling contour is quantitatively assessed using Elliptic Fourier Descriptors (Kuhl and Giardina, 1982). These traits are found to be more variable between females than within females across cycles. Swelling characteristics are linked to female age and rank, and to various condition parameters collected when trapping the animals. Some preliminary results notably show an influence of age and rank on the swelling shape. Their relationship to the length of copulation calls (sometimes presented as quality indicators), number of surviving offspring, and male preference using the occurrence of consortships in the periovulatory period will also be examined.
Journal feedback between parent and juvenile offspring on learning trajectories, behavioural acquisition and performance. Although not all juveniles matched the demonstrated solution, both groups of juveniles spent significantly more time at the targeted location being modelled for them. Parent and offspring correlated well in time spent at the modelled location. We investigated predictors of success and performance by analyzing data prior to first success. Juveniles’ exploration of the apparatus predicted well their success at the task, whereas observation of the parent had no influence. Both juvenile scrounging and adult food calling, which elicited begging, impeded learning. High adult refusals per beg also predicted task success by juveniles. Adults monitored their offspring’s performance and increased their refusals per begs once their offspring solved the task on their own. Cottontop tamarins also exhibited some behavioural scaffolding. Solving the task was clearly influenced by an intricate behavioural feedback between parent and offspring independent of maturational changes.

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Comparing the Role of Alloparenting in Apes and Monkeys

J.E. Hutchinson, A.W. Fletcher

Department of Biological Sciences, University of Chester, Chester, UK
E-Mail: j.hutchinson@chester.ac.uk

Key Words: Western gorilla · Captivity · Alloparenting · Infant care

Alloparenting, the handling and caring of infants suckled by another, is a common phenomenon among K-selected, slow growing species. In mammals, the adaptation of non-maternal infant care is proposed to enable the survival of an immature in the event of the mother’s death, when care other than nourishment may promote survival. Alloparenting is common across cercopithecine, callitrichid and colobine families; typically females (nulliparous and multiparous) interact with infants. In the apes, alloparental care and adoptions have been documented, but quantifiable data are lacking, particularly in gorillas. Using data from captive gorillas, and considering other ape species, we ask if ape alloparenting occurs in a different form or differs in adaptive function compared to monkey species. Ad lib sampling of five captive western gorilla (Gorilla gorilla gorilla) groups, between March 2005 and April 2006, provided over 900 observation hours. Each group had at least one infant and several older immature gorillas. Five out of seven infants were carried by male and female immature conspecifics, but not by adult females or the silverback. Alloparents initiated the majority of infant interactions regardless of alloparent sex and age, but a reduced frequency of infant contact occurred with increased alloparent age, particularly in males. No differences in the frequency of alloparenting were found between maternal and non-maternal siblings of the infant in question, although maternal siblings often cared for infants for longer than non-maternal carers did. This study supports findings from other ape and vervet monkey studies, that male and female immatures are both regular alloparents, with females and kin generally being the most persistent carers. We propose that alloparenting will be beneficial to the development of alloparent and infant: where alloparent and infant are related; where risk to the infant is minimal and where non-nutritional care is beneficial for infant survival.
Using Multi-Dimensional Scaling to Map Spatial Proximities in Captive Gorilla Groups

J.E. Hutchinson, A.W. Fletcher
Department of Biological Sciences, University of Chester, Chester, UK
E-Mail: j.hutchinson@chester.ac.uk

Key Words: Gorilla • Silverback male • Social relationships

Measures of proximity have been used in numerous primate studies to represent social relationships between individuals. Many reports analyse proximity between dyads, whereas primate social groups often consist of several individuals varying in age, sex and social status. Thus, demographic factors likely influence the spatial proximity of an individual in relation to other available group members. Here we present a Multidimensional Scaling (MDS) application, which demonstrates spatially the proximity relationships between several different individuals, promoting a clearer understanding of primate group dynamics. Scan data were collected from 44 gorillas (Gorilla gorilla gorilla) at 20-min intervals for over 900 observation hours at five European zoos. Proximity matrices were constructed for all five captive gorilla groups, using the percentage of scans that were within 5 m, for each available dyad. We used Proxscal, SPSS V.14, to analyse the similarity matrices and produce two-dimensional spatial maps for each gorilla group. It was found that the spatial orientations of four gorilla groups were similar, with a core containing the silverback male and adult females with their dependant offspring. Juvenile and adolescent males were found further from their parents and peers with increasing age, whereas juvenile females often remained close to juveniles and infants in the core. The fifth gorilla group was different in demographic composition to the others, and this was reflected in the greater spatial disparity of all group members in the spatial map. Spatial mapping of social species using MDS enables a visual interpretation of the structure of social relationships, to which further statistical analysis can then be applied. This application is a useful tool for the comparison of primate social relationships within groups or between groups, over time.

Life History Pace and Brain Size: From Correlation to Causation

Karin Isler, Carel van Schaik
Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: kisler@aim.uzh.ch

Key Words: Brain size • Encephalization • Life history parameters • Longevity

A positive correlation between relative brain size and life history parameters, such as development time, age at first reproduction and longevity, has been confirmed by a number of comparative studies in primates, and also in birds and in mammals in general. However, the causal link between the two is open to debate: Does a larger brain enable a species to reduce its mortality rate, and thus slow down its pace of living? Or is a longer development and maturation period a necessary prerequisite to grow a relatively larger brain? Here we show that the correlation between brain size and life history pace does not hold in several groups of altricial mammals. A comparison between taxa with different strategies of offspring care demonstrates that the energetic demands of growing and maintaining a relatively large brain lead to prolonged development only in large, precocial mammals with no helpers, such as most primates or ungulates. In altricial carnivores without helpers, an increased brain size is correlated with smaller litters. In both cases, the reduced annual fertility rate is then compensated for by a longer life span. On the other hand, larger-brained carnivores with helpers are also able to increase the number of offspring produced annually, but do not exhibit a longer life span. In conclusion,
with the aid of new, large data sets and comparative techniques that take the influence of phylogenetic relatedness into account, we can now show that larger brain size does indeed lead to prolonged development and extended adult life span, but only in large, precocial mammals. By linking these findings with an energetic viewpoint on brain size evolution, we are able to explain why a high degree of encephalization is observed in only some primates and cetaceans.

**Human Observer-Primate Relationship in the Field: An Interactionist Approach of the Habituation Process**

F. Jankowski  
EHESS (Paris), La Garenne Colombes, France  
E-Mail: frederique.jankowski1@aliceadsl.fr

**Key Words:** Baboon • Habituation process • Social organization

In order to observe primate behaviour at close range, field primatologists have to habituate animals to their presence. The techniques and processes involved have only rarely been described. The success of habituation seems to depend on different factors such as habitat structure, previous experience of the primate with humans or the species studied. Some primates are easy to habituate, whereas others remain sensitive to human presence. It is likely that primates are somewhat idiosyncratic in their response to humans. Two processes of habituation have been initiated on populations of baboons: *Papio anubis* in the 'Parc National de la Comoé' in Ivory Coast and *Papio papio* in an open area of northwestern Guinea. We carried out a crossed analysis of field data using ethological and anthropological methods. Ethological methods enabled statistical testing of certain indices – such as the baboons’ first reaction to observers or flight distance – used to evaluate the habituation level of primates to observers. Results show that indicators can be influenced by many variables. Using behavioural measures as a crude index of habituation has a number of potential limitations. It seems important to reconsider these indicators regarding species-specific traits (preferential habitat use, anti-predator behaviours or social cohesion). Individual variability to the presence of an observer seems to depend on social organisation, and, in some way, on the interaction patterns of baboons. We considered the degree of similarity between patterns of intraspecific interactions and those of interspecific relationships. The use of anthropological methods offers a new understanding of habituation, defined in a relational perspective which allows one to understand how both human observer and non-human primate adjust their behaviours to each other. We defined the forms and dynamics of interactions between human observer and baboons. The articulation between structural and cognitive aspects of the interspecific interaction is questioned: we analysed how humans and baboons use physical and social behaviour in order to adapt their actions to the context of the encounter.

**Environmental Enrichment and the Welfare of Laboratory Macaques**

Lukáš Jebavý, Pavel Kubček, Martina Kuncová, Lucie Libichová  
a Czech Agricultural University, Prague, b Lukas Jebavy Consulting, Kolin, Czech Republic  
E-Mail: lukas@jebavy.cz

**Key Words:** Macaques • Environmental enrichment

From findings based on observations of rhesus macaques (*Macaca mulatta*) in the laboratory and of Barbary macaques (*Macaca sylvana*) in a zoo, with access to an outdoor enclosure with different types of enrichment, we can say that enrichment of the cages results in increased activity. However, to be really effective, many types of enrichment must be used because ma-
Chimpanzees will quickly lose interest in toys. In a zoo, the primates usually have room to move around and they have a reasonable social environment. In contrast, in most instances, laboratory conditions cannot provide the full natural species-specific behaviour of animals, because there are limitations imposed due to the needs of the many different experimental set-ups. However, though these experiments are an inevitable part of research work, especially in medicine, it is still necessary to continually improve the environment of the laboratory animals.

‘Human and Primates in Perspective’:
A Team Research Project in Europe and West Africa
Frédéric Joulian
Programme de Recherches Interdisciplinaires ‘Evolution, Natures et Cultures’, SHADYC, (UMR 8562, CNRS-EHESS) Sociologie, Histoire et Anthropologie des Dynamiques Culturelles, Centre de la Vieille Charité, Marseille, France
E-Mail: frederic.joulian@ehess.fr

Key Words: Cultural heritage · Natural heritage · Social sciences

This presentation will report the different lines of work we have developed since 2001 at the interface of social and biological sciences. Mostly, our field research is concerned with working on the interactions between non-human primates and humans, in different time scales, cultures and social surroundings. First, our main concern is to unfold and to explain paradoxes we have revealed between anthropological data (from prehistory, paleoanthropology or social anthropology) and behavioural data (from ethology and ecology of primates). Our second concern is to collect information from history, sociology, ethnology, archaeology, ethology and ecology with the aim of reintroducing historical and sociological factors into the phylogenetic debate, which, increasingly, artificially separates biological ideas from cultural ones. Different concepts (‘sociality’, ‘culture’, ‘imitation’, ‘intentionality’) migrate from one field to another without any idea of the history or meaning of their original use. In many respects, nowadays, they are used in a very inadequate and ineffective manner. For example, the culture concept is extensively used in ethology but refers to a remote idea that was largely abandoned in anthropology in the sixties. Sociobiology seems to ignore the complexity of ecological and historical dimensions of primate communities, although ethnographic and sociological studies continue to widen the range of ideas and attitudes toward nature and animals. Here, our attempt is to illustrate that evolutionary anthropology is possible, as long as it is based on empirical studies, and we link social and behavioural sciences to the same scientific goal. West African examples will be used and compared to European concepts of animals and humanity and discussed in relation to the questions of conservation and administration of our natural and cultural heritage.

Chimpanzees Know What Others Have Seen but Not What Others Believe
J. Kaminski, J. Call, M. Tomasello
Max Planck Institute for Evolutionary Anthropology, Department of Developmental and Comparative Psychology, Leipzig, Germany
E-Mail: kaminski@eva.mpg.de

Key Words: Chimpanzee · Children · Mental state · Belief test

What chimpanzees understand about other individuals’ mental states is a highly debated issue. The hallmark for the presence of true mental state attribution is surely false belief...
understanding. In our study, the behaviour of chimpanzees and six-year-old children in a non-verbal false belief test was compared. In the current paradigm, two individuals (subject and competitor) sit opposite each other. Between them is a board which can be slid back and forth between the two individuals. Three cups are placed on this board (one of them potentially containing a high quality reward (e.g. banana)) and one cup is placed on an additional board next to the subject (containing a low-quality reward (e.g. apple)). Both individuals have visual access to the initial baiting of the high-quality reward. After that, the high-quality reward is re-placed. During this final baiting, two factors (knowledge state of the competitor as well as type of manipulation of the reward) were systematically varied resulting in the competitor having either a true or a false belief about its final location. After the baiting was completed, the competitor chose first and out of view of the subject. After that the subject could decide between the cup where she had last seen the reward or, anticipating that the high-quality reward will be gone, the cup which contained the low-quality alternative. The chimpanzees’ choice was mainly based on the competitor’s visual access to the final baiting and they did not differentiate between conditions in which the competitor’s knowledge about the reward’s final location was true or false. The behaviour of the children was different from that of the chimpanzees as they significantly preferred the cup where they had last seen the reward in the condition in which the competitor’s knowledge about its location had been false.

The Social Organisation of Sifakas (Propithecus verreauxi) at Kirindy Forest

Peter Kappeler
Department of Behavioural Ecology and Sociobiology, German Primate Centre, Göttingen, Germany
E-Mail: pkappel@gwdg.de

Key Words: Sifaka · Social organization · Life history · Kirindy

The social organisation of a species is defined by the size, composition, cohesion and genetic structure of a social unit. For most primates, the relevant social unit is the group they currently live in. Because group-living evolved independently among the primates of Madagascar, information on lemur social organisation can contribute important comparative perspectives on general principles of primate socio-ecology. One general aim of this ongoing field study is to characterise the social organisation of Verreaux’s sifakas (Propithecus verreauxi) by combining demographic, life history and genetic data. Individually known subjects from 10 groups of sifakas at Kirindy forest have been regularly observed since 1995, so that nearly all births, deaths, immigrations and emigrations can be precisely timed. Moreover, genetic analyses of mitochondrial and nuclear DNA yield information on paternity and matrilineal ancestry. In this talk I will present data on the size and composition of sifaka groups, characterise their genetic structure and outline male and female life histories. Because sifakas are characterised by even adult sex ratios, the presence of single matrilines and occasional female transfer, I will discuss why these features may differ from the modal pattern among anthropoid primates.
Ground-Nesting in the Chimpanzees (Pan troglodytes verus) of the Nimba Mountains, Guinea, West Africa: New Findings

Kathelijne Koops\textsuperscript{a}, Tatyana Humle\textsuperscript{b}, Elisabeth H.M. Sterck\textsuperscript{c}, Tetsuro Matsuzawa\textsuperscript{d}

\textsuperscript{a}Department of Biological Anthropology & Leverhulme Centre for Human Evolutionary Studies, University of Cambridge, Cambridge, UK; \textsuperscript{b}Department of Psychology, University of Wisconsin, USA; \textsuperscript{c}Department of Behavioural Biology, University of Utrecht & Ethology Research, Animal Science Department, Biomedical Primate Research Institute, Utrecht, The Netherlands; \textsuperscript{d}Primate Research Institute, University of Kyoto, Kyoto, Japan

E-Mail: kk370@cam.ac.uk

Key Words: Chimpanzee \cdot Pan troglodytes verus \cdot Ground-nesting \cdot Ecology \cdot Nimba Mountains

Chimpanzees of the Nimba Mountains (Pan troglodytes verus) commonly make both elaborate (‘night’) and simple (‘day’) nests on the ground. We investigated whether ecological or social factors influence ground-nesting in Nimba. We tested two ecological hypotheses: (1) Climatic conditions, such as higher wind speeds at higher altitudes, might deter chimpanzees from nesting in trees; (2) lack of appropriate arboreal nesting opportunities might drive the chimpanzees to nest on the ground. Third, we explored possible social correlates of ground-nesting. We investigated whether ground-nesting might be a sex-typical pattern and we investigated the spatial association between tree and ground nests. Data were collected between August 2003–May 2004 and March–August 2006. Quadrats (20 × 20 m) were marked around ground nests to assess tree availability. Two weather stations at low and high altitudes provided data on rainfall and wind speed. The sex of ground-nesting individuals was determined using DNA extracted from hair samples. Occurrence and distribution of ground nests were neither affected by climatic conditions nor by a lack of appropriate nest trees. Ground-nesting appears to be a sex-biased behaviour, as males built over 90% (15/16) of ground nests. Moreover, ground nests were made closer to tree nests than tree nests were to other tree nests within the same nest group. These results support the hypothesis that ground-nesting in Nimba is socially, rather than ecologically, determined.

Nesting Height Selection in Male and Female Chimpanzees (Pan troglodytes schweinfurthii) in Kibale Forest NP, Uganda

Kathelijne Koops\textsuperscript{a}, William C. McGrew\textsuperscript{a}, Ian C. Gilby\textsuperscript{b}, Richard W. Wrangham\textsuperscript{b}

\textsuperscript{a}Leverhulme Centre for Human Evolutionary Studies and Department of Biological Anthropology, University of Cambridge, Cambridge, UK; \textsuperscript{b}Department of Biological Anthropology, Harvard University, Cambridge, MA, USA

E-Mail: kk370@cam.ac.uk

Key Words: Chimpanzee \cdot Pan troglodytes schweinfurthii \cdot Nest-height \cdot Social factors \cdot Kibale Forest

Nest-building is a universal behaviour in wild chimpanzees, which usually takes place up in the trees. Nesting height selection in chimpanzees may be affected by a number of ecological factors (e.g. predation pressure, thermoregulation, anti-vector strategy). In addition, social factors (e.g. sex, age, nest group composition) may influence nesting height variation between individuals. For example, ground-nesting at Nimba (Guinea) appears to be a sex-specific behaviour performed mainly by males (Koops et al., 2007). Surprisingly, sex differences in chimpanzee nesting height remain to be investigated on a functional level. We set out to explore a possible sex difference in nesting height and to address the effect of social factors on male and female nesting heights in the
chimpanzees (*Pan troglodytes schweinfurthii*) in Kibale Forest National Park in Uganda. We used the long-term data set on these habituated chimpanzees and analyzed 5 years of (night) nesting data from the period 1996–2006. We examined the effects of sex, age and reproductive status, as well as the effect of nest group composition on the nesting height of both male and female chimpanzees. Our results show that nest-building appears to be a flexible behaviour, and social factors seem to play a more prominent role in nesting height selection in chimpanzees than previously thought.

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**Self-Regarding Consolers – Chimpanzee Post-Conflict Third-Party-Initiated Affiliation Benefits the Affiliators**

Sonja E. Koski\(^a\), Elisabeth H.M. Sterck\(^a,b\)

\(^a\)Utrecht University, Department of Behavioural Biology, Utrecht, \(^b\)Ethology Research, Department of Animal Science, Biomedical Primate Research Institute, Rijswijk, The Netherlands

E-Mail: koski.sonja@gmail.com

**Key Words:** Chimpanzee • Affiliation • Aggression • Conflict • Consolation

Chimpanzees (*Pan troglodytes*) exhibit third-party-initiated affiliation (a.k.a. consolation) to former participants of an aggressive conflict. This triadic affiliation is usually assumed to benefit the recipients of affiliation, and it is suggested that it is evoked by affiliators’ empathic response to conflict participants’ distress. Yet the function and the cognitive mechanism of third-party-initiated affiliation are unknown. Recently we found that third-party-initiated affiliation may not benefit the recipients the way it has been assumed to. We tested an alternative hypothesis, addressing whether affiliation benefits the affiliators by protecting them from further aggression by conflict opponents. We studied a colony of chimpanzees in the Arnhem Zoo, The Netherlands with the standard PC-MC method. We found support for the ‘self-protection hypothesis’, in that affiliators targeted specifically those opponents who were more likely to direct further aggression to them, and affiliation significantly decreased the affiliator’s chance of receiving post-conflict aggression. Third-party-initiated affiliation thus provided an effective self-protection strategy. The self-protection function applied to most third-party-initiated affiliation events. However, a subset of affiliation, provided to victims by their own kin, may reflect reasons other than self-protection, since kin received redirected aggression significantly less often and yet they frequently affiliated with victims. These results provide evidence for a direct self-benefit for affiliators, contrasting the previous assumption of the benefit for the recipients. In addition, the results question the hypothesis of cognitive empathy prompting the behaviour, with the possible exception of kin-associated affiliation.

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**Influences of in vivo Joint Load History on the Form of the Shoulder Joint in Cercopithecid Primates**

C. Krause, M.S. Fischer, M. Schmidt

Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Germany

E-Mail: co.krause@uni-jena.de

**Key Words:** Cercopithecid • Glenohumeral joint • Humeral head • Bone density

Previous studies of the shape and size of the glenohumeral joint in cercopithecids showed remarkable differences in the curvature of the humeral head. Whereas terrestrial species like *Theropithecus* and *Papio* show a cranial and caudal flattened surface area, other more arbo-
real species show a more spherical joint surface curvature with a flattened surface in the centre of the surface area. To investigate the relationship between curvature of the shoulder joint and locomotor dynamics at joint loading, the bone mineral density was examined by using computed tomography. This is a validated method for determining in vivo load history for individuals. Greater compressive loads result in a relatively greater subchondral bone density. It is hypothesized that differences in the curvature are correlated to differences in subchondral bone density. *Theropithecus* and *Papio* are habitually terrestrial although able to move arboreally, the loading forces are higher in the forelimbs compared to habitually arboreal species, which are able to shift their loads more posteriorly. In terrestrial species, compressive loading forces are concentrated more locally. This results in a local increase in bone density which therefore effects the curvature of the humeral head. More arboreal species deductively show a more diffused pattern of bone density.

