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Prevalence of Helminthes Infection among Non-Human Primates in Southwest Nigeria

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Key Words: Zoological gardens · Parasitic infection · Season

We sampled three selected zoological gardens in southwestern Nigeria with the aim of documenting the prevalence of helminth parasite infections in their non-human primates and assessing the risk of transmission to humans. We subjected freshly voided faecal samples of the primates to diagnostic tests, namely modified formal ether sedimentation, floatation technique and larvae faecal culture method to facilitate helminth identification. Six helminths were identified in the primates. These were *Taenia* sp., *Strongyloides* sp., *Heterodera* sp., *Trichuris trichuria*, *Ancylostoma duodenale* and *Ascaris* sp. We observed the highest prevalence (40%) in the primates at Oyo Themes Parks and Gardens Zoo, followed by 16.6% in the primates at the University of Ibadan Zoo, while 0% was recorded in primates at the Obafemi Awolowo University Zoo. We recorded a high prevalence in the wet season and a low one in the dry season. We also observed that the zoo setting and the number of animals housed influenced the prevalence of helminth infections in the primates.

Gastrointestinal Parasites and Ectoparasites in Wild Javajjn Slow Loris (*Nycticebus javanicus*)

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Key Words: Strepsirrhines · Nocturnal · Asia · Faecal flotation

We present the first results of analyses of faecal samples from the free-ranging Javan slow loris (*Nycticebus javanicus*), for evidence of gastrointestinal and ectoparasites. Javan slow lo-

risers are nocturnal primates weighing between 850–1,100 g. The study animals consumed a diet comprised mainly of exudates and nectar, followed by animal material and a small proportion of fruits. In June 2012, we sampled eight individual *N. javanicus* for parasites at Cipaganti, Garut District, Java. We found seven individuals infected with gastrointestinal parasites. We report hookworm (*Necator* spp.) – eggs and adults, pinworms (*Enterobius vermicularis*) – eggs and adults, and *Trichostrongylus* – eggs and adults. One adult male Javan slow loris presented a skin rash and we took samples for ectoparasite diagnostics. The ectoparasite species could not be identified, but had a close resemblance to a skin mite species. The rash had disappeared completely by his next tri-monthly check-up. Subsequent health checks of *N. javanicus* revealed a prevalence of *E. vermicularis* during seasons with heavier rain, suggesting seasonal changes in parasite loads. This is the first study of parasites of this highly endangered primate taxon. The population, however, resided in an extremely disturbed human-dominated landscape. A next step would be to compare these results with a study in a less disturbed area to understand if lorises regularly cope with such parasite loads, or if this is another consequence of the habitat loss faced by *N. javanicus*.

Do Rank and Age Affect Primates' Inhibitory Control? Japanese Macaques (*Macaca fuscata*) and Chimpanzees (*Pan troglodytes*) Compared

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Key Words: Inhibitory control · Japanese macaques · Chimpanzees · Age · A-not-B error task

Inhibitory control allows the suppression of a prepotent response in favour of an alternative response that may be more effective as a means to obtain a goal in a given context. It is, therefore, relevant for problem solving. How primate species compare with regard to inhibition is hard to interpret based on previous studies with usually small sample sizes and strong individual variation. Particularly, age and rank have been suggested to play an important role in subjects' inhibitory skills. In order to investigate this, we tested a large sample of chimpanzees ($n = 64$, 33 females and 31 males, 4–31 years-old) from the Ngamba Island Chimpanzee Sanctuary, Uganda, and the Sweetwaters Chimpanzee Sanctuary, Kenya, and Japanese macaques ($n = 21$, 13 females and 8 males, 4–24 years-old, assigned to rank categories by expert observers) from Koshima, Japan. We presented them with two tasks that required the inhibition of prepotent responses related to space. In the 'A-not-B error task' subjects saw food disappear under one of three aligned cups and were allowed to retrieve it. In the first three trials, the food was hidden always under the same cup but on the fourth trial, just before the retrieval, the experimenter visibly changed the location of the food. Most subjects of both species solved the problem on their first attempt in the two sessions given. In the 'cylinder task', subjects saw food enter a cylinder and were allowed to retrieve it. For the first four trials, the cylinder was opaque but, subsequently, we offered ten trials with a transparent cylinder. We measured the number of retrievals in which subjects did not try to get the food directly, bumping their hand against the front of the transparent cylinder. Whereas most chimpanzees also solved this task, macaques showed an effect of age, with younger individuals performing better than older ones.

Prosocial Behaviour across Six Primate Species: The Effect of Different Paradigms

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Key Words: Prosocial behaviour · Token exchange · Apes · Spider monkeys · Capuchin monkeys

Prosocial behaviour is any behaviour performed by one individual to alleviate others' need or improve their welfare (Cronin, 2012). In the lab, prosocial behaviour has been studied with different paradigms to analyse whether individuals spontaneously provide food to their partners at no extra cost for themselves. Some paradigms provided individuals with the chance to pull a sliding table, retrieve food and decide whether partners should also receive food. With these paradigms, prosocial behaviour was usually not elicited (e.g. Jensen et al., 2006; but see Burkart et al., 2007). Other authors have therefore questioned the validity of these paradigms (e.g. because they were not natural enough), and used tokens to provide individuals with the chance to donate or not donate food to partners by selecting tokens and exchanging them with the experimenter (e.g. Horner et al., 2011). Here, we will present the results of a study in which six different species (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo abelii*, *Cebus apella* and *Ateles geoffroyi*) have been tested with two different paradigms (sliding tables and tokens) that have usually provided contrasting results even with the same species. We aimed to analyse (i) whether using different paradigms elicited different responses in terms of prosocial behaviour, (ii) whether prosocial behaviour varied across species or as a function of other factors (e.g. sex, age, quality of relationship). No invasive procedures were used, contact with the animals was limited to food and token exchange, individuals were never food or water deprived and took part on a completely voluntary basis.

How to Make Comparative Cognition Really Comparative

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Key Words: Comparative cognition · Procedural differences · Intra-specific variation · Inter-specific comparisons

Research on comparative cognition has increased dramatically in the last few years. However, we have only just begun mapping cognitive skills in different taxa and we still have a limited understanding of what factors affect the distribution of cognitive skills and their evolution. Here we aim to critically review some recent literature on animal cognition by also providing original data in support of our affirmations. In particular, we identify and discuss the importance of those factors which can limit and bias further developments of research on comparative cognition: (1) procedural differences in cognitive tasks can significantly affect the reliability of comparisons across taxa; (2) intra-specific variation in terms of socio-ecological characteristics can importantly affect the distribution of cognitive skills across conspecific individuals and popula-

tions; (3) only few taxa have been systematically studied, while data on the cognitive skills of most taxa are still patchy. Finally, we propose a series of possible solutions to these issues that can guide future research on comparative cognition, including the use of automatized machines, the simultaneous collection of ecological, social and cognitive data from the same populations and the use of more tasks to test specific cognitive skills across different taxa.

Research Contributions from Lola Ya Bonobo

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Key Words: Bonobo · Research · African sanctuary · Captive primates · Democratic Republic of Congo

Lola Ya Bonobo (Lola) is the only bonobo sanctuary in the world. It is located in the Democratic Republic of Congo and is home to ~60 bonobos. Besides aiding in conservation efforts and providing a safe haven to bonobos who have lost their mothers to the rampant bush meat trade, Lola offers researchers an invaluable resource to understand our evolutionary history better. Since 2007, there have been 40 publications from Lola. These studies implemented at Lola have covered a variety of scientific interests including today's most cited bonobo publication. Lola's most well-known publication examined behavioural and cognitive differences between chimpanzees and bonobos. Through this study, scientists discovered the bonobos' natural knack for cooperation and food-sharing (FS). A complimentary study, examining the role of hormones that accompany the behavioural differences of FS, was later conducted showing differences in chimpanzee and bonobo endocrine shifts during FS events. Lola also aided scientists by providing them with blood samples to decode the bonobo genome. The results revealed that we share 98.7% of our DNA. Of further note, bonobos from Lola have been studied to monitor emerging diseases that may affect humans in the future. Finally, scientists have gathered evidence that education programmes from the sanctuary have had positive conservation effects on the local populations. Although Lola has made such great progress in the scientific field, it is the hope of the sanctuary to continue facilitating researchers. In the future, in collaboration, we hope to understand how to battle deadly diseases that harm bonobos and other great ape species, how to use contraceptives to control inbreeding and how to use the research to help the Congolese want to conserve the unique bonobo.

Weight-Bearing Mechanisms of Infant Carrying in Quadrupedal Primates: The Case Study of Olive Baboons

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Key Words: Infant carrying · Weight-bearing · Primates · Biomechanics

Many primates carry their infants over long distances until they become autonomous and relatively heavy; therefore, an efficient carrying mechanism is probably of great adaptive value.

This may also have been of crucial importance in the course of the evolutionary transition to permanent bipedal locomotion in hominins. Comparative experimental data for several locomotor models could provide quantitative data on the impact and potential adaptive mechanisms. Unfortunately, such data are almost completely lacking. We addressed this lack by a biomechanical analysis of the weight-bearing mechanisms of quadrupedal walking of loaded (infant: newborn to 12 months) and unloaded female olive baboons. During 8 months in captivity at the Primate Station (CNRS, France), 11 females regularly walked on an instrumented walkway. Motion capture was performed with a video recording system (200 fps, HD) and a force plate available at the technical platform. Two mechanisms are involved during infant carrying depending on both the position and the mass of the infant: (1) when the females carry non-autonomous infants on their abdomen, both their hind and fore limbs become more flexed than in the unloaded condition while the distribution of normalized vertical ground reaction forces (GRF) is not affected, with the posterior component slightly superior to the anterior one, and (2) when the females carry heavier infants, then on the lumbar portion of their back, the hind limbs bend while the normalized GRF increase posteriorly. Both mechanisms prevent increasing constraints on the forelimb that could be expected while carrying a load quadrupedally. Consequently, despite carrying a load, the mother's regular activities are not affected since the hands are kept as free as they are in the unloaded condition.