**Feeding Ecology and Seed Dispersal of Pigtail Macaques (Macaca nemestrina) in Khao Yai National Park, Thailand**

Alice Latinne*, Marie Claude Huynen*, Tommaso Savini*, b

*University of Liège, Faculty of Science, Department of Environmental Science and Management, Biology of Behaviour Unit, Liège, Belgium; bKing Mongkut’s University of Technology Thonburi, School of Bioreources and Technology, Conservation Ecology Group, Bangkok, Thailand

E-Mail: marie-claude.huynen@ulg.ac.be

**Key Words:** Pigtail macaques • Seed dispersal • Feeding ecology • Frugivory • Germination

Seed dispersal has a profound influence on structure and diversity in tropical environments. Although all frugivorous primates disperse seeds, the contribution to forest regeneration of dispersal by some species is still being discussed. For instance, baboons and macaques are controversially described as seed dispersers or as seed predators. We studied the seed dispersal by a troop of pigtail macaques (Macaca nemestrina leonina) in the Khao Yai National Park (Thailand) in order to describe the mode of seed dispersal and the fate of the seeds of each fruit species consumed by macaques, including the assessment of potential germination enhancement of dispersed seeds. Pigtail macaques disperse seeds either via faeces, by swallowing seeds, or via cheek pouch storage, by spitting out seeds after processing the fruits in the mouth. Preliminary results of our study show that pigtail macaques in the study troop disperse the seeds of at least 15 species. For some species (Nephelium melliferum, Baccaurea ramiflora), macaques use the 2 modes of seed dispersal simultaneously. While some of the seeds excreted are intact and viable, as shown by the cut test, some are destroyed during mastication and digestion, and therefore it seems that macaques are to be considered as both seed dispersers and predators. The size of dispersed seeds ranges from the largest defecated seed (Nephelium melliferum) at 22 mm long and 13 mm wide to the smallest (Dissocheta divaricata) less than 1 mm long and 0.5 mm wide. In the future, the Tetrazolium test will also be used to assess seed viability, and the germination enhancement for seeds defecated or spat out will be assessed using a germination test. Germination rate and germination delay will be compared for defecated, spat-out and control seeds. The last are seeds from non-consumed fruits collected from trees foraged in by the macaques.
Anthropological Dimensions of Spatial Interactions between Chimpanzees and Humans – A Case Study from the Boké Region, Northwestern Guinea

Vincent Leblan
Interdisciplinary Research Programme ‘Evolution, Natures and Cultures’, Paris, France
E-Mail: vincent.leblan@free.fr

Key Words: Chimpanzee • Fula • Landuma • Boké • Guinea

Chimpanzee societies occur in a wide range of ecological contexts, from tropical lowland forests to dry and sparsely wooded savannas, which have, historically, been shaped by human activities. Although this has already been acknowledged as an evolutionary problem (Sept and Brooks, 1994), it has seldom been taken into account in ethological and ecological studies of chimpanzee behaviour. But human-induced environmental change can no longer be separated from what has been construed as a chimpanzee realm driven by natural forces, whether for theoretical reasons or for conservation matters. This field study was conducted in two different village sites (in 2003–2004 and 2005), in areas open to interactions with Fula and Landuma farmers of the region of Boké (Northwestern Guinea). The analysis of local land tenure practices and of the spatial distribution of human subsistence activities allows us to deal with social uses of ‘nature’. Ethological data were collected from unhabituated chimpanzee communities, working from their material traces (nests, feeding remains, faeces, drumming locations), collected using two sampling methods: systematic (transects) and opportunistic (ad libitum). They were analyzed in their ethnohistorical context using remote sensing technology and GIS (Geographic Information Systems) methods. Confronted with data collected in protected areas, we suggest that this kind of approach can provide useful insights into primate adaptation processes and by correlation into conservation matters. Data analysis revealed unexpected adaptation capacities in chimpanzees, both demographically and spatially speaking. Population densities were equal or higher than those found in the nearest protected areas. Chimpanzees were also found to exploit a much wider range of environments than the gallery forests that they are usually thought to prefer in open habitats.

How Does a Bonobo Mother (Pan paniscus) Manage a Conflict between Her Son and One of Her Female Coalition Partners?

L. Legraina, L. van Eilsackerb, J. Alegria Iscoa
aDepartment of Psychology, Université Libre de Bruxelles, Bruxelles, bCentre for Research and Conservation, Royal Zoological Society of Antwerp, Antwerp, Belgium
E-Mail: lalegrai@ulb.ac.be

Key Words: Bonobo • Hierarchy • Conflict • Coalition • Pan paniscus • Social organization

In bonobos (Pan paniscus), females form coalitions in such a way that they always have the upper hand over the males; and mothers play a significant part in the male hierarchy by supporting their sons. With such a social organization, an interesting question arises: what will be the reaction of a mother in the case of a conflict between her son and a female with which she forms a coalition? We made the assumption that in these situations the mother would have a conflict of interest and so would not intervene. For two months, we observed a captive group of eight bonobos in the Planckendael Animals Park (Belgium). We used ‘all occurrence sampling’, watching the group from when they woke up until they went to sleep and observed that the bonobo mother always supported the female with which she forms a coali-
From a cognitive point of view, this support could be ‘bluff behaviour’ by the mother who could thus avoid her son being injured by the female. By supporting the female, the mother takes the lead in the conflict and limits the agonistic behaviours. Indeed, when the mother does not intervene in these conflicts, the reaction of the female partner towards her son is much more violent. So, by supporting the female partner with moderated agonistic behaviour, the mother achieves the protection of her son.

Explaining the Despotic/Egalitarian Continuum: A New Model

Hagen Lehmann, Joanna J. Bryson
Artificial Models of Natural Intelligence, University of Bath, Bath, UK
E-Mail: h.lehmann@cs.bath.ac.uk

Key Words: Despotism · Egalitarianism · Hierarchy · Reconciliation · Affiliation

The despotic/egalitarian continuum, first described by van Schaik (1989), describes a difference in primate social organization documented in a wide variety of species. ‘Despotism’ is characterized by strict dominance hierarchies, infrequent but violent and normally unilateral conflict. ‘Egalitarianism’ is characterised by looser hierarchies that are ill-defined under the top few animals, more frequent but less-violent and frequently bilateral aggressive interactions, and a significantly higher frequency and variety of reconciliation behaviours after conflict. In egalitarian species, reconciliation also happens between non-kin. There are many theories about the origin of these different social styles, each hinging on a different characteristic of the continuum. Hemelrijk (1999) suggests that environmental stress leads to greater violence in some species, which in turn required a more structured society, while de Waal and Johanowicz (1993) suggests that the learning or evolution of reconciliation behaviours by some species allowed for a reduction in violence and in turn reduced selective pressure on strict hierarchies. After extensive literature review we have developed an ecological theory of this continuum. We have also supported our theory through artificial life (agent-based modelling) software simulations. Our simulations are freely available over the internet. We believe the primary selective pressure is simply distance between animals – which is far greater in despotic species than in egalitarian. Where predation is not a severe risk, distance is an advantage as it allows each animal greater resources. However, where there is predation pressure, the ability to stay close together is adaptive. Thus greater violence (forcing neighbours apart) or a drive for reconciliation and affiliation (bringing neighbours near) may be more adaptive depending on the ideal intra-animal distance for a particular ecosystem. When food resources are not evenly distributed or are monopolizable (e.g. fruit trees), despotism also derives extra advantage. Early simulation results also show differences in the selective advantage of being a dominant animal in the various conditions.

Innovation in Orangutans

Stephan Lehner, Judith Burkart, Carel van Schaik
Anthropological Institute, University of Zürich, Zürich, Switzerland
E-Mail: slehner@aim.uzh.ch

Key Words: Orangutan · Novel behaviour · Learning · Innovation · Culture

When a novel learned behaviour spreads through a population by social learning, typically a single individual will have initiated this diffusion. Thus, this diffusion requires two processes: (1) the novel behaviour is invented by an individual, which is described as an innovation;
(2) the innovative behaviour spreads in the population between individuals by social learning. In contrast to social learning, innovation, as the first step in the chain eventually leading to culture, has not received a similar amount of attention. This is likely to be explained by the difficulty of assessing whether an observed behaviour is an innovation. Van Schaik et al. (2006) developed two criteria to distinguish behavioural innovations from other behaviour patterns. For a behaviour to be an innovation, we expect it to be non-universal, which means it is completely lacking in some populations, or if it occurs in all populations, then it is found at low prevalence, shown by a few individuals only; and second, individuals that do not perform the behaviour do so because they do not know it. On the basis of these criteria, we aimed to verify the list of behaviours classified as innovations in wild orangutans. In a comparative zoo study, we assessed which of these innovative behaviours occurred spontaneously in several captive populations, and which could be induced experimentally. Further we aimed at characterizing the innovative individuals in terms of age, sex, and social rank. So far this question has been addressed by Reader and Laland (2001), who searched the literature for examples of innovation. They found the reported incidences of innovation in primates to be higher in males and adults and in individuals of low social rank. In contrast, our preliminary results from behavioural observations of captive orangutans suggest that innovators are those with a high social rank.

**EUPRIM-NET – European Primate Network: Establishing Specialized Infrastructures and Procedures for Biological and Biomedical Research**

Ines Lein, Stefan Treue, Robert Teepe

German Primate Centre, Göttingen, Germany

E-Mail: euprim@dpz.eu

**Key Words:** Primate network · EUPRIM-NET · Europe

The Integrated Infrastructure Initiative Project EUPRIM-NET networks eight publicly funded European primate centres that combine research and breeding. Due to the multitude of biological and biomedical research activities carried out, these centres bring together extensive research resources as well as substantial experience in primate housing and breeding. The intention is to expand the network to include even more partners. The project aims to improve the ability of its eight partners to provide the best services and to support the best science that meets the highest ethical standards for primate-based animal research. With this aim in mind, the project has the following central objectives:

- The optimization of non-human primate husbandry and reproduction, taking into considering animal welfare and ethical guidelines.
- The development and provision of training courses for researchers and caretakers working with primates.
- The development and standardisation of procedures and methods for the use of non-human primates in biomedical research.
- The improved access to non-human primates of high quality and to primate material for biomedical research.

These central objectives will be met through network activities, access activities and research activities as follows. **Network Activities:** These will take the form of workshops and specialised training courses for scientists and other staff involved in primate research. The idea is to develop best practice methods and procedures and advance their standardisation across Europe. **Access Activities:** A biobank will be established providing access to biological material from primates to external users. The collection will comprise tissue, DNA, RNA, cDNA, serum, and cell lines from healthy as well as diseased animals. Users or user groups will be able to apply for samples via the internet. PRIMOCID will offer access to non-human primate models of chronic immune disorders. **Research Activities:** Two research programmes focus on the viral
and microbacterial state and the genetic profile of the primates bred and housed at European primate centres, as well as imported animals. Detailed knowledge of individual animals is critical, particularly for infection studies the success of which depends on the availability of animals with a defined viral, microbacterial and genetic status. Telemetric monitoring devices will be developed in a third research programme.

All of these activities make a major contribution to the 3R-concept (Refinement, Reduction, Replacement). More information can be found at: www.euprim-net.eu.

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**Use of Two Specialized Fingers in Aye-Ayes (Daubentonia madagascariensis) in Madagascar**

Stanislav Lhota\(^a\), Tomáš Jůnek\(^b\), Aleš A. Kuběná\(^b\), Luděk Bartoš\(^b\)

\(^a\)Department of Zoology, Faculty of Biological Sciences, University of South Bohemia, České Budějovice, \(^b\)Ústí nad Labem Zoo, Ústí nad Labem, Czech Republic

E-Mail: stanlhota@yahoo.com

**Key Words:** Aye-aye • Daubentonia madagascariensis • Madagascar • Finger use

The aye-aye (Daubentonia madagascariensis) is a lemur with highly specialized hands. Two of its fingers, the third and fourth, are used in a way not paralleled by any other primate. We observed finger use in various activities in four free-ranging aye-ayes on an island in a river near Mananara-Nord. The thin third finger was used exclusively or preferentially for tapping, cleaning teeth and probing for nectar, kernels and insects in bamboo, twigs and in live wood. In contrast, the robust fourth finger was used preferentially when eating jackfruit and probing for invertebrates in soft plant tissues. In dead wood, both fingers were used in similar proportions. To extract coconut flesh, the two fingers were apparently used for different tasks. We conclude that the third finger is specialized for tasks requiring high mobility, sensitivity and precision, whilst the fourth finger is specialized for tasks requiring strength, a scooping action and deep access. We compare the use of the specialized fingers in aye-ayes with analogous adaptations in two other mammalian groups, the stripped possums of New Guinea and Queensland and the Early Tertiary apatemyids of Europe and North America.

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**Play and Aggression in Orphan Chimpanzees at Chimfunshi Wildlife Orphanage, Zambia**

Diana Lisensky

Oxford Brookes University and Chimfunshi Wildlife Orphanage, Oxford, UK

E-Mail: lisendi@earlham.edu

**Key Words:** Chimpanzee • Sanctuary • Conservation • Aggression • Chimfunshi • Zambia

Chimfunshi Wildlife Orphanage Trust in Zambia provides sanctuary for over 100 chimpanzees confiscated from poachers or rescued from inhumane conditions around the world. While sanctuaries are often lauded as the way forward in primate conservation, behavioural studies of chimpanzees in sanctuaries are sadly lacking. In this study, 8 orphans and 9 non-orphans between the ages of 4–9 were observed and occasions of Lone Play, Social Play and Play Aggressions were recorded for each group. The orphan group was found to have higher levels of all categories than the non-orphans. This difference is probably a result of the rougher play
the orphans engaged in due to the absence of mothers. This may indicate higher levels of stress
for the orphan group, though with non-orphans exhibiting lower levels of these play categories,
the behavioural difference may be self-corrected by the second generation of captive individ-
uals.

Prevalence and Genetic Diversity of Simian Immunodeficiency Virus Infection in Wild Red Colobus Monkeys (Piliocolobus badius badius) from the Taï Forest, Côte d'Ivoire

Sabrina Locatelli, Florian Liegeois, Bénédicte Lafay, Amy D. Roeder, Michael W. Bruford, Pierre Formenty, Ronald Noé, Eric Delaporte, Martine Peeters

a UMR 145, Institut de Recherche pour le Développement (IRD), and University of Montpellier 1, b UMR CNRS-IRD 2724, Montpellier, France; c Cardiff School of Biosciences, Cardiff, UK; d Ebola Taï Forest Project, Abidjan, Côte d’Ivoire, and WHO, Department of Communicable Diseases, Surveillance and Response (CDS/CSR), Geneva, Switzerland; e Ethologie des Primates (DEPE-IPHC-CNRS UMR 7178) and University of Louis Pasteur, Strasbourg, France

E-Mail: sabriloc@hotmail.com

Key Words: Piliocolobus badius · Simian immunodeficiency virus · Taï Forest

Numerous African primates are infected with simian immunodeficiency viruses (SIVs) and it is now well established that the clade of SIVs infecting west central African chimpanzees (Pan troglodytes troglodytes) and western gorillas (Gorilla gorilla gorilla) represent the progeni-
tors of human immunodeficiency virus type 1 (HIV-1), whereas HIV-2 results from different cross-species transmissions of SIVs from sooty mangabeys (Cercocebus atys atys). We present here the first molecular epidemiological survey of simian immunodeficiency virus (SIVwrc) in wild western red colobus monkeys (Piliocolobus badius badius). These colobus are frequently hunted by the human population and represent a favourite prey of western chimpan-
zees (Pan troglodytes verus). Faecal samples (n = 88) were collected and individual discrimina-
tion was assessed by microsatellite analyses and visual observation. The inferred 53 adult indi-
viduals belonging to two neighbouring habituated groups were tested for the presence of SIVwrc infection by viral RNA (vRNA) detection. Viral polymerase (pol) (650 bp) and/or envelope (env) (570 bp) sequences were amplified in 14 individuals, resulting in a minimal prevalence of 26% among the individuals sampled. With a few exceptions, phylogenetic analysis of pol and env sequences revealed a low degree of intragroup genetic diversity and a general viral clustering related to the social group of origin. However, a higher intergroup diversity was found. Behavioural and demographic data collected previously from these communities indicate that red colobus monkeys live in promiscuous multi-male societies, where females leave their natal group as subadults and where extra-group copulations or male immigration have rarely been observed. The phylogenetic data we obtained seem to reflect these behavioural characteristics. Given the suspected high SIV prevalence among this species, the frequent association with other monkey species, the predation pressure exerted by chimpanzees and by poachers around and inside the park, simian to simian and simian to human SIVwrc cross-species transmission cannot be excluded.
**Parasite-Mediated Sexual Selection in Primates?**

_The Effect of Intestinal Parasites on the Reproductive Success of Wild Lemurs (Eulemur fulvus rufus)_

Dagmar Lorch*, Peter M. Kappeler*, Michael Heistermannb, Lutz Walterc

*a Abteilung Verhaltensökologie and Soziobiologie, b Abteilung Reproduktionsbiologie, c FG Primatengenetik, Deutsches Primatenzentrum, Göttingen, Germany

E-Mail: dlorch@gwdg.de

**Key Words:** Eulemur fulvus rufus • Sexual selection • Parasites • Endocrinology

Parasites are a driving force in sexual selection, but they can have negative impacts on their hosts. Hence, females should choose mates displaying good health and an ability to resist parasite infections. Assuming a genetic basis for parasite resistance, partners with low parasite infections should be preferred over others in order to obtain resistance genes for their offspring (parasite-mediated sexual selection). With our interdisciplinary approach we will contribute to understanding both determinants of individual parasite infections and mechanisms of parasite-mediated sexual selection in primates. Specifically, we analyse faecal samples of free-ranging red-fronted lemurs (Eulemur fulvus rufus) to characterise their intestinal parasite fauna by means of the formalin-ethyl-acetate sedimentation technique. Parasite infections are being correlated with (1) genetic correlates at the interleukin-4 locus, which is involved in parasite resistance, (2) proximate endocrine factors (testosterone and cortisol) that co-vary with the functioning of the immune system, and (3) socio-demographic data, such as sex, age and population group size of the hosts that may influence parasite infestations. Moreover, we examine whether primates use honest signals, such as conspicuous colourations, in order to assess their mate’s genetic quality. Using data from paternity analyses of the study population, we will be able to link parasite infection with reproductive success of males with different genetic and endocrine constitutions. As data collection was just about finished at the start of this conference, the presentation will give an overview of the project and present preliminary data.

**Spatial Memory in Grey Mouse Lemurs (Microcebus murinus)**

Mia-Lana Lührsa, b, Melanie Dammhahnb, Claudia Fichteb, Peter M. Kappelera, b

a Department of Sociobiology & Anthropology, University of Göttingen, b Department of Behavioural Ecology & Sociobiology, German Primate Centre, Göttingen, Germany

E-Mail: mia-lan@gmx.de

**Key Words:** Microcebus murinus • Spatial memory

In the wild, primates and other animals face the challenge of locating feeding sites distributed across broad spatial and temporal scales. Spatial memory allows animals to find a goal, such as a productive feeding patch, even when there are no goal-specific sensory cues available. Because there is little experimental information on learning and memory capabilities in free-ranging primates, the aim of this study was to test whether grey mouse lemurs (Microcebus murinus), as short-term dietary specialists, rely on spatial memory in relocating productive feeding sites and what kind of spatial representation might underlie their way of orientation in their natural environment. We used an experimental approach and set 8 free-ranging M. murinus a memory task by presenting them with two different spatial patterns of baited and non-baited artificial feeding stations under exclusion of sensory cues. Positional data was recorded by focal animal observation of radio-collared individuals within a grid system of small foot trails. A change in the baiting pattern revealed that M. murinus primarily
used spatial cues to relocate baited feeding stations and that they were able rapidly to learn a new spatial arrangement. Spatially concentrated, non-random movements revealed preliminary evidence for a topological restriction in mouse lemur space; the exact kind of spatial representation, however, remained unclear. Based on a high travel efficiency found in this study, we propose that mouse lemur spatial memory is based on some kind of mental representation that is more detailed than the route-based network of a topological map.

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**Interspecies Communication with Gorillas Reveals Advanced Cognitive Abilities and Thought Processes: Longitudinal Study of Acquisition and Usage of American Sign Language by Western Lowland Gorillas**

Susan Lutter

Director of Strategic Alliances, The Gorilla Foundation, Woodside, CA, USA

E-Mail: susan.lutter@koko.org

**Key Words:** Gorilla · Gesture · Communication · American Sign Language

The spontaneous use of untaught gestures by zoo-living gorillas suggests that gestural communication is an innate ability of gorillas and that apes and humans share an advanced talent for mapping action mentally and reproducing it physically in communication. A 35-year study of interspecies communication between gorillas and humans using American Sign Language (ASL) has demonstrated gorillas’ ability to understand the concept of gestural language as a representation of objects, actions and ideas, and to use that language to participate in meaningful two-way communication with humans. This shared ability for gestural communication provides significant opportunities for improving the quality of care for gorillas in captivity.

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**Sociality and Stress in Macaques and Baboons**

A.M. MacLarnon¹, S. Semple², K. Shutt³, M. Heistermann⁴, J.P. Higham⁵

¹School of Human & Life Sciences, Roehampton University, London, UK;
²Department of Reproductive Biology, German Primate Centre, Göttingen, Germany

E-Mail: a.maclarnon@roehampton.ac.uk

**Key Words:** Grooming · Stress · Barbary macaque · Papio hamdyras anubis · Social relationships

The primary role of grooming in primates is generally thought to be the servicing of social relationships, whereby the grooming of other individuals can be traded for social support or other services. It is commonly assumed that being groomed by another animal is relaxing or stress-reducing, and there is some evidence from captive studies of such effects over the short term. We recently presented results of a study of female Barbary macaques (*Macaca sylvanus*) in Gibraltar showing that medium-term physiological stress levels, measured as faecal concentrations of cortisol metabolites, were correlated with the amount of grooming given by individuals, but not with the amount of grooming received. In this case, the directionality of benefit from grooming is therefore the opposite from that previously assumed, or demonstrated in captive situations. Here we test the generality of our findings on Barbary macaques by investigating whether similar relationships occur in female olive baboons (*Papio hamdyras anubis*) at Gashaka-Gumti National Park, Nigeria. We also explore grooming behaviour in greater depth in both species in relation to a range of other factors including behavioural as well as physiological measures of stress. We consider our results in the light of dominant ideas about the role of grooming in primate sociality.
Gesture Use in Two Differentially Reared Groups of Infant Chimpanzees

Vanessa Maguire, Kim A. Bard
Centre for the Study of Emotion, Department of Psychology, University of Portsmouth, Portsmouth, UK
E-Mail: chimponaut1@yahoo.com

Key Words: Chimpanzee · Infant · Communication · Gesture use

Due to the high degree of evolutionary similarity between humans and other primates, primate communication has become an emerging area of interest. However, the main emphasis of these studies has been on vocal communication. Here we report on gestural data collected from infant chimpanzees raised in two different groups: (1) a nursery setting in which gestures, postures, facial expressions, and eye gaze of young chimpanzees developed during ‘guided participation’ type interactions with human research assistants especially trained to respond to communicative intentions; and (2) a setting in which infants were raised by their biological mothers within a large group of chimpanzees, with additional daily interactions with human researchers. The focus was on gestures involved in social interactions (e.g., appropriate responses and initiations, which we label as ‘social manners’). Three questions were asked of the resulting data: (1) were there individual differences in the form of the gestures (e.g., did a ‘wrist present’ gesture look the same when exhibited by each of the chimpanzees); (2) were the same behaviours used flexibly across contexts (e.g., was the ‘rump present’ gesture found in submission contexts, as well as feeding, grooming, etc. contexts), and (3) were gestures used similarly across the two groups. All subjects (n = 15) acquired at least 1 variant of submissive ‘social manners’ gestures by the end of their first year of life. Approximately half of the gestures were used flexibly (11 of 20). In some cases, the context in which they were used differed between the groups. The form of the gestures did not differ between individuals. This study provides developmental milestones for social gestures, postures and facial expressions not previously known for captive non-language-trained chimpanzees.