Primate Pragmatics: Female Putty-Nosed Monkeys Use Contextual Information to Disambiguate the Cause of Male Alarm Calls

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Key Words: Information · Pragmatics · Primate communication · Functional reference · Contextual information

Animal calls vary widely in their potential to convey information reliably depending on a number of factors including the degree to which they are acoustically distinct from other call types, and also whether they are given in a narrow or wide range of contexts. Calls that are easily distinguishable and context-specific have been termed functionally referential, and have received considerable attention because they offer a potential link with human symbolic communication. In the context of predator detection, they have commonly been described as predator-specific alarm calls and are thought to refer to specific predator types that require different escape strategies. However, in putty-nosed monkeys (*Cercopithecus nictitans*, a forest primate) adult males have a very restricted repertoire of vocalizations which are given in response to a wide variety of disturbances which include, but are not limited to, predators under conditions of poor visibility. Yet, to respond adaptively, listeners must find ways to identify the cause of a signal. In order to investigate this process, we carried out a series of field playback experiments on females in a habituated group in the Gashaka Gumti National Park, Nigeria, in which male alarm calls were presented either alone, or following acoustic contextual information that simulated the presence of predators or the occurrence of a natural, but non-threatening, disturbance. We demonstrated that listeners appear to integrate contextual information in order to distinguish among possible causes of calls. We conclude that, in many cases, pragmatic aspects of communication play a crucial role in call interpretation and place a premium on listeners' abilities to integrate information from different sources.

Not All Who Wander Are Lost: The Socio-Spatial Dynamics of Home Range Establishment by Young Female Bornean Orangutans at Tuanan

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Key Words: Spatial association · Sexual activity · Female philopatry · Home range establishment · Home range overlap

Adult female orangutans are philopatric, living in home ranges that overlap with those of their female kin. The process through which maturing females actually establish their home ranges, however, has not yet been clarified. This study combines ranging data with behavioural and social data in order to gain a better understanding of the process of home range establishment among young female Bornean orangutans (*Pongo pygmaeus wurmbii*). Detailed ranging, behavioural, and social data focusing on 3 mother-daughter (now independent) pairs were collected over a 9-year period at Tuanan, Central Kalimantan, Indonesia, totalling over 6,000 h of data per dyad. Ranging behaviour for each female was analysed using probabilistic methods, focusing on changes over time in the females' home ranges, as well as the spatial distribution of time spent ranging in association with conspecifics. Although individual variation between the three maturing females was apparent, three phases can be recognized. First, during early independence, a young female's association time with her mother decreases substantially over time, but she continues to range within her familiar natal range, which is also her mother's home range. Second, during her first phase of sexual activity, she explores far outside of her natal range, often accompanied by others, especially her mother or an adult male. Finally, after the birth of her first offspring, her home range shrinks in size as she settles into an area that is adjacent to and highly overlapping with her mother's current home range, although her association time with her mother remains relatively low. This study lends insight into how these maturing semi-solitary animals negotiate their spatial distribution and association time.

Effects of Habitat Degradation and Reproductive Seasonality on Faecal Glucocorticoid Metabolite Levels of *Eulemur collaris*

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Key Words: Habitat degradation · *Eulemur collaris* · Littoral forest · Glucocorticoids · Reproductive stages

The littoral forest of south-eastern Madagascar is among the most threatened habitats on the island and today is only represented by isolated archipelagos of fragments. Since the endangered collared brown lemur *Eulemur collaris* is the largest seed disperser of the Malagasy south-eastern littoral forest, its survival in this habitat is crucial. In this study, we compared faecal glu-

corticoid metabolite (fGCM) levels, a measure of physiological stress, between groups of collared brown lemurs living in a degraded forest fragment and groups occurring in a more pristine area. To this end, we analysed 279 faecal samples collected year-round from 4 groups of collared brown lemurs using a validated 11-oxoetiocholanolone enzyme immunoassay and tested if fGCM levels were influenced by reproductive period, gender and habitat degradation. The lemurs living in the degraded forest had significantly higher fGCM levels than those living in the more pristine area. As predicted, in males highest fGCM levels were recorded during the mating period at both sites. In females, high fGCM levels were present during the gestation period in the degraded forest while much lower levels were recorded at the more pristine site. Since mating and gestation phases are both occurring during the lean season in the littoral forest, these results likely reflect a combination of ecological and reproductive pressures. Our findings provide a clear indication that habitat degradation has additive effects to the challenges found in the natural habitat. Since increased stress hormone output can have long-term negative effects on population health and reproduction, our data emphasize the need for effective conservation plans for the species and may add to the development of them.

Study of the Morphology of Gustatory Lingual Papillae in *Pan troglodytes* by Scanning Electron Microscopy

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Key Words: Tongue · Gustatory papillae · Scanning electron microscopy · Chimpanzee

The chimpanzee is the primate with the greatest resemblance to humans in feeding habits, since the herbivore part of its diet is complemented by proteins of animal origin from meat, insects, eggs and honey. There are five types of lingual papillae, two are mechanical (filiform and conical) and three gustatory (fungiform, foliate, and vallate). The latter are the objective of the present study, since the variety of foods that constitute the diet of chimpanzees suggests that taste is very well developed. The tongues of five adult chimpanzees (*Pan troglodytes*) that died in zoological parks from natural causes, 3 males and 2 females, were studied through scanning electron microscopy (SEM). Fungiform papillae are distributed among filiform ones throughout the surface of the tongue, and on its surface gustatory pores appear. Foliate papillae are located in the edges of the posterior third of the tongue and adopt the form of 4–6 parallel folds among which gustatory pores are observed. Vallate papillae are located in the posterior third of the back of the tongue, their number and distribution is very variable, and they adopt 'Y' or 'V' shapes, generally asymmetric and of different sizes, in many cases with a double nucleus. Gustatory pores are located in the external wall of the median sulcus that separates the central nucleus from the peripheral pad. In the base of the three types of papillae, secretory pores and microridges were observed. Overall, the three types of papillae studied are very similar in morphology and distribution to those described in other primate species, including humans.

The Effects of Lived Experiences on Primate Social Cognition

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Key Words: Joint attention · Chimpanzees · Infancy · Culture

The prototypical form of infant social cognition is coordinated joint engagement, in which infants coordinate attention to a social partner with attention to an object or event. Current theories on the evolution of primate social cognition ignore the possible influences of lived experiences (past and current socio-emotional factors) on both human and non-human primates. We observed human infants with 3 different cultural experiences (from Western urban, Subsistence farming, and Hunting/Gathering societies) and chimpanzee infants with 4 different rearing experiences (Zoo, Enriched Laboratory, Wild, and Human-raised) in their everyday settings, at 1 year of age, to document the role of lived experiences on joint engagement. Human and chimpanzee infants were equivalent in their rate of joint engagement, and also in their rate of infant-initiated joint engagement, i.e., humans and chimpanzees were equally motivated to engage jointly with social partners. Interestingly, in three of the groups (Western urban, Subsistence farming humans and Human-raised chimpanzees) the topic of joint engagement was objects more often than social events. In the other groups (Hunting/Gathering humans and the 3 group-living chimpanzees), the topic was social events more often than objects. Positive emotion from social partners during joint engagement was significantly higher for infants living in object-focused groups compared to those living in social-focused groups. There was significant variation within each species in the topic and the emotion surrounding joint engagement. In building evolutionary scenarios, therefore, we must be mindful of the significant impact of socio-emotional factors, lived experiences, on developing social cognition.

Differential Manipulative Strategies in Great Apes during a New Complex Tool Use Task

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Key Words: Tool use · Great apes · Manipulative strategies · Dexterity

A high level of manual function and dexterity is an important adaptation in primates. Some authors suggest that these abilities have coevolved with bipedalism, tool-making and use, hand preference, brain enlargement and language in humans. All primates use a great variety of grips and hand movements. Studying a new complex task of tool use in apes helps to understand better the evolution of this parameter in humans. We created a specific tool-using task consisting of the recovery of nuts positioned in a wooden maze outside the cage (grid with a mesh size of 5 × 5 cm) with a stick. Here, we describe manual strategies (hand preference, hand posture and in-hand movement) of four species of great apes (8 bonobos, 4 orangutans, 8 chimpanzees and 3 gorillas). Not only did the bonobos and orangutans have the greatest interest in the mazes, moreover, only these two species changed their tool (branch) during the experiment. According to the subjects and

the species, we quantified and described different forms in-hand movements in relation to a change in grip of the object for more precise trajectories. In addition, we show a preference towards the right hand for almost all the subjects in all species. Orangutans (arboreal) and bonobos (terrestrial and arboreal) had been considered infrequent tool users until recently, yet they seem to be excellent manipulators. Some current hypotheses suggest a link between the mode of locomotion (terrestrial versus arboreal) and manipulation in primates, with a tendency for an exaptation of manipulation strategies in arboreal species. The results of this study are discussed in relation to hypotheses about the emergence of tool use in primates and especially in relation to the mode of locomotion.

Local Adaptation to Forest Life during the Reintroduction Process of *Pongo pygmaeus morio* at Kehje Sewen Forest – Restorasi Habitat Orangutan Indonesia East Kalimantan

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Key Words: *Pongo pygmaeus morio* · Reintroduction · Adaptation · Daily activity · Histories

The population of *Pongo pygmaeus morio* is steadily declining and it is classified as an Endangered species (IUCN 2012), which makes the reintroduction programme of *P.p. morio* a concern of orangutan conservation. The monitoring of newly released rehabilitant orangutans allows us to observe every step of their adaptation to the new environment and is also important to evaluate the procedure of such reintroduction programmes. During our observation work, we investigated activity patterns, food choice, travel height and the nest-building abilities of six orangutans, ranging between eight and twelve years old, at Kehje Sewen – Muara Wahau in East Kalimantan. Our results show that all individuals spent most of their time feeding (52%) with fruits accounting for the largest proportion of all food items (53%) which did not differ from the habits of wild orangutans. Furthermore, we observed that most of our focals were able to build their own nest (41%), although some individuals improved (20%) or just reused (15%) an old nest. Moreover, they spent 17% of their total activity time on the ground and 66% of the time in the trees up to 10 m. The animals' adaptation to their new environment was further influenced by factors such as age, rehabilitant or wild individuals and the time they spent in quarantine or on special rehabilitant islands, but also by the type and the productivity of the new habitat. An important indicator for a successful release of an orangutan into a new habitat is its ability to build its own sleeping nest.