The Differential Use of Gestures in Chimpanzees Based on Their Intended Audience

Vanessa Maguire, Kim A. Bard
Centre for the Study of Emotion, Department of Psychology, University of Portsmouth, Portsmouth, UK
E-Mail: chimponaut1@yahoo.com

Key Words: Chimpanzee · Gesture use · Communication

Recent research on gestures in great apes has included a focus on audience effects. When the intended recipient is looking away, then the initiator of the gesture tends to use more audible ‘attention-getting’ gestures, such as hand clapping or bronx cheers. When the intended recipient is in close proximity or maintaining visual contact, then visual gestures are used, such as extended hand. However, these studies do not address any aspects of the characteristics of the recipient; specifically does the initiator tailor their gesture depending on who is the intended audience? The focus of this study was 3 infant chimpanzees housed with 11 adult chimpanzees (3 males, 8 females) in a large semi-natural enclosure at the Kyoto University Primate Research Institute (KUPRI) in Japan. All manual gestures and the contexts in which they occurred between the focal animal and other group members were recorded. It was determined that the infants gestured more towards adult chimpanzees (focal initiated 303 gestures and received 392;
primarily with the mother and 1 adult female) than towards their same aged peers (focal initiated 161 gestures and received 106; with 2 other infants). The most common gestures and contexts initiated and received by the focal animal were similar with the two audience types. In that the most common gestures and contexts initiated and received between infants and adults overlapped and the same was true for gestures and contexts initiated and received between the focal infant and other infants. In general, the infants tended to use a larger number of gestures and contexts when interacting with the adults than when interacting with other infants. This study shows that chimpanzees, even from an early age, use age appropriate gestures and tailor their gestures based on whom their intended audience is.

**Group Size Effects on Behaviour and Demography in Primates: A Meta-Analysis**

Bonaventura Majolo\(^a\), Aurora De Bortoli Vizioli\(^b\), Gabriele Schino\(^c\)

\(^a\)Department of Psychology, University of Lincoln, Lincoln, UK; \(^b\)Facoltà di Scienze Naturali, Università La Sapienza of Rome, \(^c\)Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy

E-Mail: bmajolo@lincoln.ac.uk

**Key Words:** Primates • Group size • Competition • Fitness • Social behaviour • Predation risk

Socio-ecological theories aim to predict primate social behaviour and optimal group size on the basis of various ecological parameters. Larger groups should be favoured when predation risk and/or between-group contest competition for food is high. Individuals in large groups, however, are expected to face a greater level of within-group food competition. Ultimately, the balance between benefits and costs associated with living in a group of a given size should affect the reproductive success and survival of group members. We used meta-analytical techniques in order to measure the effect of group size on behaviour and individual fitness in primates. To this end, we reviewed the primatological literature from 1940 to 2006 using PrimateLit (http://primatelit.library.wisc.edu). In order to be included in our meta-analysis, papers had to contain data on the behaviour and demography of at least four troops, living in the same habitat, relying on natural food and with data collected within the same time window. One hundred papers met these criteria and were included in the analysis. Group size had a significant effect on daily travel distance: larger groups tend to travel further than smaller groups. Conversely, group size had no significant effect on demography. These results are interpreted in relation to species-specific differences in diet, habitat characteristics and social system.

**Assessing the Impact of Hunting on Harvest-Sensitive Primates within Protected Areas and Indigenous Land in the Colombian Amazon**

Angela Maldonado, Simon Bearder

Oxford Brookes University, Department of Anthropology and Geography, Oxford, UK

E-Mail: amaldonado@brookes.ac.uk

**Key Words:** Lagothrix lagothicha • Alouatta seniculus • Saguinus nigricolis • Subsistence hunting • Conservation • Community

Subsistence hunting has been identified as a global conservation issue not only for the stability of tropical ecosystems, but also for securing the long-term livelihood of local people. In
the Colombian Amazon, long-term studies have revealed significantly low densities of large vertebrates even in unhunted areas. However, little is known about the impact of subsistence hunting within protected areas and on indigenous land. During 2005–2007 primate densities were determined using a transect sampling method. Censuses were carried out in overlapping areas between two Tikuna indigenous communities in Amacayacu National Park, southern Colombian Amazon. Harvest of large mammals was quantified simultaneously in the two indigenous communities. Preliminary results suggest that large-bodied primates such as woolly monkeys (Lagothrix lagothicha) and howler monkeys (Alouatta seniculus) are present in significantly lower densities in comparison with other Amazonian sites exposed to similar levels of hunting and edaphic conditions. In contrast, small-bodied species such as black-mantled tamarins (Saguinus nigricolis) were present in densities comparable to unhunted sites. Encounters with large primates were more frequent in the study sites located in the indigenous territory where a hunting ban for woolly monkeys was implemented as a local initiative. The implications of subsistence hunting for harvest-sensitive primate species are discussed considering their life history traits and ecological constraints. Recommendations for the design of conservation strategies for overlapping areas are examined.

Effect of Human Interaction on the Behaviour of a Colony of Common Marmosets (Callithrix jacchus)

Arianna Manciocco, Augusto Vitale
Section of Behavioural Neuroscience, Department of Cell Biology and Neuroscience, Istituto Superiore di Sanità, Rome, Italy
E-Mail: arianna.manciocco@iss.it

Key Words: Common marmosets • Callithrix jacchus • Environmental enrichment

Human interaction as an environmental enrichment for non-human primates is widely promoted and believed to be of value, but it has been subject to little quantitative evaluation. This study assessed the effects of positive human interaction on the behaviour of a colony of common marmosets (Callithrix jacchus). Subjects were housed indoors in social groups of different sizes and composition. The study was composed of three phases: a first one (baseline condition), where the level of human interaction was represented by routine care and management (i.e. in the process of cleaning, feeding, and monitoring). A second phase (test condition), four weeks long, in which a familiar caretaker spent an additional 20 min per day, five days a week, with each group, interacting actively and positively. A last phase (data recording), in which the test condition was followed by data recording sessions. In order to assess potential durable effects of such interaction outside the testing period, data were collected only when the caretaker was absent. The sampling method used was 30-sec scan sampling, with daily sessions 30 min long. Following the testing period, the marmosets showed an increased level of grooming and playful activities, generally considered signs of increased level of welfare; however, they also showed lower levels of aggressive displays towards the observer, self-scratching and locomotion. A trend towards reduced territorial vocalisations was also observed. These results suggest that simple, unstructured positive interactions between humans and marmoset monkeys should be part of a programme aimed at increasing the level of welfare of captive non-human primates.
Do Enclosures in European Zoos Guarantee Safe Public-Primate Interactions?

O. Martín-Carrera, F. Guillén-Salazar
Unidad de Etología y Bienestar Animal, Facultad de Ciencias Experimentales y de la Salud, Universidad Cardenal Herrera, Moncada (Valencia), Spain
E-Mail: omartin@uch.ceu.es

Key Words: European zoos • Primate enclosure • Visitors

The Directive 1999/22/EC, related to the keeping of wild animals in zoos, requires institutions to accommodate their animals under conditions which aim to satisfy the biological and conservation requirements of the individual species and to prevent escapes. With the aim of analysing the accomplishment of these requirements we evaluated the security of all primate enclosures (192) from 18 zoos which were members of the European Association of Zoos and Aquaria (EAZA), the main professional zoo association in Europe. The zoos are based in Spain (9), Holland (7) and Belgium (2), and represent 75% of the EAZA zoo member institutions with primates in their collections in these countries. The evaluation was done by three trained observers from September 2003 until September 2005. We analyzed the presence of an adequate physical barrier that contains the animals within the desired enclosure, the presence of standoff barriers (or staff in case of walk through exhibits) in order to avoid direct contact between visitors and hazardous animals, and the possibility for members of the public to release the animals from their enclosures. The results reveal that almost 10% of the enclosures do not have an appropriate physical barrier to prevent the escape of the animals and avoid possible ecological threats to indigenous species. We also found that it was possible to establish physical contact with the primates in almost 20% of the enclosures. This physical contact cannot only compromise the animal’s health and its future role in the species’ conservation, but the public’s physical integrity as in 8% of the enclosures it was possible to touch a hazardous species (following EAZA’s criteria). We will aim to present ways in which zoos can improve their fulfilment of the current European legislation regarding the security of primate enclosures.

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How Great Apes Perform in Functionally Equivalent Trap-Tube and Trap-Table Tasks

Gema Martin-Ordas, Josep Call, Fernando Colmenares
Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
E-Mail: ordas@eva.mpg.de

Key Words: Great apes • Tool use • Trap-table • Trap-tube

Using a tool to bring a reward within reach while avoiding a trap is one of the ways in which researchers have investigated animals’ causal knowledge. Previous studies on tool using have shown that certain task features have masked the causal knowledge that subjects may have. However, procedural modifications (e.g. trap-table task) may not only remove task constraints but also simplify the problem conceptually. The goal of this study was to investigate the great apes’ performance in a variation of the trap-table that was functionally equivalent to the trap-tube task. In this platform task, subjects had to decide where to insert the tool and in which direction the reward should be pushed. We also administered a trap-tube task that allowed animals to push or rake the reward with the tool to compare the subjects’ performance on both tasks. We tested six orangutans (Pongo pygmaeus), six chimpanzees (Pan troglodytes),
five bonobos (*Pan paniscus*) and three gorillas (*Gorilla gorilla*). Our results showed that apes performed better in the trap-platform task than in the trap-tube task and tended to be faster solving the platform problem than the tube problem. Subjects solved the tube task faster than in previous studies and they also preferred to rake in rather than to push the reward out. However, there was no correlation in the level of performance between the two tasks. We suggest that apes possess some specific causal knowledge of traps but may lack the ability to establish analogical relations between functionally equivalent tasks.

A Comparative Analysis of Positional Behaviour of Captive Common Chimpanzees (*Pan troglodytes*): Effect of Structural Change in the Enclosure

Richard Marvan\textsuperscript{a,b}, Tomáš Polák\textsuperscript{c}, Hana Marsault\textsuperscript{d}, Jana Kantorová\textsuperscript{d}, Václav Vančata\textsuperscript{b}

\textsuperscript{a}Department of Anthropology and Human Genetics, Faculty of Science, and \textsuperscript{b}Department of Biology and Ecological Education, Faculty of Education, Charles University in Prague, \textsuperscript{c}Premier Research Group, \textsuperscript{d}Czech Radio 2, Prague, \textsuperscript{e}Department of Publicity and Education, Brno Zoo, Brno, Czech Republic

E-Mail: r.marvan@seznam.cz

Key Words: *Pan troglodytes* · Positional behaviour · Arboreal substrate · Environmental enrichment

Proper housing of captive non-human primates is essential for the development of appropriate positional behaviour (PB; i.e., locomotion and posture) patterns that are good indicators for primate welfare. After reconstruction in 2000, Chester Zoo (Cheshire, UK) provided its well-established chimpanzee (*Pan troglodytes*) colony with a complex outdoor yard, which included many structural features and increased vertical spatial opportunities. It had been expected that it would promote species-specific PB patterns and lower aggression. The present study aimed to verify these assumptions. In July of 1999 (i.e., Pre-phase), 2002 and 2003 (i.e., Post-phase), we collected a total of 621 observation hours of behavioural data. 15-min focal animal sampling of juvenile, adolescent and adult chimpanzees of both sexes (*n* = 21 and 24, Pre- and Post-phase, respectively) was used to record frequency of 20 arboreal and terrestrial PB categories in social, play and agonistic contexts. The effect of the structural change in the enclosure was tested using Hierarchical Classification Design of GLM-ANOVA. The results showed that only juveniles’ and adult males’ mean frequencies of PB significantly increased in the Post-phase in comparison with those in the Pre-phase. In contrast, we found a significant decrease in adolescents and no significant difference in adult females. Only juveniles and adolescents used arboreal substrates significantly more often in the Post-phase. Mean frequency ratio of social behaviour on arboreal (vs. terrestrial) substrates was significantly higher in juveniles and adults in the Post-phase. An increase of this ratio for play behaviour in the Post-phase was significant in all age-sex classes, except adult males where a significant decrease was found. Finally, in adults the ratio for agonistic behaviour was significantly lower in the Post-phase compared with that in the Pre-phase. Our findings extend the amount of available information on the importance of exploitable vertical space for chimpanzees and thus may assist managers of captive facilities in providing appropriate housing for our closest living relatives.

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The Role of Subordinate Males in *Propithecus verreauxi verreauxi* in the Kirindy Forest, Madagascar

Vanessa Mass, Peter Kappeler

Department of Behavioural Ecology and Sociobiology, Deutsches Primatenzentrum (DPZ), Göttingen, Germany
E-Mail: vanessamass@hotmail.com

**Key Words:** Sifaka · *Propithecus verreauxi verreauxi* · Group size · Paternity · Sex ratio

In primates, the size and composition of groups have direct consequences for the fitness of their members. Optimal group size and composition is determined by both the costs and benefits of group living. In group-living lemurs there is a tendency towards an even sex ratio in group composition, which is in contrast to what occurs in many anthropoids. Sifakas (*Propithecus verreauxi verreauxi*) are a multi-male multi-female group-living lemur species that show this tendency towards even sex ratio despite a small average number of females per group. Genetic paternity data also suggests high reproductive skew in favour of dominant males. Therefore, although dominant males are able to monopolize reproduction, they don’t exclude subordinate males from group membership. These findings challenge the predictions put forth by sexual selection theory. We have, therefore, focused on social and reproductive tactics of both natal and non-natal subordinate males and the benefits that they may be providing the group by their membership. Preliminary data, based on both demography data collected over a 12-year period and behavioural observations, will be presented, addressing the active role that subordinate males play in relation to group productivity, resource defense and group stability. The aim of this study is to gain a better understanding of the relationships between males within groups and thus enable a greater insight into certain lemur idiosyncrasies.

Post-Conflict Behaviour in Free-Ranging Male Stumptail Macaques (*Macaca arctoides*)

Lieke Mevis\textsuperscript{a,b}, Christin Richter\textsuperscript{a}, Julia Ostner\textsuperscript{a}, Oliver Schülke\textsuperscript{a}

\textsuperscript{a}Integrative Primate Socio-Ecology Group, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; \textsuperscript{b}University of Utrecht, Department of Biology, Behavioural Biology Group, Utrecht, The Netherlands
E-Mail: lieke.mevis@gmail.com

**Key Words:** Stumptail macaques · Reconciliation · Affiliation · Post-conflict · Aggression

Reconciliation (i.e. post-conflict affiliation between former opponents) has been hypothesized to serve in reducing the adverse effects of aggression in group-living animals. The aim of this study was to elucidate post-conflict behaviour in free-ranging male stumptail macaques (*Macaca arctoides*) and to complement previous work on captive groups with few or closely related males. Differences in reconciliation tendency and self-directed behaviour frequencies (as a measure of stress) after a conflict have been hypothesized to depend on the relationship between former opponents, the severity of the conflict and the role of an individual in a conflict. Additionally the influence of spatial distribution on post-conflict behaviour of former conflict partners was investigated. Observations were carried out at Wat Khua Sattayaram Temple, in southern Thailand, which was visited by two macaque groups living on the adjacent forested hills. Seven adult and two sub-adult males of the large 68-member group were observed between December 2006 and March 2007. The post-conflict behaviour of former opponents was observed using 10-min focal animal sampling after 108 male-male
conflicts (PCs); these were matched by time of day with 108 corresponding 10-min focal animal observations in non-conflict situations (MCs). Additionally 421 independent 20-min focal protocols were conducted and used to generate baseline data to supplement the matched controls. Of the 108 conflicts that marked the beginning of a post-conflict observation, 61.1% involved contact behaviours or a chase, 38% formal aggressive and submissive signals and 0.9% were unclear. In 51.4% of the PCs renewed aggression occurred. More than half of all reconciliations occurred within one dyad. Dyads with more than 3 PC/MC observations had a mean corrected conciliatory tendency (CCT) of 16.8 ± 22. The CCT found is relatively low compared to a previous study in stumpetail macaques; however, it is in the range of the CCT found for the more despotic Japanese and rhesus macaques.

The Utility of Real-Time Polymerase Chain Reaction for Molecular Studies on Faecal Samples

N. Morf, H. Morrogh-Bernard, M. Krützen
Anthropological Institute & Museum, University Zürich-Irchel, Zürich, Switzerland
E-Mail: n_morf@aim.uzh.ch

Key Words: Pongo pygmaeus • Polymerase chain • Faecal samples • DNA amplification

DNA amplification of non-invasively collected samples is difficult because of the low DNA content. In order to avoid potentially erroneous results, we used real-time polymerase chain reaction (rtPCR) to pre-screen extracts for the amount of target DNA. In a rtPCR, a target DNA molecule, in this case the c-myc proto-oncogen of Bornean orangutans (Pongo pygmaeus), is simultaneously amplified and quantified. The quantification of the target DNA relies upon the detection of a fluorescent signal, emitted from a probe which is complementary to a part of the c-myc sequence. RtPCR was carried out on 65 non-invasively collected faecal samples. We show that the amount of total DNA in the extract does not correlate with the amount of target DNA. Furthermore, the amount of target DNA in a sample allowed us to estimate the number of repetitions required for genotyping at high confidence levels.

Identifying the Economic and Social Impacts of Crop-Raiding by Non-Human Primates on Local Livelihoods, in Mount Rungwe, Southwest, Tanzania

Nadejda Josephine Msindai
Department of Anthropology and Geography, School of Social Sciences and Law, Oxford Brookes University, Oxford, UK
E-Mail: 06068706@brookes.ac.uk

Key Words: Human-wildlife conflict • Crop-raiding • Management strategy

Examining human-wildlife conflict in communities that live close to wildlife habitats is important because crop-raiding animals can cause substantial damage to agricultural crops (Hill, 2000). Mount Rungwe Forest, in Tanzania, contains the largest population of the newly-discovered species Rungwecebus kipunji (kipunji). Researchers report that colobus (Colobus angolensis sharpei) and kipunji are trapped on farms in response to crop raids (Davenport, pers. comm.). With about 1,000 kipunji remaining in the wild (Davenport, pers. comm.), it is crucial that information is collected on how the activities of primates on agricultural fields are perceived to impact upon livelihoods and economic stability of the local people (Gillingham & Lee, 1999). Fieldwork will be conducted June–July 2007. Information will be collected through semi-
structured interviews with local farmers (Hill, 2000). Interviews will be conducted in Kiswahili with a Tanzanian national acting as a translator. Each household will be asked permission for their participation in the study. It will be clearly indicated to all potential participants that participation is voluntary, and participants are free to withdraw from the project at any point without recrimination. The interviews will: (a) collect demographic information on the population within the study villages, farm sizes and their locations relative to settlements and Rungwe forest; (b) assess primate knowledge amongst those participants interviewed and their current attitudes and perceptions of primates, and (c) identify the perceived impacts on farmers when primates enter the agricultural fields and crop raid. In addition, control methods currently in use by farmers to deter primates from crop raiding will be documented. The results of this study will elucidate the issues surrounding the conflict from the farmers’ perspective, which is important for understanding and thus facilitating human-wildlife coexistence in the region. Thus, the findings will inform the development of a management strategy to mitigate people-primate conflict locally.

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**EUPRIM-Net Provides Courses Dedicated to General Primate Biology**

Britta Müller, Ines Lein, Eckhard Heymann, Deike Terruhn, Robert Teepe, Stefan Treue

German Primate Centre, Göttingen, Germany

E-Mail: euprim@dpz.eu

**Key Words:** EUPRIM-Net · Primate husbandry · Primate welfare

The ethical use of primates in research must be based on a sound knowledge of general primate biology by scientists and all other staff involved. Knowledge of morphological, physiological, behavioural and ecological characteristics of primates and of primate species which are used in biological and biomedical research is essential for the sake of animal welfare and for planning and conducting studies and experiments; knowledge of husbandry, including keeping, nutrition, breeding, and handling is essential for good scientific practice. Therefore, a series of six courses has been established and is held at the German Primate Centre to increase and broaden the competence of personnel involved in primate research. This enables them to improve housing and handling and thus the welfare of laboratory primates. The resulting increase in the quality of research contributes to the 3R-concept by ensuring excellence in all aspects of research and promotes common standards by teaching SOPs. Each course is dedicated to a special topic in primatology and includes lectures by international experts from the different fields. These include: diversity, morphology, natural history, social systems, reproduction, breeding, behaviour, environmental enrichment, ethical and legal aspects of primate research, diseases and health problems, handling and nutrition. All courses are aimed at scientists and students who want to update and extend their knowledge and to veterinarians and animal caretakers working in primate centres, industry, zoological gardens or any other institution housing and working with primates. The course series is conducted as a part of EUPRIM-Net. This infrastructure project is funded by the EU and links eight European primate centres to combine their extensive knowledge and infrastructure resources, their experience in primate housing and breeding, as well as their wide range of biological and biomedical R&D activities. Please see http://www.euprim-net.eu/network/courses.htm for more information.
Quantifying Microsatellite Ascertainment Bias between Humans and Orangutans

Alexander Nater, Michael Krützen
University of Zürich, Zürich, Switzerland
E-Mail: a.nater@aim.uzh.ch

Key Words: Humans · Orangutans · Microsatellite · Genetic markers · Conservation genetics

Microsatellites are very powerful genetic markers due to their high levels of polymorphism and abundance. The conserved nature of the primer binding sites used to amplify microsatellite repeats allows the application of these markers to study species related to those in which they were isolated (cross-amplification). However, previous studies have shown that estimates of genetic diversity obtained with cross-amplified microsatellites are negatively influenced by ascertainment bias. Since microsatellite repeats are usually selected for the highest possible polymorphism in the study species, the homologous loci in other species are on average less polymorphic. A large number of human-derived microsatellite markers is available for use in most primate species, especially great apes. Orangutans (Pongo sp.) are of special interest for conservation genetic studies due to their rapidly declining population sizes, severe habitat fragmentation and complex dispersal behaviour. In this study, we were able to show that ascertainment bias significantly reduces the measurements of heterozygosity of human-derived microsatellite markers in orangutans. Microsatellite enriched sequences of 68 clones from Pongo sp. were screened and tested for polymorphism to create two multiplex reactions with fourteen polymorphic loci in total. Sixteen DNA samples each from humans and orangutans were genotyped with both multiplex reactions and a set of twelve human-derived tetranucleotide markers. The measurements of observed heterozygosity were on average 0.14 higher in the source species as compared to cross-amplification in the other species (p = 0.04, z = 2.05). The mean number of alleles, mean expected heterozygosity and mean allele length were on average also lower when the microsatellites were cross-amplified, although not significantly. This needs to be taken into account before drawing conclusions when the genetic diversity of orangutan populations is compared to that of other species.

SIV Infection in Great Apes: A Multidisciplinary Approach for a Better Understanding of the Origin, History and Transmission of SIVgor in Wild Gorillas in Cameroon

Cecile Neel, a,b Fran Van Heuverswyn, a Yingling Li, c Brandon Keele, c Jun Takehisha, c Yangda Bienvenue, b Eitel Mpoudi Ngole, b Eric Delaporte, a Beatrice Hahn, c Martine Peeters

a UMR145, Institute for Research and Development (IRD) and University of Montpellier, Montpellier, France; b Projet PRESICA, Yaounde, Cameroon; c University of Alabama at Birmingham, Birmingham, AL, USA
E-Mail: cecileneel@yahoo.com

Key Words: Chimpanzees · Gorillas · Simian immunodeficiency viruses · Infection · Faecal samples

Numerous African primates are infected with simian immunodeficiency viruses (SIVs) and it is now well established that the clade of SIVs infecting central chimpanzees (Pan t. troglodytes) and western lowland gorillas (Gorilla g. gorilla) represent the progenitors of human immunodeficiency virus type 1 (HIV-1). The three groups of HIV-1 (M, N and O) are the result of three independent cross-species transmissions. Using non-invasive strategies, we recently
traced the natural reservoirs of HIV-1 M and N to distinct chimpanzee populations in southern Cameroon and showed that gorillas in Cameroon are endemically infected with SIVgor, closely related to HIV-1 group O. Although not yet detected in chimpanzees, the SIVgor virus seemed to have a P. t. troglodytes origin. Given their diet (herbivorous/frugivorous/insectivorous), and their peaceful co-existence with chimpanzees, the route by which gorillas acquired SIVgor remains a mystery. In order to further study SIVgor infection in relation to the socio-ecology of gorillas, surveys were extended in the site where the first positive individuals were discovered (southwest Cameroon). Field data were additionally collected on home ranges, nesting sites and group sizes of the different ape communities living in the area. This approach successfully led us to the discovery of 125 faecal samples and 19 were identified with HIV-1 cross-reactive antibodies. The positive samples were derived from 8 individuals as determined by microsatellite analysis. SIVgor viruses were amplified for 3 individuals, and new strains were closely related to the previously isolated SIVgorCP684 strain, which had been isolated in a gorilla from the same area in 2004. The new positive gorillas have been observed in a small geographic area (about 18 km$^2$) and belong to, at least, two different groups according to the field observations. A multidisciplinary approach, combining data from virology and primatology, will allow a better understanding of the natural history of SIVgor in gorillas.

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**Survey on the Abundance and Conservation of Sumatran Slow Lorises (Nycticebus coucang hilleri) in Aceh, Northern Sumatra**

K.A.I. Nekaris$^a$, V. Nijman$^b$

$^a$Oxford Brookes University, Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford, UK; $^b$Zoological Museum, University of Amsterdam, Amsterdam, The Netherlands

E-Mail: anekaris@brookes.ac.uk

**Key Words:** Slow lorises · Abundance · Sumatra · Aceh · *Nycticebus coucang*

At one time slow lorises were considered to comprise one strongly polymorphic species, *Nycticebus coucang*, ranging throughout Southeast Asia. Ongoing research has now revealed a minimum of five species. A handful of studies regarding their abundance in the wild suggests that *N.c. coucang* from the Thai-Malay Peninsula occurs at higher densities than other taxa, approximately 0.80 animals/km. This figure may be biased as most abundance estimates come from study sites that were specifically chosen for their high numbers of lorises. To examine whether *N. coucang* is uniformly abundant, we aimed to assess the abundance of *N.c. hilleri* from Sumatra, a taxon that hitherto has never been studied in the wild. In 2007, we surveyed five sites in the 6000-km$^2$ Ulu Masen Forest Complex, Aceh. We walked a total of 57.1 km, and surveyed 19.8 km from a vehicle. Slow lorises were confirmed present at an abundance of 0.39 animals/km at only one site in primary forest; slow lorises were never seen on forest edges. Overall abundance of lorises across sites covered by foot yields an estimate of 0.16 animals/km. These figures are more comparable to those from *N. pygmaeus*, *N. menagensis* and *N. bengalensis*, and not *N.c. coucang*. Despite being protected by Indonesian law, slow lorises were seen in animal markets during the study period, in addition to a number of individuals that were confiscated by the Forest Department. Collection for the illicit animal trade was the number one threat identified in systematic interviews, suggesting that absence of lorises from forest edges is related to their vulnerability to capture for the trade. In order to preserve lorises in northern Sumatra, more active patrolling is needed to deter their capture, and a clamp-down on the buying and selling of lorises at markets is recommended.
Individual and Contextual Differences in Loud Calls of Male Crested Black Macaques, *Macaca nigra*

Christof Neumann\(^a\),\(^b\), Gholib Assahad\(^c\), Kurt Hammerschmidt\(^d\), Dyah Perwitasari-Farajallah\(^c\), Antje Engelhardt\(^a\),\(^c\)

\(^a\)Department of Reproductive Biology, German Primate Centre, Göttingen, \(^b\)Institute for Biology II, University of Leipzig, Leipzig, Germany; \(^c\)Primate Research Center, Bogor Agricultural University, Bogor, Indonesia; \(^d\)Research Group Cognitive Ethology, German Primate Centre, Göttingen, Germany

E-Mail: cneumann@dpz.eu

Key Words: Macaques · *Macaca nigra* · Loud calls · North Sulawesi

In contrast to other macaque species, in *M. nigra*, loud calls are uttered by all adult males and in different contexts. In order to investigate the function of loud calls in this species, information on the degree and nature of individual and context variation in call characteristics is needed. We therefore recorded 690 loud calls from 24 adult males of three troops of wild *M. nigra* in Tangkoko Nature Reserve, North Sulawesi, Indonesia over a period of eleven months. Loud calls were given in six different contexts (feeding, position, locomotion, mating, aggression, social). Detailed acoustic analysis was carried out on 261 calls: 40 parameters were extracted and entered into a discriminant function analysis (DFA). DFA resulted in a correct classification of context by only 11.5% (chance level: 16.7%) based on cross validation. Concerning differences among individuals, DFA resulted in 63.9% correct classification in cross validation (chance level: 5.6%). Important parameters for the discrimination of individuals were delivery rate of elements within a call, mean duration of elements, sum of duration of all elements within a call, and certain spectral measures (energy distribution, mean peak frequency and the 2nd dominant frequency band). Our results suggest that although males individually vary in their call structure, loud call structure does not vary according to the context in which the calls are given. Based on these results, we will investigate the function of loud calls in *M. nigra* in future playback experiments.

Alarm Calls, Startle Behaviour and Predator Avoidance in Six Congeneric Arboreal Primates (Cercopithecidae: *Presbytis*)

Vincent Nijman\(^a\), K.A.I. Nekaris\(^b\)

\(^a\)Zoological Museum, University of Amsterdam, Amsterdam, The Netherlands; \(^b\)Oxford Brookes University, Department of Anthropology, Oxford, UK

E-Mail: nijman@science.uva.nl

Key Words: Langurs · *Presbytis* · Alarm calls · Social behaviour · Predators · Indonesia

One striking feature of the social behaviour of gregarious primates is the existence of alarm calls that signal the presence of predators, and that typically elicit startle behaviour in other members of the group. We studied anti-predator behaviour directed towards human observers in six species of *Presbytis* langurs in the forests of Indonesia (450 field days; 1994–2007), quantifying the occurrence of alarm calls, freezing behaviour, use of arboreal or terrestrial flight pathways, and group sizes. Langurs deploy three distinct anti-predator strategies, associated with group size and conspicuousness of pelage colour and pattern. When detected, brightly-coloured species living in large (9+ individuals) groups, such as *P. melalophos* and *P. rubicunda*, flee noisily through the upper canopy (*P. thomasi* does so along the ground), vocalising frequently. Less conspicuously-coloured species, living in smaller groups (6–8 individuals), such as *P. comata* and *P. hosei*, use the middle layer more often, and vocalise less. Occasionally
they employ ‘freezing’ to avoid detection by potential predators. The cryptically-coloured *P. frontata* lives in small groups (<4 individuals), behaves inconspicuously, freezes frequently upon detection by potential predators, and vocalises rarely during the day but frequently during the night. The conspicuous vocal behaviour in *Presbytis* most likely functions to signal detection and unprofitability directly to the predator. In a visually dense environment, alarm calls provide a conspicuous and unambiguous acoustic signal to the predator to indicate detection and the futility of a further hunting attempt. Despite drawing attention to themselves, the continuous scaffolding of the rainforest canopy allows them to enjoy an enormous locomotor advantage over ground-dwelling predators. Alarm calling behaviour in *P. frontata*, because of its cryptic lifestyle and frequent fleeing through the undergrowth, probably has been favoured by a predator avoidance effect; rare instances when they do alarm call can be explained sufficiently with interspecific warning only.

**An Ethno-Ecological Survey of Macaques in Thailand: Preliminary Data**

Françoise Noel-Lambot\textsuperscript{a}, Marie Claude Huynen\textsuperscript{a}, Tommaso Savini\textsuperscript{b}

\textsuperscript{a}University of Liège, Faculty of Science, Department of Environmental Science and Management, Biology of Behaviour Unit, Liège, Belgium; \textsuperscript{b}King Mongkut’s University of Technology Thonburi, School of Bioresources and Technology, Conservation Ecology Group, Bangkok, Thailand

E-Mail: f.noel@ulg.ac.be

**Key Words:** Macaques · Thailand · Hunting · Trade · Habitat destruction

Five species of macaques are present in Thailand (*Macaca nemestrina, arctoides, assamensis, fascicularis* and *mulatta*), and three of them are included on the list of threatened species. Since data on these species in Thai natural settings are rare, we are seeking information by soliciting popular knowledge of the environment. The aim of our approach is twofold: (1) gathering information on the monkeys’ presence, habitat and behaviour, (2) reaching a better understanding of the relationship between humans and macaques, essential in terms of conservation. The first steps of our study allowed us to detect various levels of threats to the macaque populations according to the species and their distribution in Thailand. Destruction of habitat: this affects all species in all regions. Officially protected areas (15 % of the country) are therefore of prime importance. In addition, Buddhist temples are often refuges providing protection and food for macaques in habitats degraded and occupied by humans. While this mainly concerns *M. fascicularis*, it can also be observed for other species. Sometimes two species become sympatric in temples and develop close contacts. Both isolation from other populations and hybridization threaten these small surviving populations. Hunting: for socio-cultural reasons, macaques are less hunted for food than other primate species (langurs, gibbons, and loris). However, they are often illegally killed as agricultural pests in the mountains of the north-west. Trade: possession of wild animals as pets is now prohibited in Thailand. However, macaques may be kept captive to work in coconut plantations or in monkey shows. In the south of Thailand, a high number of *M. nemestrina* juveniles are trapped from wild populations to be trained for coconut picking, and these captures often result in the death of adults. If the use of macaques is of great economic importance, breeding programmes, which are still not widespread, should be encouraged.
Food Transfer among Non-Kin in Two Natural Populations of Orangutans

Maria A. van Noordwijk, Carel P. van Schaik
Anthropologisches Institut und Museum, Universität Zürich, Zürich, Switzerland
E-Mail: vnoord@aim.uzh.ch

Key Words: Orangutans · Food-transfer · Feeding competition

Active transfer of food from one individual to another (usually a younger relative or mate) is common among birds, carnivores and cooperatively breeding primates. However, among other primates food transfer is mostly restricted to the mother-offspring context and involves active taking by the offspring. Here we report observations of non-contested transfer of food between independent and, mostly, non-related individual orangutans in two natural populations (Pongo abelii in Suaq Balimbing, Sumatra and Pongo pygmaeus wurmbii in Tuanan, Kalimantan). Orangutans are known for their solitary lifestyle, which has been attributed to their susceptibility to feeding competition. Nevertheless, individuals do spend some time in close proximity and may tolerate each other’s proximity while feeding. At the Sumatran site (Suaq) animals spend far more time in association than at the Bornean site (Tuanan). Yet, once in association, food transfer rates are similar: At Suaq, 33 cases of food transfer were observed during 3720 hours of focal association time (out of 8858 observation hours); at Tuanan, 19 cases during 2576 hours (out of 10,465 observation hours). In addition, in both populations, larger food items were sometimes fed on by two individuals taking turns or simultaneously. Food that was difficult to acquire, such as termites in rotten wood and Neesia seeds (in Suaq), was relatively more often transferred than other food items in both sites. However, food transfer was also observed for easily processed and common foods. The patterns in age-sex classes involved in food transfer were very similar in the sites as well: uncontested transfer of food from a sexually mature male to a female was most common, whereas attempts in the opposite direction typically resulted in an agonistic interaction. The data suggest a sexually asymmetric tolerance in feeding interactions. Thus, we conclude female orangutans have leverage over physically stronger males.

Feeding Ecology of Berenty Sifakas (Propithecus verreauxi) in the Wet Season

Ivan Norscia, Stefano Kaburu, Elisabetta Palagi, Daniela Antonacci
Centro Interdipartimentale, Museo di Storia Naturale e del Territorio, Università di Pisa, Calci (Pisa), Italy
E-Mail: norscia@lunet.it

Key Words: Sifaka · Feeding ecology · Food choice · Folivory

Folivory, as a peculiar form of herbivory, can be found in both primate and non-primate species and food selection criteria by folivorous species remains unclear. In fact, dietary choice can be mainly based either on food abundance or food quality. Within lemurs, folivory can be found in Hapalemur spp., Lepilemur spp. and in all indriid species. In particular, sifakas (Propithecus verreauxi) can show a pattern of either granivorous-folivory or frugivorous-folivory, depending on the food available in the different forest sites. P. verreauxi, widely studied in some sites (e.g. Kirindy CFPF and Beza-Mahafaly), has not been extensively investigated in Berenty Reserve (south Madagascar). In order to shed light on the diet of Berenty sifakas, we followed two groups (group A and group B, each composed of 6 individuals) in the Ankoba area (the northern part of the reserve; S 24.99°; E 46.29°). The individuals were observed via focal sam-
pling for one statistical day/month during the wet season (November 2006–February 2007). We gathered data on the timing of feeding activity, food and non-food items, and on the plant morphospecies selected by sifakas. We also estimated the abundance of the plant morphospecies present in the territory by performing a tree census on 0.16 ha in the home range of the two groups. Finally, via GPS, we recorded feeding tree positions, which we subsequently plotted by using Arcview 3.2a. Our results agree with those reported in previous literature, suggesting that sifakas base their food choice more on food quality than on food availability.

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**Tamarin Gait Plasticity on Oblique Arboreal Substrates**

*John A. Nyakatura, Martin S. Fischer, Manuela Schmidt*

Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Jena, Germany

E-Mail: john.nyakatura@uni-jena.de

*Key Words:* Tamarins · Quadrupedalism · Arboreal primates · Locomotion

Arboreal primate quadrupedalism is characterized by a suite of adaptations to move on narrow flexible substrates, these include a particular gait sequence pattern and prehensile extremities. However, the majority of experimental set-ups designed to investigate arboreal primate quadrupedalism feature horizontal poles, although horizontal substrates represent the minority of substrates in habitats of tree-dwelling animals. To test the influence of different inclinations on gait and its spatio-temporal parameters, we analyzed high-speed video films of cotton-top tamarins (*Saguinus oedipus*) walking and running at their preferred speeds along branchlike poles. Whereas stride length and swing phase durations are closely tied to velocity, other parameters, such as duty factor index, extent of relative protraction and relative retraction, the relation of forelimb stance phase duration to hind limb stance phase duration as well as gait sequence patterns, are adjusted to substrate inclination. The more the substrate declines, the more cotton-top tamarins display a tendency to decrease diagonality (limb phase). This leads to increased use of lateral sequence gaits (lh, lf, rh, rf) on descents. Conversely, the more the substrate inclines, the more diagonality is increased. This leads to increased use of diagonal sequence gaits (lh, rf, rh, lf) on ascents. We suggest that this behavioural plasticity was an important aspect of primate locomotor evolution.

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**Male Social Relationships in Wild Assamese Macaques**

*Assam macaques* (Macaca assamensis)

*Julia Ostner, Oliver Schülke*

Integrative Primate Socio-Ecology Group, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

E-Mail: ostner@eva.mpg.de

*Key Words:* Assamese macaques · Relationship · Matrilines · Multimale-multifemale group

Species of the genus *Macaca* share basic social and demographic traits: forming female philopatric multimale/multifemale groups sub-structured into matrilines. At the same time macaques exhibit great disparity in social relationships, varying from despotic, intolerant to relaxed and tolerant. Socioecological and phylogenetic explanations have been proposed to account for this variation, focusing either on the level of competition over resources or on phylogenetic inertia as the main determinants of the quality of social relationships. As part of an ongoing study on the behavioural ecology of Assamese macaques (*Macaca assamensis*) of Phu
Khieo Wildlife Sanctuary in northeastern Thailand, data were collected on 12 adult and sub-adult males of a multimale/multifemale group during the mating season 2006/2007 (~200 focal hours). Phylogenetically, Assamese macaques belong to the tolerant arctoides-sinica group. Results indicate a mosaic of despotic, intolerant traits and characteristics of tolerant macaques. The silent bared teeth display signaled submission in the study males, which compares well with despotic, intolerant species, such as rhesus and Japanese macaques. Based on dyadic submissive behaviour a dominance hierarchy was constructed. This was linear (p < 0.001) with a high directional consistency (0.93) and a low number of two-way relationships (<10%), again pointing towards the despotic end of the continuum, which is unexpected based on their taxonomic position. Assamese macaques, however, deviate from strictly despotic, intolerant species, as they frequently formed various types of coalitions and exhibited mechanisms of conflict resolution such as reconciliation and ‘agonistic buffering’ in order to regulate male-male relationships. 30% of all buffering interactions, however, included the alpha male and 20% included the alpha male and his main coalition partner, indicating that tolerance and support might not be a general feature of male relationships in Assamese macaques but might be a mechanism primarily used by the top-ranking males to maintain their position.

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**Parasites of Chimpanzees in Kalinzu Forest Reserve, Uganda, with Emphasis on Comensal Protozoans**

J. Petrášová, K. Pomajbíková, K.J. Petřželková, M. Jirků, I. Profousová, D. Modrý, C. Hashimoto

Department of Parasitology, Faculty of Veterinary Medicine, University of Veterinary and Pharmaceutical Sciences; Institute of Vertebrate Biology, Academy of Sciences, Brno; Liberec Zoo, Liberec; Institute of Parasitology, Biology Centre, Academy of Sciences, CR, Ceske Budejovice, Czech Republic; Primate Research Institute, Kyoto University, Kyoto, Japan

E-Mail: petrasovaj@atlas.cz

**Key Words:** Chimpanzees · Faecal samples · Parasites · Uganda · Troglodytella · Entamoeba

Individual wild, habituated chimpanzees (*Pan troglodytes schweinfurthii*) were followed and faecal samples were collected throughout the rainy season (September–October 2006) and dry season (January–March 2007) in Kalinzu Forest Reserve, Uganda. 450 samples were collected from 43 identified individuals. Samples were divided, preserved in formaldehyde and ethanol and later examined using Sheather’s flotation and Merthiolate-Iod-Formalin faecal technique. The following parasites/comensals were recorded using coprological methods: protists: *Entamoeba, Troglodytella cf. abrassarti* and trophozoites of unidentified entodiniomorphid ciliates; helminths: *Bertiella cf. studeri, Probstmayria gombensis, Strongyloides falleborni, Subulura sp., Trichuris cf. trichiura* and eggs of unidentified spirurid nematodes. Comparison of both sampled seasons revealed a higher diversity and prevalence and also a higher intensity of infections during the rainy season. Specific attention was given to the occurrence and fluctuation of entodiniomorphid ciliates; the prevalence of *Troglodytella* was 88%. Three chimpanzees were selected to study the fluctuation of *T. abrassarti* populations. In all sampled animals, the populations of *T. abrassarti* showed remarkable variability in CPG (ciliates per gram) with values ranging from 0 to 104. Negative samples were recorded irregularly in all three animals. As the cysts of *Blastocystis* were not recorded during coprological examinations, a specific PCR detection test was used to prove/exclude their occurrence and fluctuation in the three selected animals. They were detected in these animals, with a prevalence of 62% in the dry season and 7% in the wet season.