Assessing the Relationship of Positive Emotion, Emotional States and Welfare in Captive Gorillas

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Key Words: Welfare · Personality · Emotion · Breeding · Gorilla

Research in the field of animal welfare has been increasingly undertaken to assess the negative effects of captivity. Only recently has the concept of positive welfare received a sig-

nificant impetus with the introduction of new methodologies which facilitate new possibilities to assess, for example, positive emotions and emotional states of animals and their relation to animal well-being. Behavioural markers, like extroversion (play and breeding) as well as spontaneous expressions will enable researchers to look at the positive welfare status of gorillas using a multidimensional approach (a combination of visual expressions). Furthermore, a non-invasive cognitive bias experiment offers the opportunity to assess emotional states and will provide another indicator to measure positive experiences in gorillas' captive environment. Based on the fact that individual differences impact on positive well-being and quality of life of captive animals, ratings on personality and subjective well-being will help to understand the influence of personality on breeding and conservation success. In this study, information gathered out of the combination of behavioural (pleasure of play and breeding) and experimental cognitive measures, as well as the assessment of personality and subjective well-being, will increase our understanding of positive emotion and emotional states in captive gorillas and their relation to animal welfare. One outcome will be to examine whether repeated or steady positive emotional experiences lead to a global state of positive mood in captive gorillas. Furthermore, it is expected that gorillas' health can be improved if positive emotion and emotional states and experiences can be enhanced and cultivated and this can, therefore, increase the quality of the apes' life in captivity.

Growing Up in the Light of Endocrinology: Life History Features of Bonobos and Chimpanzees

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Key Words: Ontogeny · Development · *Pan* · Endocrinology

Hominoid primates are characterized by a slow life history and a long life expectancy. Life history includes specific endocrinology events such as adrenarche and gonadarche. Identification of the emergence of and shifts between certain life stages is usually based on measurements of physiological changes that are relatively consistent within and across species. The chimpanzees *Pan troglodytes* and the bonobos *Pan paniscus* share a long phylogenetic history, and there is a large overlap in terms of their morphology and physiology. Although data on patterns and timing of development in *Pan* are biased towards chimpanzees, recently, corresponding data from bonobos became available. Multiple lines of evidence show that bonobos develop more slowly and retain juvenile features in, for example, cranial anatomy for a longer time. One of the first endocrinology event during lifetime is adrenarche. So far, it has been reported to occur in only chimpanzees and humans. We used age-related changes in dehydroepiandrosterone-sulfate (DHEA-S) secretions to identify adrenarche in bonobos. Changes in DHEA-S have been related to adrenarche in humans and chimpanzees. To investigate if adrenarche exists in bonobos as well, we measured DHEA-S levels in urine samples of 96 bonobos from zoos all over the world. We found that bonobos exhibit a pattern of DHEA-S excretion which is comparable to the pattern observed in chimpanzees. This indicates that bonobos do undergo adrenarche and that the timing of onset is similar in the two *Pan* species. Furthermore, we measured urinary total T3 (triiodothyronine), an additional marker of development, in 96 samples of bonobos and 100 chimpanzees. Additionally, we will present preliminary results on the temporal variation in urinary T3 during ontogeny.

Biomechanics and Control of Walking in Olive Baboons (*Papio anubis*): New Perspectives from Trained and Instrumented Animals

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Key Words: Walking · Integrative analysis · Motor control · Training · *Papio anubis*

Non-human hominoids are ideal comparative models for understanding the bipedal walking foundations in hominines. Nevertheless, with regard to long-term investigations, full integrative analyses of locomotion (e.g. anatomy, biomechanics and motor control) are almost impossible to realize on these models. Cercopithecines, more accessible in a captive environment and facultative bipedal primates, constitute increasingly used alternative models. Motor control studied by intramuscular electromyography (EMG) is difficult to implement for long-term experiments for some developmental and ethical reasons. Surface EMG (sEMG), currently used in human motion analysis, could constitute an alternative tool. Thanks to the *Motion Analysis of Primates* platform and the facilities available at the CNRS Primate Station (Rousset, France), we want to demonstrate that long-term, full integrative analysis of locomotion can be implemented within a short period of time and provide original data on bipedal locomotion for olive baboons. Based on the positive reinforcement method, 4 young baboons have been trained to walk as freely as possible in the experimental environment and to accept wireless sEMG electrodes and a jacket. At the end of 6 months of training and testing for electrode positioning, kinematics, kinetics and muscles activity of walking were simultaneously measured for 2 baboons. During bipedal walking, we observed a single-humped GRF profile with an impact peak and a coordinated activity of the main hind limb muscles, as well as kinematics resembling those described previously. These results demonstrate that full integrative and non-invasive analyses are feasible and open new perspectives in particular for the follow-up of major phases in locomotor development of non-human primates.

Increase of Genetic Diversity over the Last 11 Years Demonstrates Gene Flow in a Small Population of *Eulemur collaris* Inhabiting the Fragmented Littoral Forest of South-Eastern Madagascar

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Key Words: Gene flow · Genetic diversity · Fragmentation · *Eulemur collaris* · Littoral forest

The collared brown lemur *Eulemur collaris* is an endangered prosimian inhabiting the littoral and lowland rainforests of south-eastern Madagascar. In the littoral forest, in particular, the

species is threatened by severe habitat fragmentation and only small populations survive in tiny fragments. These lemurs have been shown to exhibit an extreme degree of social and ecological flexibility by adopting different group size and ranging areas depending on the level of habitat disturbance. Although these medium-sized primates are considered very mobile, it is not clear whether any gene flow still exists between these populations or what may represent a barrier for the species. In this study, we analysed ~300 bp of D-loop mitochondrial DNA and 8 microsatellite loci from 83 faecal samples of collared brown lemurs collected over a period of 11 years (2000, 2004, 2008, 2011). The samples were collected from two fragments of littoral forest, Mandena and Ste Luce. Since the Mandena population was relocated in 2000 to a forest fragment where there were no resident lemurs before, we have genetic samples from all the individuals in this area and thus the initial genetic diversity. The results from the mtDNA analysis show the introduction of new lineages in the Mandena population in 2008. Similarly, autosomal results indicate an increase in diversity during the last 8 years. This suggests that genetic contacts occurred after the lemur relocation despite the matrix of savannah, exotic plantations, and roads that today surround the area. These findings offer encouraging clues for the future conservation management of this endangered lemur.

Predation in the Tree Tops

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Key Words: Lemur · Predation · Locomotion · Nails · Claws

Primates are primarily arboreal, their grasping hands and feet, sensitive pads on fingertips and toes and broad nails may aid in this arboreality, but most arboreal mammals have clawed digits. However, Cartmill's (1974) classic hypothesis claims that primate nails do not give a better arboreal ability. Madagascar's long isolation means that unique species have evolved to suit the ecological conditions. The only mammalian carnivore big enough to prey on lemurs is the fossa. How effective are its long body, short legs and clawed digits in hunting lemur prey? Do lemurs' grasping hands and feet, short trunk and long legs give them an advantage in the trees? We deployed a range of techniques, including a field study of the fossa, its scats and its lemur prey, as well as the anatomy of both prey and predator, to address this question. Our field study of two lemur species preyed by fossa indicates that supports are selected for external stability, permitting possible internal energy storage in tendons, and leaping trajectory is tuned to fine-branch density. In contrast, the fossa does not have a controlled ability to move on small peripheral branches. Fossa depend on hyper-robust claws as hooks when climbing upwards and, by foot rotation, to control descent; however, they lack the hind limb muscle mass required for controlled descent as their locomotion is, in contrast to that of lemurs, forelimb powered. Evidence suggests that fossa arboreal locomotion is expensive compared to that of lemurs since height gain is largely by high-cost near-vertical climbing. The Cartmill (1974) hypothesis is not, therefore, supported by our work. On the contrary, claws enabled effective predation, both directly and by permitting fossa to dig prey from tree-holes.

Habitat Corridor Utilisation by the Grey Mouse Lemur *Microcebus murinus* in the Littoral Forest Fragments of South-East Madagascar

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Key Words: Fragmentation · Habitat corridors · Non-native plantations · Grey mouse lemurs · Littoral forest

Tree dwelling animals which inhabit forest fragments are expected to display low levels of genetic diversity due to isolation. The grey mouse lemur *Microcebus murinus* has been shown to be resilient to some degree of habitat fragmentation and is, therefore, an ideal species to study to understand how to counteract this threat. In the south-eastern corner of Madagascar, the tiny remnant fragments of the highly threatened littoral forest are today linked by habitat corridors which consist of non-native plants, native plants or a mixture of both. Previous studies have revealed that grey mouse lemurs prefer to utilise native plants. However, as the regeneration of the native forests is slow and non-native plantations grow fast, it is crucial to regularly monitor when and whether threshold conditions for using non-native formations are reached. During this 3-month study, the effectiveness of different matrices of habitat corridors, with different composition and age, as dispersal mediums was assessed for grey mouse lemurs in the Mandena Conservation Area. Night walks and capture-recapture methods, using Sherman traps and non-invasive semi-permanent marking techniques, were undertaken. As expected, lemurs were observed at a higher frequency in corridors with higher proportions of native plant species, while corridors where non-native species prevailed were almost unused. The effectiveness of using non-native plantations as habitat corridors for endemic species is discussed.