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Head Rotations in the Play of Hanuman Langurs: A Description and an Analysis of Function

Milada Petrů, Marek Špinka, Stanislav Lhota, Petr Šípek
Department of Zoology, Faculty of Science, Charles University in Prague, Prague, Czech Republic
E-mail: milada.petru@seznam.cz

Key Words: Hanuman langurs • Semnopithecus entellus • Head rotation • Social play

Although head rotations are frequent patterns in play behaviour in most mammalian species, and although they differ from head movements used in other contexts, they have not been quantitatively described and their function remains unclear. Based on videotaped play behaviour of free-ranging Hanuman langurs (Semnopithecus entellus), we described, semi-quantitatively, their head rotations and tested two possible hypotheses about their function. Either the head rotations serve to create unexpected situations and should, therefore, occur in both solitary and social play and be very variable, or they serve as play signals and should, therefore, occur only in social play and be ritualized. If head rotations have both functions, they should be less variable in social play. The data revealed that head rotations were very variable and were present both in solitary and social play. Furthermore, there was no difference in the variability between the head rotations present in the two types of play. The results do not support the function of head rotations as play signals, but rather, suggest that head rotations may serve to create unexpected situations in play.

Do Female Copulation Calls Influence Mating Outcome?
A Study in Free-Ranging Barbary Macaques (Macaca sylvanus)

Dana Pfefferle\textsuperscript{a,b}, Katrin Brauch\textsuperscript{b}, Michael Heistermann\textsuperscript{b}, Keith Hodges\textsuperscript{b}, Julia Fischer\textsuperscript{a}
\textsuperscript{a}Research Group Cognitive Ethology, \textsuperscript{b}Department of Reproductive Biology, German Primate Centre, Göttingen, Germany
E-Mail: dpfefferle@dpz.eu

Key Words: Barbary macaques • Mating • Copulation calls • Reproductive status

Females of many primate species, including humans, utter loud and distinctive calls during mating. A high number of non-exclusive hypotheses have been proposed to explain the functional significance of these copulation calls: e.g. being (1) a stimulus to the calling female herself, (2) a signal to other group members or (3) a signal to the mating partner. In order to shed light on this discussion, knowledge of the information context encoded in the call structure is needed. For instance, the information may include coding of male ID, mating intensity, mating outcome or/and the female’s fertile phase. Although the latter function was suggested by previous studies carried out by Semple and colleagues (1998, 2000), it remained unclear whether calls reliably advertise the female fertile phase and/or influence mating outcome. In the present study, therefore, we analysed copulation calls in relation to female reproductive status as well as in relation to mating outcome (ejaculation), in a free-ranging group of Barbary macaques (Macaca sylvanus). In contrast to the previous study, our results showed no change in the acoustic structure of copulation calls around ovulation, indicating that female Barbary macaques do not advertise their fertile phase. Instead, we found that by calling the female influences the likelihood of a male’s ejaculation. Our findings thus support a direct female choice mechanism, fundamental for the ‘signal to mating partner’ hypothesis.
Female Mate Choice in Chimpanzees (Pan troglodytes schweinfurthii) of Kanyawara, Kibale National Park, Uganda

Katharin Pieta
University of Vienna, Department of Anthropology, Vienna, Austria
E-Mail: katharin.pieta@access.unizh.ch

Key Words: Chimpanzees · Mate choice · Sexual coercion · Kibale National Park

According to sexual selection theory, females should mate selectively with high-quality males to enhance reproductive success. However, female chimpanzees mate promiscuously. Furthermore, determining female chimpanzee mate choice is challenging in the light of male strategies such as sexual coercion of females and mate guarding. I investigated sexual behaviour and female mate choice in the chimpanzees (Pan troglodytes schweinfurthii) of the Kanyawara community in Kibale National Park, Uganda. The social behaviour of 6 oestrous females was recorded continuously during 330 focal hours. During the study period, 3 parous females were likely to conceive while 3 others were unlikely to conceive (2 subadults, 1 post-partum). 664 copulations with 13 males were analysed. I calculated rates of female proceptivity and mating resistance for each female to categorize preferred and eschewed males. A female’s oestrous period was classified into a fertile and non-fertile stage. My results show that all females, whether likely to conceive or not, shifted their mating preference according to their oestrous stage. This tactic may allow females to deceive males, indicating that promiscuity among females may be more organized than previously thought. Furthermore, parous females copulated longer when they initiated the copulation, especially when the likelihood of conception was greatest. Since this was not true for the other 3 females, this may reflect a female’s strategy to get pregnant with chosen males. Males were more successful at achieving copulations when they invited those parous females who were more willing to copulate with them. In contrast, males were less successful in achieving copulations with resisting females, which implies that females were capable of influencing male mating success. Females copulated more frequently with preferred than with eschewed males throughout their oestrous period. Overall, these results suggest that female chimpanzees play the role of the passive sexual partner much less than previously assumed.

The Occurrence of Troglodytella abrassarti (Brumpt and Joyeux, 1912) in Captive Gorillas

K. Pomajbíkováa, K.J. Petrželkováb, c, T. Tokiwa d, S. Imaid, D. Modrýa, e
a Department of Parasitology, Faculty of Veterinary Medicine, University of Veterinary and Pharmaceutical Sciences, b Institute of Vertebrate Biology, Academy of Sciences, CR, Brno, c Liberec Zoo, Liberec, Czech Republic; d Nippon Veterinary and Life Science University, Tokyo, Japan; e Institute of Parasitology, Biology Centre, Academy of Sciences, CR, Ceske Budejovice, Czech Republic
E-Mail: zvonda233@centrum.cz

Key Words: Gorilla · Ethodiniomorphid ciliates · Faecal sample · Troglodytella abrassarti

The ciliates of the order Entodiniomorphida occur in the colon of large herbivorous mammals, including great apes. Recent studies suggested possible participation of ethodiniomorphid ciliates in colonic fermentation of fibre. Based on old records, it was believed that these ciliates tend to gradually disappear in captive apes due to an unsuitable diet and probably also because of anti-parasitic treatment and of antibiotics use. Fresh faecal samples from individual gorillas (Gorilla gorilla gorilla) from Prague Zoo (Czech Republic) and Paington Zoo (Great Britain) were
collected in 2005 and 2006. Samples were preserved in formaldehyde and examined by the Merthiolate-Iodine-Formalin faecal method. Based on a detailed morphological study using both light microscopy and scanning electron microscopy, the ciliates found were identified as *Trogloidyella abrassarti*. Using serial coprological examinations, we recorded transmission of *T. abrassarti* to a previously uninfected adult gorilla introduced into the Prague group from the Dvur Kralove group. To our knowledge, nobody has recorded the time of first appearance of entodiniomorphid ciliates in chimpanzee or gorilla infants in the wild or captivity. By serial sampling of the infant born in Prague Zoo we found *Trogloidyella*-positive samples from when the infant was nine months old.

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**Grooming for Aid or Grooming to Stay? Patterns of Social Grooming in Free-Ranging Red-Fronted Lemurs (*Eulemur fulvus rufus*)**

*Markus Port*a, b, Peter M. Kappeler*a, b*

*a Department of Behavioural Ecology and Sociobiology, German Primate Centre,  
b Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany  
E-Mail: mport@gwdg.de

**Key Words:** Red-fronted lemurs · Social grooming · Biological market theory · Social organization

Apart from its cleaning function, mutual grooming in primates has traditionally been attributed a socially mediating role with grooming generally being directed upwards in a social hierarchy. More recently developed biological market theory has attributed a more flexible function to grooming interactions. Specifically, grooming is considered a service on a biological marketplace, exchanged either for its own or for other social commodities or services. Market models predict that grooming should be approximately reciprocated within a dyad when no other services are being exchanged, but should be more asymmetrical if partners within a dyad have different amounts of other services (e.g. help, tolerance, mating opportunities) to offer. We analyzed a total of 435 grooming bouts, observed in four groups of red-fronted lemurs (*Eulemur fulvus rufus*) in Kirindy Forest, western Madagascar to test this prediction. A handheld computer was used to measure precisely the time that each partner within a dyad was engaged in grooming. Grooming in this species seems to take place in a highly reciprocal manner because partners within a dyad usually alternate in the roles of groomer and grome. However, partners differed in the duration of grooming given and received. In general, females groomed males more than vice versa, and, although grooming among males was generally reciprocal, dominant males received more grooming than they gave. The observed grooming patterns therefore reflect the social structure reported for this species. With respect to market theory, grooming appears to be traded by subordinates in exchange for tolerance, rather than by dominants in exchange for the subordinates’ aid.
Food Sharing in Groups: A Comparison Between Normal Captive Chimpanzees and Recently Socialised Long-Term Isolates

S. Preuschoft, S. Peterhans, C.P. van Schaik
Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: preuschoft@aim.unizh.ch

Key Words: Chimpanzees • Food sharing • Rehabilitation • Social deprivation

The way in which food is provided – its size, portability and distribution – influences the prevalence of aggression among captive group-living animals. In egalitarian species such as chimpanzees priority of access is not predicted by dominance, and overt conflicts over food may be caused by clumped feeding. Wild chimpanzees are known to call group members to join in feeding at abundant food resources, and to share food by tolerance and active transfers. While food sharing can result from the inability to monopolise the food, it is also used to forge bonds of cooperation, and pay for favours. We provided opportunities for food sharing to recently resocialised chimpanzees who had lived in social isolation since infancy, and compared sharing patterns between different social groups at Gänserndorf Sanctuary (Austria) and with an established group at Yerkes Primate Centre, Atlanta (GA, USA). Discovery of attractive food was greeted by extensive vocalisations in all groups, but ‘celebrations’ with emphatic embracing and erotic contacts varied. While active giving was rare, food transfers by tolerated taking, co-feeding, and controlled discarding were common in all groups. Transfers were elicited by begging and following, but not by aggression or bluffs. The extent of food sharing was variable. Males were usually generous, and some females tended to share more with friends. As a rule, ownership, even by subordinates, was respected. In contrast to the socially experienced individuals at Yerkes, the Gänserndorf chimpanzees rarely used offensive screaming to pressure an owner into generosity, and exhibited a general disinclination to risk overt conflicts. We conclude that feeding together and sharing of food is an inherently pleasurable situation for chimpanzees, it poses natural challenges to social intelligence and skills, and zoos should not be afraid to risk escalated fighting when providing attractive food in a clumped fashion, as long as it is abundant.

Grooming Patterns in Primates: A Model

Ivan Puga-Gonzalez, C. Hildenbrandt, Charlotte Hemelrijk
Rijksuniversiteit Groningen, Groningen, The Netherlands
E-Mail: ivanpuga@hotmail.com

Key Words: Primates • Grooming • Social organization • Aggression • Dominance hierarchy

Grooming is supposed to play a crucial role in the social organization of primates. Apart from reducing tension, it is believed to function as a currency for exchange, where grooming can be reciprocated or exchanged for commodities such as support in fights, access to food, to mates, etc. In macaque species, grooming patterns differ according to the type of society: egalitarian or despotic. Whereas in both types of societies females groom more than males and they reciprocate grooming, in despotic societies, grooming is more clearly directed up the hierarchy, occurs more frequently among individuals of similar rank and reconciliation after fights is less frequent than in egalitarian societies. These differences are explained as an effect of the hierarchical gradient on the process of exchange. In this study however, we show that all these grooming patterns may arise by self-organization if the function of grooming is only to reduce tension. We extend a previous model of aggression and grouping developed by Hemelrijk (1996), ‘Dom-
World’, by adding different rules for grooming. In the new model, ‘GrooFi World’, all the agents have a value indicating their tension. This value decreases after an agent grooms with another and it increases after fighting and over time. Two rules for grooming were compared. Only one of them (called ‘aggression rule’), led to all the grooming patterns observed in macaques and the differences between both types of societies. In this rule according to empirical observations, an active agent first decides whether to fight or not. If it decides not to fight, then it decides whether to groom or not. The emergence of the grooming patterns in the model is due to the behavioural priorities of the agents and spatial structure. This model may lead to new hypotheses to be tested in real primates.

Hand Preference in Captive Non-Human Primates: Lemur catta and Macaca nemestrina
Caterina Quaresmimia, Caterina Spiezioib, Donata Grassib
ab Biology Department, University of Padua, Padova, bResearch Department, Parco Natura Viva – Garda Zoological Park, Bussolelengo, Verona, Italy
E-Mail: anireta@libero.it

Key Words: Lemur catta • Macaca nemestrina • Hand preference • Handedness

A great majority of human beings almost exclusively use their right hands for writing and other skilled activities. Several studies have supported a relation between handedness and the complex connections to the distribution of functions in the two halves of the human brain. Comparative research with non-human species may help to answer fundamental questions about the origin and the evolution of hemispheric lateralization in humans. The aim of this research is to verify the two principal theories concerning the origin and the evolution of right-handedness: the genetic theory proposed by Annett (1985) and the postural theory proposed by MacNeilage et al. (1987). Fourteen ring-tailed lemurs (Lemur catta) and 9 pig-tailed macaques (Macaca nemestrina), housed at Parco Natura Viva, Italy, were observed during their daily activities in order to assess their individual hand preference and their group-level handedness, based on the classificatory framework provided by McGrew and Marchant (1997). Our data collection was focused on hand used for posture, locomotion and reaching for food. The results demonstrate that most of the ring-tailed lemurs and some of the pig-tailed macaques showed an individual hand preference for the behavioural categories considered. As a consequence, the group of Lemur catta seems to belong to Level 2 while the troop of Macaca nemestrina seems to belong to Level 1. However, neither of the species showed a hand preference at a group level. Nonetheless, some traces of hand preference seem to be found in lemurs and macaques.

Can Ancient DNA Aid in Documenting the Loss of Genetic Diversity in Orangutans?
Nadine van Reeuwijk, Michael Krützen
Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: vanreeuwijk@aim.uzh.ch

Key Words: Orangutan • Genetic diversity • Mitochondrial DNA

The last 100 years have seen a dramatic decline in orangutan populations in Borneo and Sumatra. The reduction in population size since 1900 is estimated to be 75%, from ca. 3,150,000 individuals in 1900 to between 50,000–70,000 in 2004. Orangutans are suffering the consequences of illegal logging, hunting and trade and also natural disasters, all of which can lead to loss of genetic diversity and extinction. Recent studies have shown that at least some orangutan populations...
have undergone genetic bottlenecks. The aim of the study is to estimate genetic diversity of orangutan populations in the early 19th century, to compare genetic diversity with recent populations and, if we detect a loss of genetic diversity, to attempt to quantify the extent. A total of 37 historic samples (14 from Borneo, 7 from Sumatra and 16 with unknown origin) have been extracted and amplified for the mitochondrial d-loop (hyper-variable region I and II) to compare haplotypes. In order to avoid amplifying human DNA that could have contaminated the samples due to previous handling, we designed new species specific primers that divide HVRI and HVRII in four small fragments of 120 to 270 base pairs. Mitochondrial DNA diversity of historic samples will be compared with recent samples that were obtained from the same area, in order to assess the change in haplotype diversity over the past hundred years. The results are particularly important for the detection of genetic changes that occurred due to anthropogenic pressures and may aid us in future conservation efforts.

Social Relationships in Free-Ranging Male Stumptail Macaques (Macaca arctoides)

Christin Richtera,b, Lieke Mevisa,c, Oliver Schülkea, Julia Ostnera

aIntegrative Primate Socio-Ecology Group, Max Planck Institute for Evolutionary Anthropology, bInstitute of Biology II, University of Leipzig, Leipzig, Germany; cDepartment of Biology, University of Utrecht, Utrecht, The Netherlands

E-Mail: celestina.richter@gmail.com

Key Words: Stumptail macaques · Dominance relationships · Conflict · Grooming

It has been shown that dominance relationships in the genus Macaca differ not only between species, but possibly also between sexes. This is not surprising considering that the sexes differ in the resources over which they compete. Whereas females may fight predominately over access to food resources, competition for mates is believed to be the dominant factor responsible for the quality of male social relationships. Stumptail macaques (Macaca arctoides) have been classified as having egalitarian social relationships based on studies in captivity and focusing mainly on females. This study set out to investigate male social relationships in a group of 68 free-ranging, naturally dispersing stumptail macaques at Wat Khua Sattayaram, southern Thailand. Continuous focal data were collected from 7 adult and 2 large subadult males, recording agonistic, affinitive and affiliative behaviour, as well as sexual interactions during 283 hours of contact (140 focal hours). Data were supplemented with ad libitum recording of agonistic and sexual behaviours. A hierarchy was constructed based on a winner-loser matrix containing dyadic decided conflicts, showing a significant but moderate linearity (h = 0.67, p < 0.01), a directional consistency index of 0.82 and 33% of two-way relationships. The steepness of the hierarchy was 0.55 and it was significant at p < 0.01. Almost all (97%) of male conflicts were dyadic, with a high proportion of them being decided (82%). Conflict rate among males equalled 1.64 per hour. To assess whether males preferentially approach dominant or subordinate males, the Up/Down Index was calculated, showing a tendency to approach lower-ranking individuals more often (0.14 ± 0.56). Grooming, one of the affiliative behaviours, was directed up the hierarchy in all males except one individual (Up/Down Index: 0.63 ± 0.73). Overall, the combination of dominance characteristics revealed in our study indicate that male stumptail macaques are more despotic than previously assumed and are also more so than their female conspecifics.
The Primate Centre of the CNR (Rome, Italy): Research and Education

M.C. Riviello, A. Wirz, E. Addessi, F. Natale, P. Poti, G. Sabbatini, M. Saporiti, G. Spinozzi, V. Truppa, E. Visalberghi

Istituto di Neurobiologia e Medicina Molecolare, CNR, Fondazione Santa Lucia, Istituto di Scienze e Tecnologie della Cognizione, CNR, Rome, Italy
E-Mail: cristina.riviello@istc.cnr.it

Key Words: Capuchin monkeys • Cebus apella • Education projects

The Primate Centre of the Cognitive Primatology Unit of the Institute of Cognitive Science and Technologies of the National Research Council (CNR) is hosted by the Bioparco of Rome. It houses a colony of about 30 tufted capuchin monkeys (Cebus apella). The Primate Centre carries out important scientific and educational activities concerning primatology. In the past six years the Centre has carried out the following five education projects (funded by the Italian Ministry for Education), involving teachers and students of primary and secondary schools: (1) Learning to know ourselves: the biological basis of human and non-human primate behaviour; (2) learning how to observe primate behaviour; (3) comparison between humans and monkeys: an on-line laboratory; (4) from observation to modelling and back in the study of the animal kingdom; (5) research and ethics: from observation to understanding and respecting. The common aim of these projects was to teach students how to carry out observations using a scientific approach. In particular, we focussed on animal behaviour, employing our capuchin monkeys as models. These educational activities led to books, CD-ROMs, educational posters, a DVD, a web site and a permanent multimedia information point. Finally, our activities promoted the distribution of information on the biology and behaviour of non-human primates to a wider audience, in order to analyse and to compare human and non-human primates in an evolutionary perspective.

Tail Marking and the Taxonomic Status of the Goeldi’s Monkey (Callimico goeldii)
Claudia Rudolf von Rohr
Anthropological Institute & Museum, University of Zürich, Zürich, Switzerland
E-Mail: claudiarvr@aim.uzh.ch

Key Words: Callimico goeldii • Sternal gland • Callitrichids • Cebids • Olfactory communication

In New World monkeys, olfaction plays an important role in communication. Whereas callitrichids primarily use the circumgenital scent glands for their olfactory communication, the cebids use their sternal scent gland. Within the New World monkeys, Callimico represents a mosaic form that combines morphological and behavioural characteristics typical either of the callitrichids or the cebids. Therefore, it has been variously classified as in either of these taxa or even in its own family. The aim of this study was to contribute to the discussion concerning the taxonomic status of Callimico within the New World monkeys by assessing whether the biology of the scent marking behaviour in Callimico resembles most that of other callitrichids or that shown by cebids. In particular, this study focused on ‘tail marking’, a specific scent marking behaviour in Callimico, involving the sternal scent gland, and on its specific function. We compared the sternal scent gland of Callimico morphologically, histologically and functionally to that of other callitrichids and to that of the cebids. Within the callitrichids, Callimico appears, phylogenetically, to be most closely related to the genus Callithrix. Thus, the sternal scent gland of Callithrix jacchus in particular was examined and compared. The results of this study show
that (1) the specific ‘tail marking’ behaviour involving the sternal scent gland in *Callimico* is unique within the New World monkeys, (2) the function of ‘tail marking’ in *Callimico* can be understood as territorial behaviour and (3) the morphology and ethology of the sternal scent gland in *Callimico* mostly resembles those of the cebids and not those of the callitrichids. Thus, from a morphological and ethological point of view it makes sense to consider *Callimico*, despite recent molecular genetic surveys, as a more distantly related basal member of the callitrichids.

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**A Pilot Study of the Sahamalaza Sportive Lemur (*Lepilemur sahamalazensis*) – Population Density, Habitat Requirements, Ethogram and Vocalisations from Four Forest Patches of the Sahamalaza Peninsula, Northwest Madagascar**

F.S. Ruperti³, F.P.M. Rabenandrasana³, S. Renaudineau³, T.K. Beade³, N. Schwitzer³, C. Schwitzer³,e

³Nocturnal Primate Research Group, Oxford Brookes University, Oxford, UK; ⁴Département de Biologie Animale, Université d’Antananarivo, Antananarivo, Madagascar; ⁵Laboratoire de Neurobiologie de la Cognition, Université de la Provence, Marseille, ⁶Association Européenne pour l’Etude et la Conservation des Lemuriens (AEECL), Mulhouse, France; ⁷Bristol Zoo Gardens Research Office, Bristol, UK

E-Mail: fruperti@yahoo.com

**Key Words:** *Lepilemur sahamalazensis* · Population density · Sleeping sites

The Critically Endangered Sahamalaza sportive lemur (*Lepilemur sahamalazensis*) was first discovered in 2004 and no studies other than genetic and morphological descriptions (Andriaholinirina et al., 2006) and a brief survey (Olivieri et al., 2005) have been carried out to date. The species is included in the most recent list of the world’s 25 most endangered primate species (Mittermeier et al., 2006). The present study aims to establish its population density with DISTANCE analysis by means of transect walks in four forest fragments of varying degrees of disturbance. Habitat characteristics will be measured at intervals along each transect to gain a quantitative measure of forest structure. The abundance of *Lepilemur* will be compared between fragments to gain an insight into basic habitat requirements and tolerance. Furthermore, the characteristics of sleeping sites will be described and microhabitat characteristics surrounding sleeping trees will be compared to representative samples of each forest patch in order to understand this species’ habitat selection within fragments. A basic ethogram, activity budget and vocalisation recordings of *L. sahamalazensis* will also be included to facilitate and encourage further research.

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**Bridging Science and Tourism – A Preliminary Study of the Black and White Ruffed Lemur at Monkeyland Primate Sanctuary, South Africa**

F. Ruperti³, E.L. Nelson³, M.A. Novak³

³Monkeyland Primate Sanctuary, Plettenberg Bay, South Africa; ⁴Oxford Brookes University, Oxford, UK; ⁵University of Massachusetts, Amherst, MA, USA

E-Mail: fruperti@yahoo.com

**Key Words:** *Varecia variegata variegata* · Monkeyland Primate Sanctuary · Eco-tourism

Monkeyland Primate Sanctuary holds 11 different primate species and over 400 residents. The adjacent Birds of Eden Sanctuary, which is the world’s largest aviary, houses an additional three primate species. The sanctuaries are supported by responsible eco-tourism and strive to raise public awareness about primates and environmental education. Experienced rangers lead...
informative safaris through the 12-ha indigenous forest at Monkeyland. The sanctuary has recently begun to expand its educator role by promoting behavioural research that seeks not only to increase our knowledge of primates, but to bring science to the visiting public in an accessible, meaningful way. This presentation will discuss non-invasive scientific research as a positive tool for facilities such as Monkeyland. In a preliminary first study, the individuals of Monkeyland’s black and white ruffed lemur (*Varecia variegata variegata*) populations were identified and feeding data were collected via videotape. A brief summary of this project will be presented. The perception of scientific research by the staff and guests was then measured via self-report questionnaires and small focus groups. The impact of research on these groups will be discussed, as well as future plans for incorporating science into tourism at Monkeyland.

**Capuchins’ Use of Visual and Auditory Stimuli to Locate Hidden Food**

**Gloria Sabbatini, Elisabetta Visalberghi**

Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy

E-Mail: gloriasabbatini@libero.it

**Key Words:** Capuchin monkeys • Causal reasoning • Inferential reasoning • Sensory modalities

Inferential reasoning has been studied mainly in chimpanzees. We investigated this ability in a task requiring capuchin monkeys (*Cebus apella*) to find hidden food using different sources of physical information. Capuchins were presented with two boxes (one of which was baited) and given visual or auditory information about their contents. In the visual condition of Experiment 1, the experimenter showed the content of both boxes; in the auditory condition, the experimenter shook both boxes producing an audible noise when the box was baited. All subjects except one were above chance in the visual condition, whereas only one subject was above chance in the auditory condition. After a familiarization treatment, during which capuchins played with objects filled with noisy food or with empty ones, all capuchins were tested again. Some subjects were then above chance both in the visual and auditory condition. In Experiment 2, the experimenter manipulated the type of information concerning the location of the reward, by showing (or shaking) the baited box, or the empty box. When information concerned the empty box and success implied inferential reasoning, two subjects out of four were above chance in the auditory empty condition, and all four were above chance in all the visual conditions. Control tests showed that subjects did not avoid the shaken noiseless box, nor did they learn to use arbitrary auditory information as a cue. Overall, the achievement of our capuchins resembles that of apes when tested in the same task and suggest that these monkeys are capable of inferential reasoning.

**The Implications of Fission-Fussion Dynamics for Social Interactions in Wild Spider Monkeys**

**Colleen M. Schaffner*, Filippo Aureli**

*a Psychology Department, University of Chester, Chester, b Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Liverpool, UK

E-Mail: c.schaffner@chester.ac.uk

**Key Words:** Spider monkeys • Conflict • Social interactions • Fission-fusion dynamics

Social interactions are likely to vary depending not only on the strength of social relationships but also the degree of spatio-temporal cohesion. For example, species that live in predom-
inantly cohesive groups would be expected to exchange interactions that facilitate coordination of group movement and daily activities, cooperation and conflict management, whereas species that live in social systems characterised by a high degree of fission-fusion dynamics may require additional signals that serve to remove ambiguity when animals reunite. A framework that captures such variation can be used to facilitate the generation of testable hypotheses about the form and frequency of signals to regulate social relationships. We used such a framework to investigate social interactions in wild spider monkeys, a species noted for its high degree of fission-fusion dynamics. Data were collected on two wild communities of spider monkeys (Ateles geoffroyi) at the Otoch Ma’ax Yetel Kooh reserve in the Yucatan Peninsula of Mexico. We hypothesized that the spider monkeys would use appropriate interactions, such as embraces, to reduce uncertainties. Our data revealed that embraces were more likely between individuals reuniting at fusion and served to offset the risk of aggression at these times. We also examined contexts in which conflict was especially likely: during feeding for females and when females were present for males. We found that females exchanged embraces with one another more frequently in the context of feeding than at other times and males embraced other males more often in mixed-sex subgroups than in same-sex subgroups. Our findings demonstrate that specific social interactions may reduce escalation of conflict in risky situations in spider monkeys and illustrate the utility of the framework in generating and testing hypotheses about species living in social organisations that vary in their extent of fission fusion dynamics.

Between-Group Antagonism: Is It Affected by the Collective Action Problem?

Carel van Schaik, Barbara Hellriegel

Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: vschaik@aim.uzh.ch

Key Words: Between-group antagonism · Home range · Social system · Territory defence

Most primate species live gregariously. The resulting groups vary widely in size, age-sex composition, and use of space. Group living provides clear benefits, such as reduced predation risk or more efficient exploitation and defence of food resources and/or the supporting area. These are, however, opposed by non-negligible costs, such as competition for food and mates. Most importantly, group living entails the risk that group members will not equally share the costs and benefits. Especially in larger groups there is an incentive to free ride on the efforts of others, i.e. a so-called collective action problem arises. We chose to test this idea in the context of between-group antagonism to defend a common home range. Because males are often involved in this activity, we expected to find a decreased defensive effort in multi-male, as compared to single-male, bisexual groups. We selected home range overlap as an indirect measure of effectiveness of range protection, and analysed 80 cases, from 56 non-human primate species, collected from the literature. As possible factors determining the degree of the home range overlap between neighbouring groups we included home range size, defendability, group size, number of males and females, and social system. In all of our analyses, social variables (social system or number of males or females) emerged as a highly significant correlate of home range overlap, more so than the expected effect of defendability. These results are consistent with a collective action problem affecting between-group antagonism related to territory defence.
Signal Content of Red Coloration in Female Mandrills
Joanna M. Setchell
Evolutionary Anthropology Research Group, Department of Anthropology, Durham University, Durham, UK
E-Mail: joanna.setchell@durham.ac.uk

Key Words: Mandrill • Mandrillus sphinx • Animal coloration • Evolution

Animal coloration has played a special role in the history of evolutionary biology. Although many primates exhibit striking coloration, including brightly coloured pelage and red, pink, purple and blue areas of bare ‘sexual skin’, our understanding of the function and evolution of these traits pales into insignificance in the face of knowledge about colour in other taxa. However, recent years have seen an increase in the number of studies of individual variation in primate colour and evidence is accumulating that these traits can act as important signals to conspecifics. Female mandrills (Mandrillus sphinx) possess facial coloration that is highly variable between individuals, ranging from black to bright pink. Over 19 months, I used bi-weekly photographs of 52 semifree-ranging females aged >3 years in combination with long-term demographic and behavioural data to evaluate the potential signal content of coloration in female mandrills. Results show that colour is not related to female rank or quality (body mass index, age at first birth or mean inter-birth interval). However, colour does increase significantly with age and primiparous females are darker than multiparous females. Colour may therefore signal reproductive quality, as younger females are less fertile and produce smaller offspring. Colour was brighter during the follicular phase than during the luteal phase, suggesting that it may signal fertility. Colour also varied across gestation and peaked at 4 and 8 weeks post-parturition, suggesting that it may signal approaching parturition and lactation. I will also examine whether colour is related to measures of parasite infection, and whether males are more attracted to redder females. I will conclude with a discussion of similarities and differences in the information conveyed by facial colour in female and male mandrills.

Preliminary Information on the Current Status of the Yellow-Tailed Woolly Monkey (Oreonax flavicauda) at Yambrasbamba, Peru
N. Shanee, S. Shanee, A.M. Maldonado
Neotropical Primate Conservation, Kfar Saba, Israel
E-Mail: nogashanee@gmail.com

Key Words: Oreonax flavicauda • Deforestation • Yambrasbamba • Peru • Forest refuge

The yellow-tailed woolly monkey (Oreonax flavicauda) is classified as critically endangered (IUCN, 2006) and is listed by the IUCN Primate Specialist Group as one of the top 25 most endangered primate species in the world (PSG, 2006). Its distribution is restricted to the Tropical Andes Biodiversity Hotspot. Between March and June 2007 we conducted a preliminary survey of O. flavicauda in Amazonas and San Martin states, Peru. Forest fragments which are part of the distribution range of O. flavicauda were surveyed and secondary data on current habitat threats were collected using semi-structured interviews. Since the last field survey of this species (Leo-Luna, 1980) the area has undergone high levels of deforestation and many populations of the species now exist in isolated forest patches. The preliminary results of this pilot study suggest that the area of Yambrasbamba is one of the last remaining forest refuges for O. flavicauda and, considering the species habitat requirements, represents a critical area for its survival. On Yambrasbamba’s lands we encountered a large area of intact habitat where O. flavicauda still persist. The area lies between the Alto Mayo Protected Forest and the proposed
Cordillera de Colan Reserved Zone, forming a natural corridor. The main threats facing *O. flavicauda* are the continued immigration of people from the highlands and associated habitat destruction. The main income sources for the local inhabitants are timber extraction, followed by clear cutting for cattle ranching and commercial coffee cultivation. Soils are poor and susceptible to erosion, requiring further encroachment into forested areas. Other threats include mining and road construction and subsistence hunting by neighbouring indigenous groups. Owing to the paucity of protection and updated information on the conservation status *O. flavicauda*, we recommend immediate protection of this area alongside the implementation of alternative income strategies and a sustained public awareness campaign.

**Primate Reciprocity: General Patterns and Proximate Mechanisms**

*Gabriele Schino*

Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy

E-Mail: gschino@casaccia.enea.it

**Key Words:** Primates · Altruistic behaviour · Reciprocal grooming · Aggression

Primates exchange a variety of putatively altruistic behaviours, e.g., grooming, agonistic support, and tolerance. Here, I first review recent research that explored the general rules followed by primates in distributing altruistic behaviours among group members and their intraspecific and interspecific variability. Second, I present data on the temporal patterning of reciprocity, and discuss how this relates to the proximate mechanisms underlying reciprocity. Meta-analyses of published data on grooming distribution showed that primates: (1) groomed preferentially higher-ranking animals and kin, and competed for access to preferred grooming partners; (2) reciprocated the amount of grooming received, and (3) exchanged grooming for agonistic support. Phylogenetically controlled analyses of interspecific variability and simple analyses of intraspecific variability showed that the tendency to groom up the hierarchy was positively related to the slope of the dominance hierarchy and negatively related to the tendency to reciprocate grooming, although these relations were not entirely consistent. Data on the temporal patterning of reciprocity showed that Japanese macaques supported preferentially those individuals that groomed them most, but that no short-term temporal relation existed between grooming and agonistic support. These results are discussed in terms of the emotional or cognitive mechanisms that may underly reciprocation.

**Female Social Relationships in Two Species of Asian Colobines, *Trachypithecus auratus* and *Presbytis melalophos***

*Oliver Schülke, Carolin Fischer, Julia Ostner*

Integrative Primate Socio-Ecology Group, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

E-Mail: schuelke@eva.mpg.de

**Key Words:** Langurs · *Trachypithecus auratus* · *Presbytis melalophos* · Social relationships · Dominance style · Agonistic interactions

Variation in female social relationships and specifically in dominance styles has been proposed to result mainly from phylogenetic inertia rather than ecological factors in the genus *Macaca*. This study aims at testing the generality of the phylogenetic hypothesis with an independent sample on colobine social relationships. To this end, between June and October 2006,
data were collected on two large groups (1m:7f) of *Trachypithecus auratus* and *Presbytis melalophos* with a diet rich in fresh leaves that were kept in large enclosures at Howletts Wild Animal Park, UK. All adult and older juvenile females were subjected to focal animal sampling (448 h in total) with continuous recording of all social interactions and proximity behaviours as well as instantaneous recording of general activity and spatial behaviour. Females of both species formed roughly age-inverted linear dominance hierarchies and the few related females present did not rank together. Linearity indices, directional consistency indices and the proportion of two-way relationships in the dominance matrix did not differ between species. Rates of agonistic interaction were significantly higher than expected in the feeding context than in the non-feeding context in both species and higher again when food was provided than when feeding on the trees in the enclosure. The intensity of aggression generally was low. The species differed, with female *P. melalophos* showing agonistic interaction rates twice as high as those of *T. auratus* and displacement rates that were three times higher. Furthermore, *P. melalophos* females showed mutual avoidance after conflict, whereas female *T. auratus* regularly showed reconciliatory behaviour. A comparison with published information on other Asian colobines (*T. phayrei* and *P. thomasi*) shows more similarities between congeneric species than between more distantly related species. Possible drivers of these similarities, other than phylogenetic inertia, are discussed.

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**Ethology between Science and Practice: Different Kinds of Objectivation of Animal Behaviour (West-African and Western Europe Examples)**

Véronique Servais, Frédéric Joulian
Anthropologie de la Communication, Université de Liège, Liège, Belgium
E-Mail: v.servais@ulg.ac.be

*Key Words:* Ethology • Objectivation • Animal behaviour • Habituation

The aim of this communication is to present, in parallel, three different ways of objectifying and understanding animal behaviour. Behaviour is a bizarre object of science that has not been well thought out, neither by anthropology nor by ethology or epistemology. For example, the definition of behaviour, as opposed to simple movement, is problematic. The history of scientific ethology throughout the 20th century shows different trends, from positivist to empathic ones, with different ways of coming into contact with animals in the wild (the habituation processes in particular). This multiplicity illustrates the difficulty scientific ethology meets in treating animals and behaviours as completely neutral objects of inquiry. Scientific ways of objectivating behaviour will be compared to common sense ones, in our case with the discourses and observations we collected at the zoo from visitors commenting on primate behaviours and in West-Africa, Ivory Coast (Guéré, Dan, Baoulé), where animal behaviour (primate behaviour principally) is questioned and analyzed in very different directions. In varied indigenous contexts (daily life, hunting activities, rituals, forbidden food) we shall discuss the most salient knowledge people have about primates and what it means in term of ‘objective understanding’ of behaviour. We shall also raise the question of what it could mean to objectivate ethological knowledge in a nonscientific context and how to make the comparison with ethological science possible.
The Barbary Macaque: Working towards a Solution
Ania M. Sharwood Smith, Geert P.J.M. Jonkers
Rescue and Rehabilitation, AAP, Sanctuary for Exotic Animals, Almere, The Netherlands
E-Mail: ania.sharwood@aap.nl

Key Words: Macaca sylvanus • Welfare • Conservation • Barbary macaques

Research into the numbers of Barbary macaques (Macaca sylvanus) in Northern Africa shows local decreases of at least 70% over the last few decades. Fragmentation of their natural habitat, logging and overgrazing are some of the factors causing the fast population declines. AAP, a European sanctuary for primates in The Netherlands, has been experiencing an increasing demand for placement of wild-caught (confiscated and donated) Barbary macaques. Subsequent research into this showed that around 300 animals are brought into Europe yearly, mostly from Morocco, and most of them destined for the pet trade. The high capture rate was demonstrated to be exceeding sustainability. The Barbary macaque’s misfortunes have developed into a welfare crisis and a pressing conservation issue. Together with IUCN, local and international authorities and others, AAP is involved in an extensive programme aimed at stopping the trade, educating relevant parties, and finding solutions for local animal-human conflicts in Barbary macaque habitat.

The Problem of Quality and Comparability of Chimpanzee Faecal Samples before Hormonal Analysis – Variability and Standardisation
Jiří Škvor¹, Václav Vančata², Richard Marvan², Jana Trilčová¹,², Tomáš Polák³, Barbora Láznová³, Claudio Tennie⁴
¹Department of Anthropology and Human Genetics, Faculty of Science, ²Department of Biology and Ecological Education, Faculty of Education, Charles University in Prague, ³Premier Research Group, Prague, Czech Republic; ⁴Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
E-Mail: skvor@natur.cuni.cz

Key Words: Pan troglodytes • Behavioural endocrinology • Faecal sampling • Hormonal analysis

Due to the dissimilar nature of analysed faecal material (soaked vs. dried samples) used in different studies it may be difficult to obtain comparable results. In the initial part of the study, we analysed 70 fresh faecal samples collected in the morning from 6 mature male and female common chimpanzees at the Liberec Zoo (Czech Republic). After deeply frozen samples were thawed, they were extracted by a non-aqueous solvent. After vortexing and centrifugation, supernatants were transferred into new vials, evaporated and the residue was redissolved with phosphate-buffered saline. Aliquots were analysed for concentrations of testosterone and cortisol with competitive enzyme-immunoassays. Firstly, the extraction procedure was sufficient for testosterone EIA sensitivity; however, the absorbance values for cortisol were at the limit of detection or undetectable in about 95% of the samples tested. Secondly, the samples were markedly variable in content of water and the amount of undigested particles. In the following part of the study, 286 fresh morning faecal samples from 12 mature male and female common chimpanzees were collected at the WKPRC, Leipzig Zoo (Germany). Due to our previous findings, these samples were processed according to a modified extraction protocol, including a lyophilisation step with subsequent removal of the biggest undigested particles. We hypothesised that such modification eliminates the variability of the samples. To test our hypothesis (before we removed the undigested particles), we made a comparative analysis of the variability of soaked samples.
and lyophilised samples' weights (m). Prior to data analysis the following standardisation method was applied: \( m_{\text{standardised}} = (m_i - \text{mean}) / \text{SD} \). The analysis showed statistically significant differences in the variability of soaked and lyophilised samples' weights; the variability for the lyophilised samples was significantly smaller (modified-Levene equal-variance test, \( p < 0.0001 \)). Therefore, we conclude that lyophilised and 'purified' faecal samples compared with soaked ones are more suitable to obtain reliable results of steroid hormone assay. The findings of our study emphasise the importance of maximum possible sample standardisation.

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**Food, Sex and Violence: Influences on Intergroup Encounters in Tamarins (Saguinus spp.)**

Andrew C. Smith\(^a\), Hannah M. Buchanan-Smith\(^b\)

\(^a\)Department of Life Sciences, Anglia Ruskin University, Cambridge, \(^b\)Department of Psychology, University of Stirling, Stirling, UK

E-Mail: a.smith@anglia.ac.uk

**Key Words:** Tamarins · Intergroup encounters · Diet · Seasonality · Mixed species troops

Interactions with conspecifics are a key part of an animal’s ecology. We examine factors affecting intergroup encounters in two mixed-species troops of saddleback (Saguinus fuscicolis) and moustached tamarins (S. mystax). The monthly mean number of intergroup encounters per day for saddleback tamarins accounted for a significant amount of the variation in the monthly mean number of intergroup encounters per day for the moustached tamarins within each mixed-species troop. The majority of intergroup encounters occurred in the first quarter of their active period. More long calls were given on those days when the tamarins engaged in an intergroup encounter than when they did not. The distribution of encounters between the two categories of interaction, aggressive and calm, was not significantly different between the two species, nor was it affected by location within the home range, proximity to major fruiting trees or oestrus period. Durations of encounters were not affected by the category of interaction, season, location within the home range, proximity to major fruiting trees or oestrus period. Frequency of encounters was affected by season and oestrus period differently for each of the two study troops. Dietary indices were not affected by intergroup encounters. These findings are discussed with respect to the ecology of these species, particularly their diet, social structure and reproductive biology.

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**An Assessment of Conservation Initiatives and Priorities, and the Habitat Risks of Human Land Use to the Primates (Colobinae, Hylobatidae and Pongoide) of Kalimantan**

D.A. Smith\(^a\), S. Thompson\(^b\), K.A.I. Nekaris\(^a\)

\(^a\)Oxford Brookes University, Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford, \(^b\)Oxford Brookes University, School of Life Sciences, Spatial Ecology and Landuse Unit, Oxford, UK

E-Mail: 06053013@brookes.ac.uk

**Key Words:** Colobinae · Hylobatidae · Pongidae · Kalimantan · Deforestation · Oil palm plantations · Conservation

The island of Borneo is ranked in the top 25 list of global ‘hotspot’ regions – areas of mega-biodiversity, with special reference to endemic species. It is home to 13 primate species, eight of which are endemic. However, in the last 50 years Borneo has lost over 56% of its pri-
mary lowland rainforest as a result of deforestation and mass burning events. Logging of the forests and the cultivation of oil palm are inextricably linked, with over two thirds of all logging concessions across the Indonesian archipelago involved in conversions to oil palm plantations. Palm oil production has risen exponentially in the last 15 years, and Indonesia is at the forefront of the industry. Consequently, the pressure on its rainforests is extreme. In response, the Malaysian, Indonesian and Bruneian governments have committed to the ‘Heart of Borneo’ (HoB) agreement, which will gazette up to just under one third of the island into a series of protected area networks. Here, we used a Geographic Information System (GIS) to map the distribution of eight of the 13 primate species present in the Indonesian territory of Kalimantan, using data from the Southeast Asian Mammal Databank (SAMD). Logging concessions and oil palm plantations were mapped in relation to primate distributions, showing the impact of human activities on habitat areas. Accordingly, it was possible to predict future expansions of oil palm cultivation, and to present alternative areas for any plantations likely to convert primate habitat. Further to this, the HoB network was mapped to assess its efficacy in the protection of primate species, especially regions where species distributions’ overlap. Finally, Gap analysis highlighted conservation priority areas of primate ‘hotspot’ zones across Kalimantan which are not currently under protected area networks. The success of the HoB network and potential actions for primate conservation are discussed accordingly.