Do Adults and Youngsters Equally Pay Attention to Vocal Exchange Rules? The Case of Call Matching in Japanese Macaques

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Key Words: Vocal development · Vocal exchange · Call matching · Playback experiment · Japanese macaques

Social vocal learning in non-human primates is a matter of intense discussion, especially around early evidence of innately guided vocal production. However, socially determined flexibility is found when the debate is moved from vocal structure to vocal usage. Recent studies suggest that the appropriate context of call utterance, notably concerning call exchange rules, may be the result of a socially-guided development process. For example, the young Campbell's monkeys *Cercopithecus campbell* and the Japanese macaques *Macaca fuscata* more often break the turn-taking rule than do adults. Among those rules, call-matching is found to be of primary importance in a growing number of species, including Japanese macaques, with interacting females matching the frequency contour of their own call with another female's preceding call. Here, we tested for the ability of different age-class subjects to discriminate between vocal exchanges following or not the matching rule. We performed playback experiments with 10 adult and 10 one-

year-old captive Japanese macaque females. Each subject was successively exposed to two stimuli, a pair of calls respecting call-matching (i.e. two calls from two individuals with matched frequency modulations) and another pair of calls that did not respect call-matching. Behavioural responses of subjects were recorded. Only adults displayed different levels of interest when hearing playbacks respecting or not the matching rule. The latency to look towards the direction of the loudspeaker was shorter after the playback of vocal exchanges that did not respect the matching rule in adults, but not in youngsters. Additional behavioural analyses are ongoing. Our findings support the conclusion that the matching rule is cognitively relevant for adults, whereas it does not seem to make any sense for socially inexperienced young monkeys.

Intentional Communication in Olive Baboons (*Papio anubis*)

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Key Words: Gestural communication · Intentionality · Language · Perceptual attention · Old World monkeys

Although non-human primates' gestural communication is often considered as a likely precursor of human language, the intentional properties in this communicative system have not been entirely elucidated to date, especially in monkeys. Here, we drew on three experimental situations of a requesting food paradigm to address this issue in olive baboons (*Papio anubis*). We relied on behavioural criteria used for prelinguistic children to assess whether baboons gesture intentionally: (1) gestures are produced to an attentive audience, (2) gestures are supported by visual orienting behaviour alternating between the partner and an external target, and (3) gestures are goal-directed and persist until the goal is reached. Experiment 1 manipulated the presence of an audience and showed that requesting gestures were not driven by the sight of food but were exclusively produced in the presence of both a human recipient and food. Experiment 2 manipulated the communicative goal and showed that baboons produced more requesting gestures when the goal had not been reached than when their communicative bids were successful. Experiment 3 manipulated the attentional state of the human and showed that baboons produced more gestures and alternations of gaze when the human was visually attending. Most importantly, baboons elaborated and used more attention-getting gestures when the human was not visually attending or not responding. This is, to our knowledge, the first report of monkeys elaborating novel attention-getting signals to compensate for communication breakdown. These findings offer solid evidence that requesting gestures are produced intentionally and flexibly by baboons and that they are capable of attributing perceptive attention to others.

Behavioural Adaptability of Pre-Release Orphaned Chimpanzees

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Key Words: Chimpanzee · Reintroduction · Behaviour · Adaptability · Monitoring

Although African ape reintroduction is a complicated and controversial process, returning captive apes to their native habitats can be advantageous in terms of both welfare and con-

servation. Overcrowded African sanctuaries house hundreds of captive chimpanzees and, as a result, attempts to reintroduce these primates back into their natural environment are increasing. Lack of careful planning and systematic documentation has led to the majority of African ape reintroduction programmes being unsuccessful though and thus criticised as being in need of appraisal. One release programme, H.E.L.P (Habitats, Ecologie et Liberté des Primates) Congo has, however, already successfully reintroduced 37 chimpanzees back into the wild. H.E.L.P is continuing its work and currently has a group of six young orphaned chimpanzees in the first phase of release, namely adaptation to the wild. Since a fundamental aspect of any primate release programme is the examination of the behavioural adaptability of the individuals to be released, these chimpanzees were studied in their pre-release environment. Observations focussed on diet choice, activity budgets and social relationships within the group. Based on the results of this study, we show that behavioural studies allow the identification of suitable candidates for release and facilitate the final release process and post-release monitoring of orphaned chimpanzees.

Impacts of a Recent *Streptococcus* Outbreak in a Commensal Population of Long-Tailed Macaques (*Macaca fascicularis*) in Bali, Indonesia

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Key Words: Human-macaque commensalism · Epidemic disease · Population dynamics · Behaviour · *Macaca fascicularis*

The quest for coexistence between humans and non-human primates requires an extensive analysis of the impacts of the growing commensalism phenomenon. In South-East Asia, the long-tailed macaque *Macaca fascicularis* adapts successfully to anthropogenic habitats. The low predation pressure in zones of human-macaque interface and the inclusion of human food in the macaques' diet can lead to local overpopulation. On the other hand, the risk of epidemic disease simultaneously increases with high primate density and proximity with human vectors. Data presented here reflect the population dynamics of a commensal-living population of macaques in the Ubud Monkey Forest (Indonesia) over a 25-year period. Over this period, the population has experienced a dramatic growth with an average annual increase rate of 11%. In June 2012, we counted 615 individuals divided into 5 groups with the very high density of 61 macaques per hectare. However, two *Streptococcus* outbreaks were also reported over the same period, temporarily limiting the steep positive demographic trend of this population. The first epidemic episode appeared in 1994 and the second in July 2012, the last one resulting in 14% mortality in 3 out of 5 groups of the population (563 macaques in October 2012). The comparison between the pre- and post-outbreak periods in 2011–2012 shows changes in the macaques' ranging and behaviour. After the outbreak, the affected groups used smaller and more peripheral home ranges, while the non-affected groups centred their home ranges on the human provisioning places. Besides anthropic factors promoting population growth, epidemic diseases play a significant role in shaping the dynamics and behaviour of this synanthropic population and could have important implications in the future in terms of both management and local conservation status.

Links between Tolerance, Inhibition and Prosociality across Primate Species

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Key Words: Inhibition · Social tolerance · Prosociality · Mechanism

Some link between tolerance, inhibition and prosociality seems intuitively plausible. Social tolerance may require individuals to inhibit prepotent action tendencies in response to the behaviour of conspecifics, or it has been argued that prosociality may directly result from social tolerance. Most obviously, in order to behave prosocially by offering food, a donor may have to inhibit its own interest in the food. We explored these relationships in different experimental contexts, i.e. in group service experiments that assessed prosociality and social tolerance in 19 groups of 11 species of primates, and by comparing the outcome of prosocial games played with common marmosets with their performance in inhibition tasks. The results were as follows: first, social tolerance is a precondition for prosociality both within and across species, but not a sufficient one because high levels of social tolerance do not automatically lead to prosociality. Second, social tolerance was not linked to brain size as a proxy for inhibitory control across species. Third, performance in dyadic prosocial games is not correlated with inhibitory control (detour reaching and A-not-B tasks) in common marmosets. Likewise, there is no correlation across species between prosociality and inhibition (i.e. brain size). This result is not consistent with the idea that prosociality in food contexts critically requires the inhibition to eat the food oneself, but instead suggests that it can be regulated at a purely motivational level: a prosocial motivation may simply override the competing motivation to eat the food oneself. We discuss our results in light of the heterogeneity of the concepts of inhibition, prosociality and tolerance.

Flexible Social Roles in Captive Gibbons with Varied Family Composition (*Hylobates moloch*, *Nomascus leucogenys* and *Symphalangus syndactylus*)

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Key Words: Hylobatidae · Behaviour · Parental investment · Social play · Family roles

Life history theory predicts that when offspring care is required, parents divert their finite energy from other activities into parental investment. In cooperatively breeding primates, this cost to the breeding pair is reduced through allocare provided by other group members. As part of a study of behavioural development of captive gibbons, we investigate how family social roles differ when parents have offspring of differing dependency. Seven family groups in zoos across Australia and New Zealand were observed for 1,136 h. The data include some longitudinal sampling of families as group compositions changed. We compare the time parents and sub-adults spend in energetically expensive behaviours (movement and play) in groups of differing composition. Non-gravid females with one offspring (of <6 years) spent 3.3% of their time playing with their offspring. Females who were pregnant or breastfeeding spent less time playing ($\mu = 0.01$ and 0.03% , respectively; $p = 0.005$). Paternal play did not increase when the mother was pregnant or lactating; however, it exceeded that of pregnant or lactating mothers. Females did not decrease the amount of time they spent moving when pregnant or lactating. This suggests

that pregnant and lactating females reduce their investment in activities that can be substituted by other group members. Paternal play decreased when siblings played with each other. This was not limited to young siblings; a male sub-adult siamang with younger siblings spent more time in social play than a similarly aged male sub-adult siamang with no younger siblings. Social roles in gibbon families may alter in response to group composition; females may reduce their investment in juveniles and adolescents when fathers or siblings are available to share the cost.

Social Tolerance and Inhibitory Control in Primates: Variation, Sociality, and Its Relation to Socio-Ecology and Cognition

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Key Words: Inhibitory control · Socioecology · Apes · Monkeys · Social tolerance

Social tolerance and inhibitory control are two topics that have over the years figured prominently in primatologists' research agendas. However, with a few exceptions, they have been investigated separately and from different perspectives. Whereas social tolerance has been mostly studied from a socio-ecological perspective, inhibitory control has been studied from a psychological perspective. Recently, we measured social tolerance (as indicated by co-drinking in proximity) and inhibitory control (measured by means of a five-task test battery) in seven primate species. We found that those species with higher levels of social tolerance scored higher in inhibitory control. This finding will be the starting point to explore the following three aspects about the relationship between social tolerance and inhibitory control: (1) the variation at the individual and species levels; (2) the social dimension of tolerance and inhibitory control, and (3) the connection of tolerance and inhibition with other aspects of a species' socio-ecology and cognition.