New Approaches to Understanding Tooth Development and Life History in Hominoid Evolution

Tanya M. Smith
Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
E-Mail: tsmith@eva.mpg.de

Key Words: Hominids · Great apes · Neanderthals · Imaging technology · Tooth development

Because teeth remain behind in the fossil record long after soft tissues, scientists have puzzled over the scarce dental evidence of our ancestors for over a century. The enamel of the tooth crown is the most highly mineralized tissue in the body; it is almost completely ‘fossilized’ during formation, and undergoes little change during an individual’s lifetime. Tooth size, shape, chemistry and structure may be used to infer taxonomy, body size, environment and even the diet of the individual. Furthermore, dental tissues faithfully record their formation at the level of daily and even sub-daily growth (reviewed in Smith, 2006). Developmental rate and time are permanently recorded by incremental lines that remain unchanged for millions of years. These lines represent a ‘time machine’ for scientists to look backwards into the daily life of an individual while it was growing and developing. Dental development in humans and great apes begins prior to birth and continues throughout adolescence. Dean and Wood (1981) published a seminal radiographic study of developing hominoid dentitions, suggesting that incremental development may provide novel information on differences in crown and root formation between apes and humans. Subsequent histological studies have begun to provide a new understanding of hominoid dental development, largely driven by the goal of characterizing fossil hominid dentitions. For example, it is now clear that ape and human molars do not form in the same manner or over the same period of time. Moreover, there is variation within the molar row, and among cusps of a single tooth (e.g., Smith et al., 2007). Differences in the thickness of hominoid molar enamel and the speed of extension lead to differences in the duration of crown growth. Unfortunately, the lack of comparative data on wild ape populations remains a limiting factor in our understanding of hominoid dental development. This information is essential to interpreting developmental variation in limited ape and human fossils. Analyses of dental development, molar eruption and age at death also inform our understanding of life his-
tory and developmental change in the human fossil record (reviewed in Dean, 2006). Studies on Plio-Pleistocene hominids and Neanderthals have indicated that the relatively slow developmental rate and prolonged duration of modern human crown formation may be a fairly recent and unique development. These studies are complemented by advances in imaging technology, including the application of virtual histology, revealing that the modern human developmental condition originated before 160,000 years ago (Smith et al., 2007). This extended period of dental development and, by implication, childhood may relate to social, biological, and cultural conditions necessary to support highly dependent children with prolonged opportunities for social learning. Ongoing research on dental development in juvenile hominids, which aims to assess when and where these changes occurred, will be presented.

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**Problem-Solving and Social Learning in Cotton-Top Tamarins**

*Caterina Spiezio, Francesca Fornalé, Donata Grassi*

Research Department, Parco Natura Viva, Garda Zoological Park, Bussolelengo, Verona, Italy  
E-Mail: spiezio@parconaturaviva.it

**Key Words:** Cotton-top tamarins • *Saguinus oedipus* • Social learning • Problem-solving

In the last decade, progress has been made in understanding social learning abilities in animals. Recently it has been found that social context and individual characteristics are important in acquiring new behaviours by observing others. In this study we investigate the social learning strategy adopted by cotton-top tamarins (*Saguinus oedipus*) in acquiring new behaviours to solve tasks through observation. Eight cotton-top tamarins, housed at Parco Natura Viva – Garda Zoological Park, Italy, were employed in two different experiments of problem-solving tasks in order to obtain a reward. The subjects saw a human demonstrator solve the tasks several times before they had a chance to interact with the apparatus. Furthermore, they could observe each other during the experimental sessions. Our results show significant differences across subjects in learning how to solve the tasks. However, cotton-top tamarins were able to solve problems in order to obtain the reward especially after having observed their conspecific’s interaction. Thus cotton-top tamarins can learn new behaviours by observing others. As findings of this study show that there was a homogeneous pattern of behaviour in the manipulation of the apparatus, it seems that observation could play an important role in spreading new behaviours within a colony.

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**Perceptual Grouping Ability in Humans (*Homo sapiens*) and Monkeys (*Cebus apella*): The Role of Gestalt Factors**

*Giovanna Spinozzi*, *Carlo De Lillo*, *Valentina Truppa*, *Giulia Castorina*

aIstituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy; bUniversity of Leicester, Leicester, UK; cDipartimento di Psicologia Generale, Università di Padova, Padua, Italy  
E-Mail: giovanna.spinozzi@istc.cnr.it

**Key Words:** Cebus apella • Visual perception • Perceptual grouping • Gestalt principles

In order to visually identify objects and to segregate them from the background, organisms must be able to group their component parts into perceptual wholes. General principles regulating perceptual grouping have been identified in humans and must pertain, to some
extent, to non-human species with relatively sophisticated visual systems. Nevertheless, comparative studies have shown important differences between humans and non-human primates in this domain. In order to assess whether interspecies differences in perceptual grouping could be accounted for by the prevalence of different grouping cues in different species, we carried out a comparative investigation aimed at evaluating the relative ease of processing proximity, shape similarity and orientation grouping cues in humans (*Homo sapiens*) and tufted capuchin monkeys (*Cebus apella*). We used a figure-ground segregation task requiring the subjects to identify the global shape of a multi-element pattern displayed on a background of other elements. According to the different conditions of the task, the proximity, the similarity of shape or orientation between the elements of the compound patterns and the background elements was manipulated in order to provide different grouping cues as the basis for the segregation of the global figures. Results indicate that, in capuchins, grouping by proximity and shape similarity, but not grouping by orientation, facilitated the discrimination of compound patterns. By contrast, in humans, proximity grouping was more efficient than grouping by similarity of shape and of orientation. Overall these findings point to some differences in the perceptual grouping processes required to segment an entity into its constituent parts and to integrate these parts into a coherent whole by humans and capuchin monkeys. Such interspecies differences seem to reside in a different sensitivity to shape similarity as a grouping cue.

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**Vigilance in Mixed-Species and Single-Species Groups of Moustached Tamarins (Saguinus mystax) in Peruvian Amazonia: Preliminary Results**

*Mojca Stojan Dolar, Eckhard W. Heymann*

Department of Behavioural Ecology and Sociobiology, Deutsches Primatenzentrum (DPZ), Göttingen, Germany  
E-Mail: mojca.stojan@arnes.si

**Key Words:** *Saguinus mystax* · *Saguinus fuscicollis* · Vigilance · Competition · Alarm calls

Collective vigilance is considered to be one of the major advantages of group living in animals. Bigger groups are safer due to both the detection and the dilution effect. This allows individuals to be less vigilant and spend more time engaged in other activities. The same benefits also apply to mixed-species associations with an additional advantage: the avoidance of increased intra-specific competition which inevitably appears in larger groups of conspecifics. The question however remains whether heterospecifics can really play the same role as conspecifics in increasing safety. The aim of this study was to examine the differences in vigilance behaviour between a population of wild moustached tamarins (*Saguinus mystax*) that form mixed-species groups with saddleback tamarins (*Saguinus fuscicollis*) and an island-living population that does not associate with another species. In the former population, the two species spend up to 100% of their time together and recognize each others’ alarm calls. A comparative study under mixed- and single-species conditions allows us to evaluate whether it is the number of conspecifics or the total mixed-species group size that determines vigilance behaviour. Preliminary results that will try to elucidate the importance of predation pressure and interspecific collective vigilance for forming mixed-species associations of tamarins will be presented.
**Group Coordination in Chacma Baboons**

Sabine Stückle, Dietmar Zinner

Research Group Cognitive Ethology, German Primate Centre, Göttingen, Germany

E-Mail: sabstu@gmx.de

**Key Words:** Chacma baboons • Group coordination • Leadership • Dominance

Group members need to synchronise their activities to keep the group cohesive. In mammals, individuals mainly conduct ‘consensus-decisions’ by making trade-offs to perform collective activities, and leadership is one possibility for reaching a consensus. Two forms of leadership have been proposed, ‘personal leadership’, where a single individual uses its high dominance status or experience to lead the troop, and ‘distributed leadership’, where a group of individuals or all group members make trade-offs to reach a collective decision. In baboons, the best studied taxon in this respect is the hamadryas baboon. Their coordination of troop movement seems to be accomplished by ‘distributed leadership’, with harem leader males having the most influence in the decision-making process. Less is known about the decision making in savannah baboons. We therefore observed the matutinal departure process of a group of chacma baboons (*Papio hamadryas ursinus*) in De Hoop Nature Reserve, South Africa. Individuals were defined as making a start attempt if they moved over a certain distance beyond the periphery of the group. We distinguished between successful and unsuccessful initiations, depending on the number of followers an individual recruited. Approximately 75% of the adult individuals performed a start attempt, with 62 out of 92 start attempts being performed by males. Irrespective of the absolute number of attempts, on the average, two out of three attempts were successful. According to the above definitions, the coordination process in chacma baboons can be regarded as ‘distributed leadership’ to reach a consensus. The travel direction seems to be a vote of the majority and appears to be coordinated merely through individuals setting an example by moving off.

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**Social Learning of Tool Making in Great Apes and Human Children: The Loop Study**

Claudio Tennie, Josep Call

MPI EVAN, Department of Comparative Psychology, Leipzig, Germany

E-Mail: tennie@eva.mpg.de

**Key Words:** Great apes • Human culture • Learning • Imitation • Tool use

Human (cumulative) culture largely rests on the human ability to acquire complex behaviour through social learning – especially imitation. The lack of cumulative culture within great ape traditions in the wild is consistent with the view that great apes do not engage in imitation. However, there is growing experimental evidence that great apes can and do socially learn to solve some problems, some of them even involving tool use. What type of social learning they use in such experiments is currently still unclear and also was not the focus of the study presented here. Instead, in the current study, we focused on the generality of social learning of human children and great apes with regard to tools. We used a task that involved not only tool use but also tool making. The task was to acquire a desired object by pulling it with a loop that subjects had to form from a piece of wooden wool. We demonstrated the solution to children and four species of great apes. Only the children were able to succeed. The apes failed to copy the tool making, which might be due to some restricted copying skills or else to a general failure to understand the physics of the task.
Modelling Slow Loris (Genus *Nycticebus*) Distributions in Borneo, Java and Sumatra: A Tool for Assessing Threats and Setting Conservation Priorities

J. Thorn, K.A.I. Nekaris

Oxford Brookes University, Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford, UK
E-Mail: james.thorn@brookes.ac.uk

Key Words: Slow loris · *Nycticebus* · Taxonomic revision · Distribution · Conservation

Three species of slow lorises (*Nycticebus*) are recognized in Indonesia; the greater slow loris (*N. coucang*) and Javan slow loris (*N. javanicus*) are classified as Endangered (A2cd), and the Bornean slow loris (*N. menagensis*) is classified as Vulnerable (A2cd) (IUCN Red List, 2006). In light of the on-going taxonomic revision of *Nycticebus*, the emergence of new species will further restrict individual geographic ranges. The geographic distribution of a species is a crucial determinant of global population size and, therefore, global extinction risk. Combined with the present threats of habitat loss and unsustainable harvesting for the wildlife trade, slow lorises are being subjected to high levels of ecological pressure. Accurate data on their geographical distribution are fundamental in evaluating their conservation status. In response to the paucity of information surrounding Indonesian slow lorises in the wild, this project modelled their distribution in order to identify priority areas for further research and conservation initiatives. Occurrence data for slow lorises were obtained from specimens held in zoological collections, published literature, and through analysis of questionnaires completed by field researchers. These data were entered into Maximum Entropy (MAXENT) ecological niche modelling software, along with selected environmental variables, in order to predict the distribution of slow lorises across Indonesia. The resulting predicted distributions were projected onto a Geographic Information System (GIS), and transposed with layers of current vegetation, protected area boundaries, and current land usage. Gap analysis was applied to identify gaps in the protection of each species. Analyses of the predicted distributions using GIS highlight populations most at risk from anthropogenic activities. The findings lay the foundations for further surveys and research to be carried out in priority areas, in order to establish a true picture of conservation status, behavioural ecology and species diversity.

The Primate Brain Bank


*Department of Behavioural Biology, †Department of Veterinary Science, ‡Emeritus Professor of Ethology & Socio-Ecology, Utrecht University, §Department of Pharmacology and Anatomy, Rudolf Magnus Institute of Neuroscience, University Medical Centre Utrecht, Utrecht, The Netherlands
E-Mail: i.b.toxopeus@uu.nl

Key Words: Primates · Neurology · Brain bank

In consideration of the vast possibilities for neuroscientific research offered by the brains of primates living in Europe we established the Primate Brain Bank. By conserving brain material of deceased primates in a standardised way and accompanied with good documentation the Primate Brain Bank hopes to stimulate (neuro)scientific research and a more efficient use of available material. In recent years the Primate Brain Bank has been successful in storing over 200 brains from primate species ranging from the pygmy marmoset to the orangutan and gorilla. With these brains the Primate Brain Bank has provided valuable material to a range of projects stemming from neurology, (evolutionary) anthropology, archaeology, animal behav-
bour, anatomy and veterinary science. Next, the Primate Brain Bank aims to establish a European network of brain banks to increase the influx of material. This will allow for more flexibility in conservation methods, and an even larger number and variety of projects that can be supplied. We invite everyone who is interested in our material to contact us and we call on the European zoos and scientific institutes to join the European Primate Brain Bank.

Preferable and Predictable Enrichment in Captive Common Chimpanzees: How Affiliative and Agonistic Behavioural Patterns May Be Elicited Using the Piñatas Enrichment Device

Jana Trilčová a,b, Richard Marvan a,b, Tomáš Polák c, Claudio Tennie d, Václav Vančata b

a Department of Anthropology and Human Genetics, Faculty of Science, b Department of Biology and Ecological Education, Faculty of Education, Charles University in Prague, c Premier Research Group, Prague, Czech Republic; d Department of Developmental and Comparative Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

E-Mail: jana.trilcova@centrum.cz

Key Words: Pan troglodytes · Feeding enrichment · Anticipation · Affiliative behaviour · Agonistic behaviour

Several studies have suggested that enrichment may facilitate a reduction in abnormal behaviours, e.g. coprophagy, self-mutilation or stereotypic behaviour. Thus, this study considered the possible effects of enrichment with respect to both affiliative and agonistic behaviours in a group of 11 mature chimpanzees (Pan troglodytes) at the WKPRC, Leipzig Zoo (Germany). During spring 2006, a total of 168 observational hours of behavioural data were gathered in 84 days, which in turn were divided into two alternating 14 day intervals. This resulted in 3 baseline periods and 3 experimental periods. During both periods (baseline and experimental) the apes’ habitual food supply was provided. However, enrichment in the form of 10 piñatas (these are paper boxes containing favoured food such as dry fruits or nuts) was additionally given during the experimental periods. The piñatas were provided in a predictable and monopolizable way on every second day during the experimental period, resulting in a total of 21 days with piñatas (EN) and 21 days without them (NE). A combination of focal-animal and all-occurrence sampling was used to score frequency and duration of allogrooming and the frequency of other affiliative and agonistic behaviours. The behaviour that occurred during one hour prior to the predictable feeding time and during one-hour post feeding was recorded. Wilcoxon signed-rank test was applied to compare relative frequencies of affiliative and agonistic behaviours between the baseline and the experimental period as well as within these periods. The results suggest: (1) Frequencies of affiliative behaviour were higher in the experimental than in the baseline period; (2) pre-feeding frequencies of affiliative behaviour were higher and frequencies of agonistic behaviour were lower, when compared with those during post feeding, and (3) pre-feeding during the EN period, frequencies of affiliative behaviour increased and frequencies of agonistic behaviour decreased, when compared with pre-feeding in the NE period. We conclude that, in captivity, application of a predictable and preferred enrichment device may promote social dynamics and thus reduce behavioural stereotypes.

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Picture-Object Recognition in Tufted Capuchin Monkeys (Cebus apella)
Valentina Truppa, a, b, Giovanna Spinozzi, a, Tommaso Stegagno, a, Joel Fagot, c
a Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, b Dipartimento di Psicologia Generale, Università di Padova, Padua, Italy; c Centre for Research in Cognitive Neurosciences, CNRS-CRNC, Marseille, France
E-Mail: valentina.truppa@istc.cnr.it

Key Words: Cebus apella • Pictorial stimuli • Picture-object recognition

Although pictures are frequently used in place of real objects to investigate various aspects of cognition in different non-human species, only a few experiments explicitly address the question of picture-object recognition in animals. Furthermore, available data on this topic do not provide clear evidence that non-human species treat pictorial stimuli as a representation of the real objects. We present the results of four experiments designed to assess picture processing in tufted capuchin monkeys (Cebus apella), a New World monkey species, using a simultaneous Matching-to-Sample task. The results of the first three experiments indicated that capuchins were able to associate real objects with their colour photographs and vice versa, and that such an association was not based on confusion between the pictures and the objects they represented. The results of the fourth experiment showed that capuchins were able to recognize objects in their pictures with a high level of accuracy even when less realistic images, such as black-and-white photographs, silhouettes and line drawings, were used as bi-dimensional stimuli. Overall these findings suggest that capuchin monkeys are able to establish a correspondence between the real objects and their pictorial representations.


Grooming Body Site Preferences among Captive Adult Common Chimpanzee Females
Jan Tůma, a, Richard Marvan, b, c
a Department of Anthropology, Faculty of Philosophy and Arts, University of West Bohemia, Plzeň, b Department of Anthropology and Human Genetics, Faculty of Science, Charles University in Prague, Prague, Czech Republic
E-Mail: nemazat.tuma@seznam.cz

Key Words: Pan troglodytes • Dominance hierarchy • Allogrooming sites

The goals of the present study were to verify the existence of allogrooming site preferences and whether dominance rank affected the choice of body sites being groomed. The subjects were 5 adult females of the common chimpanzee (Pan troglodytes) group at Pilsen Zoo (Czech Republic, n = 7). Data were collected over a period of three months, during 92 observation hours. The frequency and duration of grooming at different body sites were recorded using whole-day focal following. Females’ dominance ranks were determined on the basis of observed frequencies of submissive behaviours. The results showed that the proportions of grooming frequencies and duration were highly positively correlated. Therefore, only frequencies were used for statistical analysis. To test for a preference of grooming body sites, Friedman ANOVA was used. For the effect of rank on the grooming distribution, the Spearman rank correlation test was carried out. The results suggested (i) a clear female preference for grooming sites such as forelimbs, hindlimbs and shoulders, and (ii) that lower-ranking females groomed the others significantly more often than did higher-ranking females. However, the only significant correlation was found between rank and grooming the back and head: the lower the rank the groomer occupied, the more she preferred
to groom back and head sites. We conclude that subordinate females might have a tendency to avoid eye contact with dominant ones by grooming them preferentially at back and head sites. This behaviour also enables dominant females more than the others to profit from the hygienic function of grooming of body parts that are difficult to access themselves. The results are discussed in the context of the findings of other studies.

The Ontogeny of the Postcranial Skeleton in Two Neotropical Primates (Callimico goeldii and Saguinus fuscicollis)

Bernardo Urbani

Department of Anthropology, University of Illinois at Urbana-Champaign, Urbana, IL, USA
E-Mail: urbaniglobal@yahoo.com

Key Words: Neotropical primates • Callimico goeldii • Saguinus fuscicollis • Ontogeny • Postcranial skeleton

Ontogenetic studies of callitrichine anatomy are limited to research focused mainly on the adult postcranial skeleton. The goal of this study is to compare the ontogeny of postcranial skeletal development in Goeldi’s monkeys (Callimico goeldii) with data on saddle-back tamarins (Saguinus fuscicollis). The intermembral, humerofemoral, brachial, crural and ulna-radius indices of Goeldi’s monkeys and saddle-back tamarins were calculated and compared among different age-classes in order to assess the implications for their ecology and behaviour. Ontogenetic trajectories, including age at growth cessation, were also calculated. It is shown that for a given hindlimb length, S. fuscicollis has longer forelimbs than C. goeldii, maintaining this proportion across all age classes. In S. fuscicollis, relatively elongated forelimb may serve a mechanical role in reducing the force of impact when landing on large vertical substrates. In contrast, hindlimb length and pattern of hindlimb development (such as derived features of the ankle that enhanced stability) in C. goeldii appear to play a critical role in propulsion during trunk-to-trunk leaping. These differences may affect niche partitioning, foraging strategies and substrate use.

Scent-Marking in Mandrills (Mandrillus sphinx): Preliminary Reports of a Chemical and Ethological Investigation

Stefano Vaglio, Francesca Romana Dani, Yitzhak Yadid, Jacopo Moggi Cecchi, Brunetto Chiarelli

a Laboratory of Anthropology and Ethnology, Department of Animal Biology and Genetics ‘Leo Pardi’, b Mass Spectrometry Centre, University of Florence, Florence, c Bioparc Foundation, Rome Zoo, Rome, Italy
E-Mail: stefano.vaglio@unifi.it

Key Words: Mandrillus sphinx • Scent-marking • GC-MS analyses • Cutaneous glands

Mandrills (Mandrillus sphinx) are one of the few Old World monkeys to have cutaneous glands. The presumed function of these very complex glands and of the behaviour associated with them is scent-marking. Both females and males older than seven years mark the substrate with their sternal glands, but alpha males scent-mark most frequently. This study on the olfactory communication of mandrills was carried out in order to investigate the functions of scent-marking. Both chemical and behavioural approaches were used. The research was carried out on the group of mandrills housed at Rome Zoo. Using all occurrence sampling, we observed all olfactory behaviours for 250 h in the pre-mating season (from October to December 2006) and
in the mating season (from March to May 2007). To collect the olfactory secretions, we placed filter paper on special supports and males marked them spontaneously. The epidermis of the triangular area in the middle of the chest and the modified hairs of an adult female were sampled directly. Volatile compounds from the secretions were analysed by gas chromatography-mass spectrometry (GC-MS). Behavioural observations showed that sternal marking was almost always performed by alpha males in specific places on the enclosure boundary when visitors were present. Moreover, GC-MS analyses showed the presence of some volatile compounds in the males’ secretions that have a pheromonal function in other mammals. In contrast, there were no interesting volatile compounds in the females’ samples. As a consequence, we confirm the hypothesis, previously suggested by other authors, that scent-marking affirms the status of the dominant male and repels rivals, whilst we disagree with the hypothesis that it facilitates orientation within the home range. We also suggest that the same male scent-marking behaviour is involved in sexual pheromone communication, and that the female sternal mark is an imitation behaviour, used as a visual signal rather than a scent-marking behaviour.