Effects of Habitat Quality and Seasonality on Ranging Behaviour of *Eulemur collaris* in Littoral Forest Fragments of South-East Madagascar

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Key Words: Home-range · Daily distance travelled · Kernel analysis · Habitat degradation · Fragmentation

Degraded habitats typically show low food availability and scattered resources. This has been shown either to force animals to move further in search of food, resulting in large home ranges, or to use energy saving strategies. Lemurs are known to face pronounced seasonality and resource unpredictability which add to the overall reduction in food availability due to the

human-driven habitat disturbance in Madagascar. In order to explore lemur flexibility to habitat disturbance here we examined the ranging behaviour of *Eulemur collaris* in two differently degraded fragments of littoral forest in south-eastern Madagascar. We collected data from February 2011 to January 2012 on two groups living in a degraded area and two groups living in a more pristine forest. We followed each group for 4 full days per month and recorded their location every 30 min. We calculated annual ranges, monthly ranges and daily distance travelled via RANGES 7. We then ran a GLM using seasons as within subject factor and site and group as between-subject nested factors. We also set up five 20 × 50 m² vegetation plots within the home-range of each group to characterize the habitat. The lemurs had larger home-ranges in the degraded forest, although important differences were revealed within the same site. Distances travelled were shorter for the groups living in the degraded area and overall the animals moved less during the lean season. Our results indicate that in the degraded fragment the lemurs are able to use a habitat mosaic which also includes non-forested areas, plantations and swamps. Additionally, in the disturbed area, the animals minimize their daily path length, possibly to save energy, and move to different areas as resources become seasonally available elsewhere.

Which Social Cues Are Taken into Account by Tonkean Macaques to Communicate with a Human Partner?

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Key Words: Social cognition · Attention · Intentionality · Gestural communication · *Macaca tonkeana*

The existence of Theory of Mind in non-human primates is historically a source of debate. Studying Theory of Mind precursors such as the understanding of other individuals' attentional state in non-human primates would help in tracing back the evolutionary roots of human mind-reading abilities. The study presented here asks whether Tonkean macaques (*Macaca tonkeana*) share with us attention reading abilities. More specifically, we investigated the macaques' ability to communicate intentionally about the location of an unreachable food reward thanks to a learned pointing behaviour in various contexts that differed according to the human partner's attentional state. Six individuals have been tested in eight different attentional conditions. When attentive, the experimenter placed herself facing the subject with her 'eyes open', or followed the gaze of the subject displaying 'gaze alternation' between the hidden food and the subject or was 'informed' of the location of the hidden food. Inattentive, she placed herself facing the subject with her 'eyes closed' or her 'turned back' or she 'looked up at the sky' or she turned her 'head aside' or was 'absent'. If macaques point intentionally, they should emit fewer gestures and use other types of communicative signals, for example, auditory displays, when facing an inattentive experimenter than an attentive one. Moreover, facing an attentive human, they should point more and realize more gaze alternation between the human and the hidden food. The results of the study are currently being analysed and will be compared to those obtained in other species and will be discussed in the light of Theory of Mind precursors.

Hair as a Retrospective Cortisol Calendar in Orang-Utans (*Pongo spp.*): A New Tool for the Assessment of Stress in Captive Management and Conservation

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Key Words: Stress-monitoring · Cortisol · Hair · Orang-utans

Non-invasive methods are essential for unbiased stress measurement. Measuring the concentration of the stress hormone cortisol in saliva, urine or faeces are non-invasive tools that are traditionally used to assess stress objectively. During the past decade, studies on humans, monkeys and other mammals have documented that stressful events lead to an increased cortisol concentration in hair, too. However, detecting timed stressful events indicated by increased cortisol concentrations in distinct hair segments has never been documented for animal hair. The aim of the present study was to establish hair cortisol analysis in orang-utans and to correlate the cortisol concentration of hair segments with the individual's known history. It could be shown that it is possible to detect timed stressful events in orang-utans, as well as to measure basal cortisol concentration up to 4.5 years back into the past, depending on the individual's hair length. There was no general decline along hair shaft. The procedure requires only one hair sample of 10 mg per measured segment. Furthermore, it could be shown that on average the intra-individual variability of hair cortisol concentration is below 15%, with no statistical difference found between all tested body regions. These findings show that it is also possible to assess an individual's basal cortisol concentration using shed hair which can, for example, be found in sleeping nests even of wild non-habituated animals. Hair samples provide cortisol profiles over a longer period of weeks and months rather than days as in urine or faecal samples, which clearly reduces the effort for long-term stress monitoring. In conclusion, hair cortisol measurements provide a highly valuable non-invasive technique for conservation and captive management in orang-utans and potentially all other apes.

Nesting Patterns of Chimpanzees in Relation to Human Disturbance and Vegetation Characteristics at Lagoas de Cufada Natural Park, Republic of Guinea-Bissau

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Key Words: Human disturbance · Hurdle models · Nesting patterns · Tree choice · Western chimpanzee

Chimpanzees constitute an important model for assessing the influence of anthropogenic habitat disturbance and conversion as their ecological importance in tropical ecosystems is well appreciated. We assessed the effect of land-use change on the distribution of the western chimpanzee, *Pan troglodytes verus*, at Lagoas de Cufada Natural Park (LCNP), Guinea-Bissau, in rela-

tion to landscape-level proxies of human disturbance. We further investigated nest tree choice and the influence of vegetation characteristics (tree diversity, floristic composition, basal area) on nesting patterns. Nest counts and vegetation sampling were conducted along linear transects in 2010 and 2011. Human disturbance had a negative influence on chimpanzee distribution as nests were built farther away from settlements, roads, and rivers than if they were randomly distributed, coinciding with the distribution of the remaining patches of dense canopy forest in LCNP. Chimpanzees used 23 out of a total of 97 available tree species for nest building. Comparing tree use with its availability, 5 species were clearly selected more often than expected by chance, suggesting that tree choice was non-random. A zero-altered GLMM model that considered both true nest counts and false zeroes suggested that nest abundance was negatively correlated with basal area of tree species commonly eaten by chimpanzees. This might indicate a preference of chimpanzees to build their sleeping nests at a certain distance from fruiting trees, which could be linked to predator avoidance. Our results further imply that the continuous disappearance of suitable habitat inside the park due to human encroachment may be compromising the future of one of the most threatened Guinean coastal chimpanzee populations.

Dealing with Distress: Emotion Regulation, Consolation and Social Competency in Juvenile Bonobos

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Key Words: Emotion regulation · Consolation · Composite sociality index · Rearing · Social development

The concept of emotion regulation, commonly applied in developmental psychology, focuses on how individuals manage and modulate internal emotional processes and the impact this has on cognitive and socio-emotional functioning. Studies with human infants and adults have demonstrated a close relationship between emotion regulation and empathy-related responding, such as sympathetic concern, and that both phenomena are negatively impacted by disrupted development. While rarely applied to non-human primates, here we explore its usefulness for exploring the socio-emotional behaviours of bonobos observed at a large sanctuary in DR Congo, Lola ya Bonobo. While most individuals were orphaned, some juveniles were born at the sanctuary and mother-raised. We observed how juveniles ($n = 6$ mother-reared, $n = 6$ orphan) responded to post-conflict events to examine the relationship between responses to distress in others (as bystanders) and responses to self-distress (as the victim). We also examined whether juvenile responses to self- and other-distress were predicted by baseline social competency and emotion regulation skills, as has been shown in children. Mother-reared juveniles consoled more than orphans and rearing positively correlated with sociality. In turn, juveniles with a higher sociality index and signs of better emotion regulation were more likely to console other bonobos in distress. We found a close connection between responses to self- and other-distress, with individuals quicker to recover from their own distress more likely to offer consolation. These results highlight the role of rearing on socio-emotional development and provide novel insights into the relationship between sociality, emotion regulation and empathy-related responding in one of our closest relatives.

From Nine to Five: The Impact of Poaching and Park Management on the Declining Primate Population in Southern Burkina Faso, West Africa

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Key Words: Burkina Faso · Ivory Coast · Primates · Poaching · Reconnaissance surveys

The landlocked West African country of Burkina Faso has been presumed to harbour at least nine species of primates, although data are sparse. It is imperative to determine which primates are still present in Burkina and the threats currently imposed in order to mitigate potential long-term anthropogenic effects. Between May 11 and July 16, 2012, we conducted reconnaissance surveys of nearly 250 km within five different forest reserves across southern Burkina Faso. We recorded both direct and indirect signs of presence for both primates and poaching activities. Our surveys were supplemented with qualitative interviews with 24 farmers and forestry workers. We were able to confirm the presence of only five species: *Chlorocebus aethiops*, *Chlorocebus saebaeus*, *Erythrocebus patas*, *Galago senegalensis* and *Papio anubis*. We propose that the Vulnerable *Colobus vellerosus* and Endangered *Cercocebus atys lunulatus* are very near extirpation and that the Endangered *Pan troglodytes verus* has been extirpated from this historic range country. Encounter rates for signs of poaching ranged from zero to 0.443/km, were highest in study sites bordering Ghana and the Ivory Coast, and within which anti-poaching patrollers reported having little to no authority to approach or arrest. There was a strong inverse relationship between signs of poaching and encounter rates for *P.anubis* and *Chlorocebus* spp., most notably a significant negative correlation between shotgun shells and primate presence. We suggest that the future of the remaining Burkinabé primates will depend on improvements to park management, particularly an increase in anti-poaching patrols and in the authority of anti-poaching patrollers, as well as increased border protection within protected areas bordering the Ivory Coast.

Female Mate Choice and Male Mating Strategies in Wild Bearded Capuchin Monkeys (*Sapajus libidinosus*)

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Key Words: Mate choice · Sexual selection · Social network analysis · Capuchin monkeys · *Sapajus libidinosus*

Many theoretical and empirical studies overlook the fact that individuals differ in their social experiences. Social network analysis (SNA) can help to take this into account (Sih et al., 2009). Degree is a SNA metric that identifies how many social partners an individual has and may therefore be useful in identifying how females vary in the number of males they have access to. Also seldom evaluated empirically is the exclusivity a male has regarding the females choosing to mate with him. There is likely to be a trade-off between time spent acquiring mates versus guarding or maintaining fidelity by affiliative behaviours. We present data for a wild group of bearded capuchin monkeys (*Sapajus libidinosus*) in the Serra da Capivara National Park. Composed of multi male-multi female groups of 30–50 individuals, little is known about sexual and social behaviour for populations inhabiting the Brazilian savannah (caatinga). Focal data, with an emphasis on social interactions, were collected and scans were carried out to determine associations and sub-

groupings. We recorded 26 events of courting behaviour between identified individuals. Results indicate marked differences in the frequency with which males were targeted by oestrus females. Unlike the norm for capuchins, usually a single alpha male dominates mating within a group; here, we find several males attaining access to females, on occasions with exclusivity within their subgroups. Also atypical is that grooming was more frequent between female-male dyads (the norm being higher activity between females, the philopatric sex in capuchins), with males being particularly active. This may be one of the mechanisms involved in maintaining fidelity.

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Lack of Evidence That Macaques Understand What Others Can Hear

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Key Words: Perception · Deception · Intentionality · Social cognition · *Macaca tonkeana*

Although we know that monkeys are able to withhold information, we do not know the mechanisms by which they deceive others. A study carried out by Santos et al. (2006) concluded that rhesus macaques (*Macaca mulatta*) are able to recognize the perception of humans, and understand the connection between hearing and knowing. We replicated this study by testing captive Tonkean macaques (*M. tonkeana*) using similar methods and apparatus. We trained 18 subjects to choose one of two visually identical, transparent boxes containing identical food rewards: one box had a hinged lid covered with pellet bells that rang when the box was opened; the lid of the second box was covered with jingle bells without ringers, meaning that no jingling occurred on opening. We then tested each subject in two successive trials in which they were shown the noisy or silent opening of each box. In the first trial, a masked experimenter, i.e. relatively frightening to animals, approached and sat with her back to the subject; subjects intending to take the reward without being noticed should choose the silent box. Conditions were the same in the second trial except that the experimenter faced the subject, making any noisy versus silent box discrimination pointless. Results showed that subjects' choices did not significantly differ from random in both trials. We thus found no evidence that Tonkean macaques took experimenter hearing into account. Differences in methods used and species tested could explain discrepancies between the present and the previous study. Our results, however, indicate that the conclusion that monkeys can link seeing and hearing is premature at best. We urge colleagues to replicate these studies in other populations of primates.

Chimpanzees Distinguish Acoustically Similar Alert Hoos from Resting Hoos

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Key Words: Chimpanzee · Alarm call · Informing · Functional reference · Pragmatics

Although many animal species produce alarm calls, there are a number of motivations for a potential prey to vocalise in the face of a predator. Alarm calls produced to different classes of

predators, such as aerial or ground predators, are in many cases acoustically distinct. However, alarm calls are not always acoustically distinct from calls produced in non-alarm contexts. Here, we tested whether chimpanzee (*Pan paniscus*) 'alert hoo's produced to threats such as snakes and snares are acoustically distinct from similar sounding 'resting hoo's produced when resting. We recorded calls from chimpanzees in the Budongo Forest, Uganda, produced to snakes and when resting. Acoustic analysis confirmed that the two call types are acoustically distinct but grade into one another, as expected for the chimpanzee call system. To determine if chimpanzees could discriminate between the call types, we conducted a playback experiment using a within subjects' design. Whilst subjects were travelling down a forest trail, they heard either an alert hoo or a resting hoo from a speaker hidden 5–10 m from the trail. In line with our predictions, chimpanzees reacted for longer and showed more alert behaviour to the 'alert hoo' rather than the 'resting hoo' playback. The results indicate that chimpanzees discriminate between the two call types and react as if the calls convey different information. A previous study showed that alert hoo's are sensitive to audience effects such that signallers are more likely to produce alert hoo's when others are ignorant as opposed to knowledgeable of a danger. Signallers' use of an acoustically distinguishable call type in the context of informing others of danger is discussed with respect to functional reference and pragmatics.

'Normal' Human Foot Function and Its Evolution: Insights from Footprints and Foot Pressure

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Key Words: Biomechanics · Feet · Function · Hominin · Laetoli · Ileret

We discuss recent work on the external forces generated by the plantar foot (foot pressure) and their fossil representation (footprint trails) which has used a combination of forwards dynamic modelling, topographical statistical analysis and experimental studies of foot pressure (using a unique database of over 25,000 records) and footprint formation. We discuss the significance of Laetoli and the published Ileret footprint trails which overlap substrate conditions at the two ancient sites as a control for substrate interaction effects, and review some of the issues surrounding the interpretation of fossil footprint trails.

The Many Metrics of Social Tolerance: Are We Measuring One Concept?

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Key Words: Tolerance · Chimpanzees · Social behaviour · Fairness · Inhibition

Social tolerance has been prominently integrated into theoretical predictions about the emergence and stability of cooperation and social learning in primates. The concept of tolerance has been assessed objectively through a wide range of measures, yet it is unclear whether these measures reflect the same underlying phenomenon. Here, we apply multiple metrics of social tolerance that have been employed by primatologists to four social groups of semi-wild chimpanzees to investigate whether they generate similar conclusions about relative levels of tolerance.

Through a combination of observational and experimental approaches, we assessed: (1) social cohesion through social networks of proximity, (2) asymmetry in conflicts, (3) proximity to conspecifics at a clumped resource, and (4) equality of monopolizable food distribution. Findings indicate that these measures generate slightly different conclusions about the relative tolerance of chimpanzee social groups, and suggest that conclusions about social tolerance may depend largely on the immediate context and choice of measure. What we can learn from each of these measures, and whether any of these measures correspond to inhibition, will be discussed.

Local Extinctions of Primates: Demographic and Genetic Effects on Vegetation

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Key Words: Defaunation · Seed dispersal · Seedling recruitment · Plant genetic structure · Atlantic Forest

Combining with a high deforestation rate, poaching in the rainforests threatens most plant and animal populations. Primates, constituting 25–40% of frugivore biomass in the tropics, are not spared since poaching targets mostly large and medium mammal herbivores, seed dispersers or seed predators. Local primate extinctions may alter plant-animal interactions through reducing the number and the outcome of seed dispersal events, yet few studies have measured this impact along a defaunation gradient. Therefore, cascading effects on the demographic and spatial genetic structure of plant populations are expected, especially for large-seeded species needing large seed dispersers. This study aimed at determining the consequences of defaunation – focusing on large primates – on the recruitment dynamics and spatial genetic structure of a large-seeded species, *Cryptocarya mandioccana* (Lauraceae), along a defaunation gradient in the Brazilian Atlantic Rainforest. Specifically, we intend (1) to determine the contribution of each seed disperser (*Brachyteles arachnoides*, *Alouatta guariba*, and *Aburria jacutinga*) to the recruitment dynamics of *C. mandioccana* during two successive years; (2) to link the seed disperser occurrence and contribution to *C. mandioccana* recruitment to the spatial genetic structure. First results indicate that seed predation effect overcomes seed dispersal effect, resulting in high seedling recruitment success in the most defaunated site despite short dispersal distances. Results from the genetic data will tell us if this apparent positive demographic effect hides a negative genetic effect: the decreasing of gene flow and genetic diversity, leading to a pronounced spatial genetic structure of plant populations in defaunated areas.

Dental Evidence Indicates Evolutionary Disequilibrium among Sympatric Diurnal Lemurs in South-Western Madagascar

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Key Words: Lemurs · Dental ecology · Beza Mahafaly · Anthropogenic effects · Niche shifts

The ring-tailed lemurs *Lemur catta* at Beza Mahafaly Special Reserve exhibit severe postcarnine tooth wear and antemortem tooth loss (25%; n = 274), largely the result of processing challenging tamarind fruit. The sympatric Verreaux's sifakas *Propithecus verreauxi* show frequent

apical maxillary canine abscesses (30%; n = 77), sometimes leading to systemic infections and death. Beza sifakas consume tamarind fruit, frequently using their maxillary canines, causing heavy wear and pulp cavity exposure. Ring-tailed lemurs at Tsimanampetsotsa National Park (TNP), Madagascar and numerous localities where tamarind is rare, and at the 500 BP Ankilitelo Cave site, exhibit only minor tooth wear, and little or no tooth loss. For Verreaux's sifaka and other indriid museum samples from a variety of localities and habitats, canine abscesses are rare. Lack of tamarind and less frequent ($p = 0.05$) tooth loss in ring-tailed lemurs at TNP (4%; n = 26), Ankilitelo (0%; n = 17), and all other localities examined (3%; n = 31), and infrequent canine abscesses in Verreaux's sifaka (8%; n = 59), indicates lemurs at Beza rely on a fallback food for which they are not dentally adapted, thus displaying evolutionary disequilibrium. This discordance is likely the result of human activity over the past 2,000 years, including (1) shifts in the Beza lemur community, with extinction of all large (>10 kg) lemur species, due to habitat loss and hunting, with the remaining lemurs exploiting resources previously consumed by these large lemurs, (2) changes in the Beza forest, with domesticated tamarind now dominating the riverine gallery forest, or (3) degradation of Madagascar's southern riverine forests, leading to areas with only tamarind available as a lemur fallback food. Our data illustrate the power of using dental ecology to identify mammalian niche discordance.