**Conservation of Bonobos (Pan paniscus) through the Kyoto Protocol: The Establishment of the ‘Bonobo Peace Forest’ in the Maringa-Lopori-Wamba Region (Democratic Republic of Congo)**

*Stefano Vaglio*<sup>a</sup>, *Lorenzo Orioli*<sup>b</sup>, *Ulla Mauno*<sup>c</sup>, *Sally Coxe*<sup>d</sup>, *Michael Hurley*<sup>d</sup>, *Gian Claudio Faussone*<sup>e</sup>, *Brunetto Chiarelli*<sup>a</sup>

<sup>a</sup>Laboratory of Anthropology and Ethnology, Department of Animal Biology and Genetics ‘Leo Pardi’, <sup>b</sup>Department of Agronomy and Land Management, University of Florence, Florence, Italy; <sup>c</sup>Department of Environmental Sciences, University of Kuopio, Kuopio, Finland; <sup>d</sup>The Bonobo Conservation Initiative, Washington, DC, USA; <sup>e</sup>In.Ser. S.p.A., Turin, Italy

E-Mail: stefano.vaglio@unifi.it

**Key Words:** Pan paniscus · Kyoto Protocol · Bonobo Peace Forest · Reforestation

The reforestation project designed for the Maringa-Lopori-Wamba region in Democratic Republic of Congo (DRC) is an example of the possible use of the Clean Development Mechanism (CDM), a flexibility mechanism of the Kyoto Protocol, for biodiversity conservation. The project aims to enlarge the forest habitat of bonobos (*Pan paniscus*), a non-human primate species sharing almost 99% of the human genome, endemic to the DRC and currently under a strong risk of extinction. The reforestation plan will be based on the ‘Modified Okoumé Method’ (from the scientific name of the main species used, *Aucoumea klaineana*). New forest corridors with native species will be developed and a protected public reserve – including both new forest corridors and existing forest islands – will be established. This activity will complement existing conservation programmes including the establishment of Community-Based Reserves. One of the major threats for bonobos and other species has been the fragmentation of the forests. This project will target specific areas of degraded and cleared forests to establish corridors that may promote habitat viability for previously isolated and fragmented bonobo populations, in order to ensure a positive impact on their genetic variability. Moreover, in order to change the habits of local human populations, who use bonobos as food, we plan a multidisciplinary programme based on the introduction of cattle and other domestic animals, the introduction of economic activities and the planning of informative and educational programmes. This reforestation project was designed by applying the first approved ‘baseline and monitoring methodology’ for CDM Afforestation/Reforestation Project Activity. Implementation of the present venture as a CDM Project Activity provides an opportunity to be involved in the emission trade with emissions reduction achieved by reforestation. The proposal envisions from a reforested area of 5,000 hectares more than 4,000,000 tons of CO₂ emission reduction over the 30-year crediting period.
Tool Use Behaviour of Western Lowland Gorillas (Gorilla gorilla gorilla) in Captivity

Marina Vancatova
Faculty of Humanities, Charles University in Prague, Prague, Czech Republic
E-Mail: marina.vancatova@seznam.cz

Key Words: Gorilla · Social structure · Tool use

The cataloguing of individual spontaneous tool using activities in gorillas has shown that there are many common features in tool use among great apes under laboratory conditions, in captivity in general and in the wild. We studied behavioural and social changes in a group of western lowland gorillas (one male, three females and a juvenile male), including manipulation and tool use behaviour. We demonstrated how markedly the quality and quantity of tool use activities can be influenced by the equipment at a given zoo and by the availability of objects suitable for manipulation and potential tool use or tool making. Plastic boxes have become ‘universal’ tools for gorillas in Praha Zoo and they may be an increasing tool use tradition in Prague gorillas as well. However, this tradition has apparently no analogy in wild conditions. Plastic box use has become ritualized in many cases, for example, in agonistic behaviour, where the box is used a transmitter of aggression, being used as a drumming amplifier. We found in our study that tool use became part of various types of behaviour. It usually occurred during feeding, aggression, games or other play behaviour, and during social and comfort behaviour as well.

The Contribution of Primatology to the Question of the Gestural Origin of Language

Jacques Vauclair
Centre for Research in the Psychology of Cognition, Language & Emotion, University of Provence, Department of Psychology, Aix-en-Provence, France
E-Mail: jacques.vauclair@univ-provence.fr

Key Words: Vocal communication · Gestural communication · Language

I will first examine some of the major features of vocal and gestural communication in non-human primates by considering the underlying cerebral control both for perception and for production. I will then propose that gestural communication can be a good candidate for addressing the question of the origin of language. Several examples in relation to gestural communicative intentional gestures and their cerebral asymmetric organization will be especially developed. Emphasis will be put on the similarities and differences between the expression of communicative gestures in non-human primates and in human infants and children (comparative approach) as well as on the lateralization of these intentional gestures for the evolution of communicative systems and language (evolutionary approach).
Factors Influencing the Process of Innovation in Captive Great Apes (Pongo pymaeus abelii, Gorilla gorilla gorilla and Pan troglodytes)

Miriam de Vries, Carel van Schaik
Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: mir63@vtxnet.ch

Key Words: Great apes · Innovation · Social tolerance

Innovation in the wild appears very rarely. For this reason, studying captive animals is important. In addition, control over exposure to objects and other stimuli is much greater in captivity. Innovation can be defined as a novel learned skill an animal adopts independently without being influenced by social or environmental factors. Innovation seems to appear mostly in animal species that have high social tolerance as well as a slow life history and large brains. Beside social tolerance, several other factors, such as personality, individual abilities, sex and age, may have an influence on an animal’s innovation process. We also know about the influences of the different experiences animals may have had in their lives concerning novel objects and social and environmental effects. In my project, gorillas, orangutans and chimpanzees were compared. Baseline data were used to figure out social tolerance, rank and individual abilities as well as the tendency to explore known or novel objects and food apparatuses that had been in the enclosure for a long time. Furthermore, each animal was rated on its personality by at least 3 people. During the innovation experiments the apes had to solve tasks on novel food apparatuses in their day enclosure. The tasks ranged from simple to complex. The experiments were recorded on video tape. The analysis shows that low-ranking animals are interested, but because of harassment by high-rankers they are not able to maintain attention on the tasks. Social tolerance, personality and also age have been detected in preliminary results as important factors influencing the tendency of animals to explore and innovate.

Is There a Relationship between Gazing Behaviour and Social Structure? An Experimental Study with Common Marmosets (Callithrix jacchus)

T. De Wandelaer, J. Burkart
Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: judith.burkart@aim.unizh.ch

Key Words: Common marmosets · Callithrix jacchus · Social structure · Gaze aversion · Eye contact

Gaze aversion is a widespread ‘cut-off’ behaviour used by animals, including humans, to avoid aggressive interactions with dominant conspecifics. Several researchers have noticed that the tendency to avert gaze varies across species and have suggested a correlation between social structure and this tendency. The only quantitative study that systematically compared the reaction to a direct gaze in different non-human primate species (Miopithecus talapoin, Erythrocebus patas, Macaca arctoides, Macaca fascicularis, Macaca mulatta and Saimiri sciureus) was published by Thomsen (1974). He suggested that the propensity to establish eye contact might be linked to the social structure of a species. Our aim was to compare the gazing pattern of common marmosets (Callithrix jacchus) to that of other primates tested earlier by using an extended version of the same procedure. Because common marmosets are cooperative breeders that show marked social tolerance, we hypothesized that they might display less gaze aversion and hence establish more eye contact. We measured the frequency and duration of eye contact established by 18 common marmosets in reaction to passive continuous eye gaze of two different human ex-
Experimenters from two different distances (0.6 m and 1.8 m). Animals were tested individually in a test cage, for two periods of two minutes for each condition. Our results suggest that common marmoset, compared to its non-cooperatively breeding sister taxon (*Saimiri sciureus*), indeed show elevated levels of eye contact. Within each test condition, subjects who were more likely to establish eye contact also maintained it for longer. Furthermore, we found consistent individual differences over test conditions. Future work comparing these individual tendencies to establish eye contact with different measures of individual social tolerance in naturalistic contexts will further clarify the relationship between patterns of gazing behaviour and social structure.

**Bold and Cautious Personality Types in Primates: An Individual-Based Model**

*Jan Wantia*

Artificial Intelligence Laboratory, Department of Informatics, University of Zürich, Zürich, Switzerland

E-Mail: wantia@ifi.unizh.ch

**Key Words:** Coexistence · Competition · Personality types

In many taxa, individuals within one group differ from each other in a number of correlated traits, producing, thereby, so-called personality types. Usually, a bold and a cautious type are distinguished that differ, among other things, in their aggressiveness. It is still unresolved how both types coexist. Although several explanations have been suggested, there is no evidence that they apply to primates. The aim of my talk is to present and discuss an explanation of coexistence and its relevance to primates. In particular, I use a process-oriented model to study the explanation that each personality differs in its performance in different contexts, i.e. in competition within and between groups. I use a model, called DomWorld, because it previously showed resemblance with real primate societies and personality types (bold and cautious). The model incorporates only grouping and fighting, whereby the effects of winning and losing are self-reinforcing. To model encounters between groups, I develop a new model, called GroupWorld, which is based on DomWorld. I simulate bold and cautious personalities as attack strategies: Bold individuals attack always, whereas cautious individuals attack risk-sensitively, i.e. only when the chance to win is high. Results show that within groups bold individuals usually lose against cautious ones, but in competition between groups consisting of both types, groups with a higher percentage of bold individuals outcompete those with a higher percentage of cautious individuals. Thus, the performance of each personality type differs between contexts and this may support their co-existence. In evolutionary terms, one may speculate that coexistence of the two personality types may be favoured by selection at different levels, that of the individual and of the group.

**Factors Associated with Faecal Glucocorticoid Levels in Zoo Orangutans**

*Tony Weingrill, Michael Heistermann*

Anthropological Institute and Museum, Zürich, Switzerland; Department of Reproductive Biology, German Primate Centre, Göttingen, Germany

E-Mail: tonyw@aim.unizh.ch

**Key Words:** Orangutans · Genetic structure · Faecal hormones · Stress · Glucocorticoid levels

Orangutans survive in fragmented and isolated populations in Borneo and Northern Sumatra. While the genetic structure can predict survival chances of future generations, non-in-
Invasive monitoring of stress hormones could provide a more immediate picture of the state of these populations, since increased levels of stress might affect reproductive output. This would help wildlife managers to identify priority populations for which conservation efforts need to be intensified. A further application of this method is the assessment of the welfare status of orangutans living in captivity. However, a large unresolved issue impeding the utility of stress hormone assays in conservation biology and animal welfare is the understanding of what range of stress levels, over what period of time, are deleterious to an animal. This issue can be addressed by comparing stress levels of orangutans living in zoos, quarantine and rehabilitation stations, and in the wild. As the first step towards this approach we established a technique reliably to monitor stress hormones in urine and faeces, using samples from zoo orangutans. We then measured faecal glucorticoid levels from samples of 62 individuals, collected at 19 European zoos. We will present data on the effect of reproductive state, gender and age on glucocorticoid levels, and also the effect of group size and group composition. Furthermore, we will discuss the possibility that there is an intrinsic difference in the pattern of glucocorticoid excretion between the two orangutan species (*Pongo abelii* and *Pongo pygmaeus*).

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Anja Widdig\(^a\)\(^+\)\(^-\), Susan C. Alberts\(^b\), Peter Nuernberg\(^d\), Michael Krawzczak\(^e\)

\(^a\)Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany; \(^b\)Department of Biology, Duke University, Durham, NC; \(^c\)Caribbean Primate Research Centre, Punta Santiago, Puerto Rico, USA; \(^d\)Cologne Centre for Genomics, University of Cologne, Cologne; \(^e\)Institut für Medizinische Informatik und Statistik, University of Kiel, Kiel, Germany

E-Mail: anja.widdig@eva.mpg.de

**Key Words:** *Macaca mulatta* · Paternal kin · Phenotype matching · Paternity confusion

Recent studies have demonstrated that mammals, including primates, are capable of recognising their paternal kin as animals preferentially interact with their paternal kin when compared with non-kin in different social contexts. The most likely mechanisms underlying paternal kin discrimination are familiarity and/or phenotype matching, but they are not well understood specifically in species where females mate with multiple males during the time they are likely to conceive (confusion of paternity). Previous studies suggested that animals match phenotypes to identify paternal kin, but these studies failed to control for familiarity which could also explain the finding. Under the familiarity hypothesis, mothers would either mediate social bonding among their paternally related offspring or promote interaction between their offspring and the common father. We tested this hypothesis among rhesus macaques, *Macaca mulatta*, by following newborns of the Cayo Santiago population (Puerto Rico) during their entire first year of life (approximately 1500 focal hours). Paternity was determined using 15 microsatellites with likelihood ratios for paternity versus non-relatedness including all potential fathers. Preliminary analysis of the behavioural and genetic data suggest that mothers influence the interaction of their newborn infants, but probably not as a function of their paternity. This would further suggest that either fathers provide paternal care independent from the mothers’ presence (suggesting familiarity) and/or that animals indeed use phenotype matching to identify paternal kin.
An Assessment of Spatial and Temporal Variation in Range Use by a Group of Vervet Monkeys (Cercopithecus aethiops)

Erik Willems, Russell Hill
Evolutionary Anthropology Research Group, Department of Anthropology, University of Durham, Durham, UK
E-Mail: e.p.willems@dur.ac.uk

Key Words: Cercopithecus aethiops pygerythrus · Ranging behaviour · Predation risk · Spatial variation

Central to the study of animal ecology is an understanding of how animals use their environment over space and time. A detailed knowledge of this is not only fundamental in the study of the social organisation of a species but also, and ever increasingly more so, in directing conservation efforts. In primatology, the vast majority of range use studies has focused on identifying the social and ecological factors that affect the ranging behaviour of the animals. Group size and access to resources such as food, water and sleeping sites have commonly been reported to be of particular relevance in this respect. The significance of predation risk, on the other hand, is also well-documented. This study then set out to investigate temporal and spatial aspects of range use by a group of vervet monkeys (Cercopithecus aethiops pygerythrus) in relation to these social and ecological conditions in a South African mountain environment. Where appropriate, a spatially explicit approach within a Geographic Information System (GIS) was adopted and probabilistic measures of animal range use and predator class-specific predation risk are introduced. In addition, the explanatory value of a remotely sensed index of local primary productivity (the Normalised Difference Vegetation Index, NDVI) is assessed. Standard regression techniques were used to investigate temporal associations, whereas a spatial regression model looked at spatial relationships. Findings of these models are interpreted for their biological significance and several advantages of the variables and techniques employed are discussed.

Effect of Reproductive State on Wild Female Orangutans

Janneke T. van Woerden a, b, John Pettersson b, c
a Department of Behavioural Biology, University of Utrecht, Utrecht, The Netherlands;
b Anthropological Institute & Museum, University of Zürich, Zürich, Switzerland;
c Department of Animal Ecology, Uppsala University, Uppsala, Sweden
E-Mail: janneke@orangutan.nl

Key Words: Orangutans · Activity budget · Pregnancy · Oestrous · Lactation

Due to their large body size and unpredictable habitat, orangutans have little expendable energy (Knott, 1998). It has been suggested that this is one of the reasons for their semi-solitary system (van Schaik, 1999). The extra costs associated with reproduction are predicted to affect a female orangutan’s daily activity budget, yet little empirical data has been presented on this topic. The purpose of this study was to investigate the effects of pregnancy on female orangutan behaviour. Two wild female orangutans (P. p. wurmbii and P. abelii) gave birth in the Tuanan Orangutan Research Centre, Central Kalimantan and Suaq Balimming, Sumatra, Indonesia, respectively. The females were followed for several years before pregnancy, in oestrus (787, 955 h, respectively), during pregnancy (536, 430 h, respectively) and postpartum (376, 658 h, respectively). To compensate for environmental effects, females with semi-dependent offspring were used as comparison (Tuanan 8700 h, Suaq 3000 h total). Results indicate that female orangutans in oestrus, regardless of whether they had previously given birth, spent more time with males in the period preceding pregnancy compared to lactating females. However, wheth-
er a female had previously given birth does seem to influence which type of partners she prefers, e.g. flanged or unflanged male. Furthermore, ranging data was acquired using ArcGis 9.1 (ESRI, USA) for the Tuanan Research Area. The ranging area of the oestrous female decreased over time (oestrous > pregnant > postpartum), while the ranging area of lactating females did not differ over time. The combined data indicate that female orangutans when in oestrous make an effort to locate male conspecifics, increasing their range and indicate movement towards a flanged male’s longcall. Our results further indicate that pregnant female orangutans behave in a way similar to lactating females.

The Influence of Individual Abilities and Social Factors on Innovation among Captive Chimpanzees (Pan troglodytes)
Angela Ziltener, Carel van Schaik
Anthropological Institute and Museum, University of Zürich, Zürich, Switzerland
E-Mail: a.ziltener@access.uzh.ch

Key Words: Chimpanzees · Innovation · Exploration · Personality · Social position

Innovation is a process that generates in an individual a novel learned behaviour that is not simply a consequence of social learning or environmental induction (Ramsey, Bastian & van Schaik, 2007). Furthermore, innovation seems to be associated with long-lived, large-brained species living in variable environments. Because innovation in the wild appears very rarely and the exposure to objects and other stimuli is very difficult to control, studying innovation in captive animals is necessary. However, little is known about the individual abilities or social factors that influence innovative behaviour. The efficiency of innovation may depend on various factors, including personality, sustained attention, social position and social tolerance. Critical preconditions for innovation could be response to novelty and exploration. The aim of this study is to evaluate these two critical preconditions and to determine which factors influence the efficiency of innovation in three captive groups of chimpanzees (Pan troglodytes). Baseline observations were conducted in order to determine the social position, the personality and the friendships of the subjects. The subjects were then exposed to novel objects and different food apparatuses in the day enclosure. Preliminary results suggest that personality and social tolerance are two important factors influencing innovation. Moreover, non-tolerated low rankers appear to have less sustained attention, because they are often distracted by the high rankers and have to abandon the object/apparatus as a consequence. Finally, the type of novel object and the level of difficulty of the task can influence the novelty responses and the innovative behaviour. Additional factors affecting the individuals’ ability to solve tasks are discussed.

Ecology and Use of Day Shelters in Red-Tailed Sportive Lemurs (Lepilemur ruficaudatus)
Dietmar Zinner, Roland Hilgartner
Cognitive Ethology, Deutsches Primatenzentrum, Göttingen, Germany
E-Mail: dzinner@gwdg.de

Key Words: Lepilemur ruficaudatus · Day shelters · Thermoregulation

Red-tailed sportive lemurs (Lepilemur ruficaudatus) are pair-living nocturnal lemurs of western Madagascar. They use tree holes as day shelters and spend a large part of the daytime in their holes. These shelters may have various functions, such as protection against predators...
or facilitation of thermoregulation. To fulfil these functions, the tree holes have to provide certain minimum requirements. Between 2000 and 2005, we studied a population of 28 sportive lemurs in the Kirindy Forest, western Madagascar. More than 115 shelters were examined with respect to an array of ecological variables, such as size, height, depth, number of entrances, tree species, dead or live wood, and number and species of cohabitants, such as birds, reptiles, rodents or snails. For eight shelters we measured inside and outside temperature. We identified 22 tree species that were used as day shelters. Average inner diameter of tree holes was 10.4 ± 2.8 cm. On average, each sportive lemur had six shelters in its home-range and each shelter was used on 10 consecutive days before changing to another. Male and female pair partners used the same shelter only successively (with a few exceptions). In contrast, mothers and their offspring used shelters simultaneously.

Geographic Variation in Orangutan Diet: How Important is Culture?

Nicole Zweifel a, b, Meredith Bastian b

a Anthropologisches Institut, Universität Zürich, Zürich, Switzerland; b Department of Biological Anthropology & Anatomy, Duke University, Durham, NC, USA
E-Mail: nzweifel@gmx.net

Key Words: Orangutans · Pongo pygmaeus wurmbii · Diet composition · Food choice

Foraging decisions in rainforest primates require choosing between hundreds of possible food items of which the profitability might not be known. Some items might be hidden and/or require special feeding techniques. So far most studies on orangutan diet have focused only on special feeding techniques or tools used to process certain items. The aim of this study is to establish possible variation in diet composition within and between populations and to estimate the degree to which diet composition has a cultural basis. This study systematically compares the overall diet composition of two wild orangutan populations (Pongo pygmaeus wurmbii) in Central Kalimantan, Borneo. The two nearby sites, Tuanan and Sungai Lading, are situated in ecologically similar habitats, separated by an impassable river, which forms a dispersal barrier. Diet overlap was assessed through the observed difference between actual (items eaten at each site) and potential diet similarity (items available at each site). By collecting dry specimens of all species eaten at the two sites, all food species were identified with the aid of local botanists and by crosschecking them directly with the collection at the Wanariset herbarium. After producing a complete food list, we investigated which items were actually available at both sites during the study period. Analyses thus far indicate that diet overlap between sites is greatest for fruits and smallest for fallback food items. This indicates that variation in diet between sites increases with decreasing profitability of the potential food item.