Locomotor Versatility in Primates: Baboons Shifting to Bipedal and Tripedal Gait

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Key Words: Biomechanics · *Papio anubis* · Locomotion · Transition

Most primates are locomotor generalists and display a wide range of locomotor behaviours. Biomechanical studies, however, have focused on steady, quadrupedal locomotion, which is rather rare in nature. Here, we report on two transitions in baboon gait: (1) instantaneous dynamic changes in pedality (from quadrupedal to bipedal), and (2) the acquisition of tripedal gait due to limb loss. Do baboons perform such shifts with relative ease, as expected? We made high-speed video (200 fps) and ground reaction force recordings of olive baboons (*Papio anubis*, including one fore- and one hind limb amputee) at the CNRS Primate Station (Rousset, France), and analysed spatiotemporal gait parameters, joint kinematics and inverse dynamics for selected trials. Baboons execute transition from quadrupedal to bipedal gait in three steps by combining a forward repositioning of the hind limb and knee flexion. This results in a forward shift of the point of application of the ground reaction force; associated with this, the necessary upward rotation of the trunk occurs, probably aided by hip extensor activity. The role of the forelimbs is limited. In baboons lacking a forelimb or a hind limb, locomotor performance seems to be affected relatively little, and gait adaptations focused on a more orthograde reorientation of the trunk for both individuals. This mechanism regroups the remaining limbs closer to the vertical projection of the centre of mass, and might distribute the vertical impulse well over the remaining limbs. We suggest that the locomotor adaptations observed here in dynamic and life-long pedality changes in baboons are performed relatively easily thanks to the anatomical and functional generalist nature of primates compared to other mammals.

Tolerance and Food Sharing in a Despotic Group of Bonobos: It All Depends on the Resource?

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Key Words: Bonobo · Food sharing · Tolerance · Dominance

Recently there has been debate on whether or not bonobos are tolerant when sharing food. While some authors claim that bonobos live in an egalitarian society and will share food more tolerantly than chimpanzees, others have stated that bonobos are less tolerant around food, and will share less because they live in a more despotic hierarchy. So the social structure of dominance hierarchies has been invoked to explain patterns of food sharing, with contrasting results. While studies differ in design and experimental approach, they also differ in the kind of food that was offered to study food sharing. According to the marginal value model of Winterhalder (1996), the quantity, quality and, hence, divisibility of food will influence the degree of food sharing, with tolerated scrounging being the basic mechanism. If food distribution is selective, forms of altruism can further explain the patterns. We investigated the influence of social and food related aspects on the degree of food sharing in a captive group of bonobos at Planckendael (Belgium). We used two different food items that have previously been used in food sharing studies (bundles of willow and bags with vegetables) and applied the logic of the marginal value model to make predictions about how the different food types should be shared differently. We found a despotic social structure in the study group. In addition, we found more tolerant food sharing compared to a previous study. Preliminary results indicate that food sharing was more prevalent and tolerant when willow was fed. Tolerated scrounging was prevalent in both food contexts, but in the branch context, we found evidence of grooming up the hierarchy. We can conclude for now that differences in food items reflect differences in food sharing patterns.

Waiting for the Larger Amount: Do Capuchin Monkeys (*Sapajus apella*) Show a Magnitude Effect in a Delay Choice Task?

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Key Words: Delay discounting · Value · Intertemporal choice · Magnitude effect · Quantity · Quality

Both humans and non-human animals often face intertemporal choices, i.e. decisions between smaller immediate options and larger delayed options, and usually devalue future rewards compared to immediate ones. Apparently, however, only humans show the magnitude effect, according to which they discount larger/more preferred delayed rewards less steeply than smaller/less preferred ones. This effect has been repeatedly demonstrated in humans across cultures and with different types of rewards, such as money, cigarettes, heroin, and health outcomes. In contrast, studies with non-human animals have failed to replicate the human results. We aimed to assess whether in a delay choice task, in which individuals face choices between smaller immediate rewards and larger delayed rewards, capuchins (i) show a magnitude effect, and (ii) value more the quality or the quantity of the reward. Ten subjects were presented with four conditions: (i) 2 pieces of low-preferred food versus 6 pieces of high-preferred food (2 low-6 high); (ii) 2 pieces of

high-preferred food versus 6 pieces of low-preferred food (2 high-6 low); (iii) 2 pieces of low-preferred food versus 6 pieces of low-preferred food (2 low-6 low), and (iv) 2 pieces of high-preferred food versus 6 pieces of high-preferred food (2 high-6 high). Interestingly, capuchins valued the quality of the reward more than its quantity when the delay was implicated, in that they chose the larger delayed reward less in the condition 2 high-6 low than in the condition 2 low-6 low. However, reward quality did not enhance capuchins' willingness to wait for a larger reward, since they did not choose the larger delayed reward significantly more in the condition 2 high-6 high than in the condition 2 low-6 low, thus confirming the absence of a magnitude effect.

Golden-Headed Lion Tamarin Diet and Seed Dispersal: A Potential Role in Seed Flux and Forest Regeneration in the Atlantic Forest

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Key Words: *Leontopithecus* · Feeding ecology · Seed dispersal · Forest regeneration

Golden-headed lion tamarins (GHLTs, *Leontopithecus chrysomelas*) are arboreal primates, endemic to the Atlantic Forest of Southern Bahia and endangered due to habitat fragmentation and degradation. Groups of GHLTs can use different types of vegetation, including mature forest, degraded and regenerating areas and shade cocoa plantations. We discuss the role of GHLTs in promoting seed flux and forest regeneration in the Atlantic Forest, based on data from our own ecological studies in degraded areas and literature data from other habitats. Ecological data provide evidence for a generalized diet, encompassing approximately 300 species across all habitat types. Despite some overlap in the diet of groups ranging in different habitat types, particularly for generalist tree species, there is considerable divergence in the type of species consumed in different areas. Available information suggests that GHLTs have a flexible dietary strategy, determined mainly by the tree species composition of an area and seasonal variation in fruiting and flowering patterns, rather than particular morphological or nutritional characteristics. GHLTs disperse seeds from at least 89 plant species. Given their broad diet, and the fact that their home ranges usually contain different habitat types, GHLTs can play an important role in promoting seed flux between degraded and less degraded areas, shade cocoa plantations and future restoration areas for many tree species. The particular impact a group of GHLTs will have on seed flux and forest regeneration will depend on the composition of the landscape mosaic and characteristics such as the floristic composition and size of the home range and daily distance travelled, factors that can vary considerably between study groups and areas.

Parasite Prevalence in Lemurs: The Effect of Anthropogenic Disturbance and Natural Stress Factors from a Multi-Scale Perspective

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Key Words: Gastrointestinal parasites · Lemurs · Anthropogenic disturbance · Primates · Social organisation

Parasite prevalence and associated infectious diseases play an important role in ecological, social and evolutionary processes, but the potential drivers of parasite loads are still unclear.

However, several forms of anthropogenic habitat disturbance have been shown to increase parasite prevalence in several animal species. In systems where social primates function as hosts for many parasites species, different interactions are expected. These can be grouped into three levels of social organization: the population, the group and the individual level. On the population level, the parasite prevalence in hosts is higher in more disturbed forest fragments close to villages, compared to less disturbed habitats. From a group perspective, higher parasite prevalence is expected in larger groups and in groups with large daily travel distances and in groups of a lower social rank. On the individual level, higher parasite loads are expected in individuals with a lower body condition, social rank and immune status. We focus on a lemur species (*Eulemur rufifrons*) as a model organism to explore the general mechanisms of parasite infections and transmission. Methods include the non-invasive sampling of focal animal behaviour and collecting and analysing faecal samples to assess gastrointestinal parasite prevalence. The association between parasite prevalence and reduced host fitness, combined with the parasites' potential to spread infectious diseases among wildlife and human populations, underlines the importance of this project from an ecological, a social developmental and a conservation perspective.

Brown Tufted Capuchins (*Cebus apella*) Adapt Their Communicative Behaviour to Humans' Attentional States

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Key Words: Gestural communication · Intentionality · Attention · Social cognition · Non-human primates

Animal communication became a widely studied field of research, especially because of the associated debates on the origin of human language. Due to their phylogenetic proximity with humans, non-human primates represent a suitable model to investigate the precursors of language. This study focuses on the perception of the attentional states of others, an important prerequisite to intentional communication. We investigated if capuchins produce a learnt pointing gesture towards a hidden and unreachable food reward as a function of the attentional status of the human experimenter. For that purpose, we first trained five subjects to indicate by a pointing gesture the position of a reward hidden by an assistant. Capuchins were then tested in two experimental conditions randomly ordered. In the first condition – motivation test – the experimenter (E) was attentive to the subject gestures and rewarded him immediately when he pointed toward the baited cylinder. During the second condition – trial test – E adopted one of the following attentional states and the subject was rewarded after 10 s, regardless of its behaviour. Five attentional states were tested: (1) E absent, (2) E back to the monkey, (3) E's head away, (4) E watching above the monkey, and (5) E watching the monkey's face, as during the motivation test. Our results reveal a variation in our subjects' communicative behaviours with a sharp discrimination of the different postural clues available in our experimental conditions. This study suggests that capuchins can flexibly use a communicative gesture to adapt to the attentional state of their partner. This finding provides evidence that acquired begging gestures of monkeys might be used intentionally.

Communicating the Motivation to Play: Gestures and Facial Expressions in Bonobos

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Key Words: *Pan paniscus* · Intentionality · Play face · Emotional communication

The correct production and interpretation of communicative signals is of primary importance for social animals. Free brachio-manual gestures, so far only reported for humans and other apes, are considered as intentional signals. Facial expressions, on the other hand, although used during intentional communication, are influenced by emotional states. Play is one of the most sophisticated forms of social communication and it has also been reported to be the context in which gestures occur more frequently in two *Pan* species. Through a video-analysis of playful sessions, we investigated the use of (a) facial expressions and (b) gestures in *Pan paniscus*. Both of them were more frequent during the most risky form of play, play fighting. The redundancy of signals is effective in reducing the probability of escalation into overt aggression. The difference between the use of gestures and facial expressions emerges with the variation in number of players. Gestures tend to decrease as the number of players increases; whereas facial expressions are independent of the number of players involved. Both communicative patterns are performed mainly when the receiver can perceive them, thus suggesting the intentional nature of these displays. The importance of understanding the way apes and other primates communicate through gestures and how this capacity develops becomes central when considering that our ancestors' first linguistic expressions were probably in the gestural more than in the vocal domain.

Physiology and Sociality of Birth in Bonobos: A Comparative Perspective

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Key Words: *Pan paniscus* · Birth phases · Delivery physiology · Social behaviour · Placentophagia

Evolution is about reproduction. Birth is probably the most critical step of the entire reproductive process as in a few hours the lives of both mother and infant could be seriously threatened. From an evolutionary point of view, many competing selection pressures must have shaped the course of delivery to minimize risks and maximize the survival of mother and infant and, in the long term, of the species. In spite of its pivotal importance, very little is known about the birth process within the Primate order, except in the case of *Homo sapiens*. We video-recorded and described two deliveries in bonobos (*Pan paniscus*) at Apenheul Primate Park (The Netherlands) and La Vallée des Singes (France). During all the delivery phases, both mothers remained in their social group and were free to move around both the outdoor and indoor enclosures. This permitted us to describe in detail and temporally quantify the mothers' behaviours as well as the interactions among group members during all the delivery phases. The other group members, especially females, stayed in proximity of the mothers and frequently inspected their vaginal area. Placentophagia occurred in both cases and, in one of them, the placenta was shared with other females. The first mother-infant interactions mainly consisted of extended licking and grooming,

and contacts between the newly born and other group members were also observed. All the pre- and post-delivery events will be discussed in a comparative perspective in order to detect differences and similarities in the evolutionary pathways of *Homo* and *Pan* birth.

Phylogenetic Relationships within the *Cercocebus* Clade as Indicated by Craniodental Morphology

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Key Words: *Cercocebus* · Phylogeny · Morphology · Biogeography

Mangabeys form a diphyletic group, with white-eyelid mangabeys (*Cercocebus*) being closely related to drills and mandrills. However, to date the phylogenetic relationships among members of the *Cercocebus* clade have not been investigated in detail, particularly from a morphological perspective. Grubb (1978, 1982) considered *C. agilis* to be the ancestral species from which several taxa originated and *C. torquatus* as the most derived species, the result of a more complex branching event. Alternatively, other authors have proposed a sister group relationship between the genus *Mandrillus* and either *C. chrysogaster* or *C. torquatus*, the former species because of its unique occurrence south of the Congo River and general drill-like appearance, the latter species because it shares some similarities in cranial features with drills and mandrills. Here, we present the results of phylogenetic analyses based on 33 craniodental quantitative characters, scored separately on males and females, for four species of *Cercocebus* (*agilis*, *atys*, *chrysogaster*, *torquatus*). We used the general allometric coding method to control for allometry and conducted exhaustive searches for male, female and sex-combined data sets, with *Macaca* and *Mandrillus* constrained as successive outgroups. In all analyses, *C. torquatus* is reconstructed as most basal, while *C. agilis* and *C. chrysogaster* are grouped together as a derived clade. This is striking, given the distribution of these two species along the banks of the Congo River, but also congruent with recent genetic analyses, behavioural analyses and assessments based on the fossil record. Additional species and additional characters should be included in future analyses to gain full insight into the phylogeny and biogeography of the white-eyelid mangabeys.

MHC Typing in Various Non-Human Primate Species by a Robust and High-Throughput Microsatellite Technology

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Key Words: MHC · Microsatellites · Immunological fitness · Conservation

The major histocompatibility complex (MHC) represents a genomic region of multi-copy gene families in human and non-human primates. So-called 'classical' class I and II MHC genes are characterized by a high degree of variability (polymorphism) and encode for proteins that play a major role in immune reactions via immune recognition and host-parasite interactions. Therefore, analysing the polymorphism of these genes provides information about the immunological fitness but also about the degree of inbreeding of a population. Furthermore, the MHC

has been linked with mate choice and pregnancy outcomes and may improve mating success in captive breeding colonies. Therefore, robust and quick methods are needed to define the allelic variation of these genes. Several MHC-linked microsatellites have been extensively tested in various non-human primate species, including chimpanzees, baboons and different macaques species. One of the microsatellites, D6S2878, characterizes the most polymorphic, multicopy class II gene, DRB. Analyses with this microsatellite result in length patterns, which are chromosome (haplotype) specific. Comparable results have been gained for the MHC class I region with two A region specific microsatellites. Additionally, twelve single copy microsatellites encompassing the core MHC region have been used in various macaque species in breeding colonies, leading to the definition of hundreds of different MHC haplotypes/chromosomes. Thus, the described methodology allows a quick and robust characterization of the MHC region that may not only be useful for non-human primate breeding facilities but also for wildlife rescue and conservation programmes.

Age Differences in Locomotor Behaviour of Catarrhini: A Case Study of Bipedal Behaviour and Its Morphological Correlates in a Sample of Captive Olive Baboons (*Papio anubis*)

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Key Words: Bipedalism · Ontogeny · Morphology · Captivity · *Papio anubis*

Primates have developed particular locomotor modes such as permanent bipedalism in *Homo*, knuckle-walking in *Pan* and *Gorilla*, suspension in *Pongo*, brachiating in *Hylobates*, semi-plantigrade quadrupedalism in *Papio*, etc., each constituting the main locomotion of the adult repertoire. These modes have been linked to some traits of the species' morphology. However, catarrhines usually display a wide positional repertoire including some form of bipedalism. As an individual develops, both its locomotion and morphology change; although a general ontogenetic parallel can be made between them, especially with regard to bipedalism, their possible relationships during individual growth have been poorly investigated compared to those of adults, mainly for reasons of accessibility of the primates. As far as postnatal development is concerned, studies in captivity can provide original data at an individual level. We have conducted a cross-sectional ontogenetic study of the positional repertoire and the morphology (body mass distribution) on a sample of 22 captive olive baboons at the Primatology Station of CNRS. As a result, although the variation is marked, a general trend of change in the positional repertoire as the primates age can be depicted: infants have a wide repertoire, including more climbing and more bipedalism than adults, which are more quadrupedally specialized. When infant and adult bipedal behaviours are compared, infants use more bipedalism but for shorter periods on average. Simultaneously, mass distribution shifts caudally; this occurs from birth to 2 years of age and then stabilizes. On the basis of these individual and ontogenetic data, we discuss possible links between ontogenetic peculiarities of bipedalism and mass repartition in the frame of the human evolution.

Sex Differences in the Use of 'Whinny' Vocalizations in Spider Monkeys (*Ateles geoffroyi yucatanensis*)

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Key Words: Spider monkey · Communication · Sex differences · Food-associated · Group dynamics

Spider monkey (*Ateles* sp.) social groups are characterized by male philopatry and high fission fusion dynamics in which individuals form subgroups that temporally vary in size, composition and spatial cohesion. Whinny vocalizations are frequently produced by both males and females, and prior research has suggested that they function to recruit or maintain contact with close associates in dispersed subgroups. Females do not form close bonds, and little is known about how this affects their use of the call. We investigate sex differences in the use of the whinny vocalization by the Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) at the Runaway Creek Nature Reserve, central Belize. Using a general linear model, we compared call rates between the sexes across behavioural contexts. The effect of changes to subgroup membership on the likelihood of calling by either sex was determined using generalized estimating equation models. Compared with males, females called at higher rates in almost all behavioural contexts, but particularly while foraging. The likelihood of a female calling increased during subgroup fissions and fusions, and was positively correlated with the number of animals joining or leaving a subgroup. Neither behavioural context, nor changes to subgroup composition affected the likelihood of calling by males. The high rate of calling by females while foraging and during subgroup composition changes suggests that whinny vocalizations may function differently for males and females; i.e., while calling by males may allow close associates to maintain contact, females may call as a spacing mechanism within subgroups to reduce within-group feeding competition, with calls reflecting social anxiety at the arrival of other females on a proximate level.

Tolerance to Delay and Risk in Primates

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Key Words: Delayed exchange task · Risky barter · Inhibition

Every day animals commonly deal with predictable and unpredictable events. Delaying a reward may involve some risk, and impulsive conducts of animals are often interpreted in term of risk avoidance strategy. If risk-sensitivity affects decision-making and tolerance to delay, we know little of the cognitive processes involved. In this talk, I will present and compare the results of two studies conducted in several species of primates. The first study investigates tolerance to delay of gratification in an exchange task, the second study also uses an exchange task to investigate tolerance to risk of loss. We analyse whether individual decision-making is rational, i.e., based on the estimated chances of winning or losing an expected reward. Results of study 1 indicate that individuals can tolerate some delays and exert self-control if the expected reward is judged worth waiting for. Study 2 indicates that primates tolerate loss in risky games and take into account their odds of success when playing. The implications in terms of cognitive mechanisms involved in delayed/risky decision-making and how they may be expressed in the social context of these species will be discussed.

Geographic Variation in Orangutan Males' Monopolization Potential Is Driven by Female Choice and, Ultimately, Ecology

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Key Words: Orangutan · Ecology · Monopolization potential

Earlier, we found that Sumatran orangutan males arrest development of secondary characteristics more often and for a longer time span than Bornean orangutan males do. This difference is caused by variation in the monopolization potential of high-ranking males, leading to differences in stability of male dominance and competition styles, as well as different options for unflanged males. Here, we try to understand the reasons underlying the variation in monopolization potential. We examine the effect of forest productivity on association times, mating frequencies and the duration of female sexual activity, all of which are higher in Sumatra than Borneo. The results show that in Suaq, the Sumatran site, all females approached the dominant male and proceptively copulated with him, whereas in Tuanan, on Borneo, females showed less directed preference for the highest-ranking male and also less proceptive mating behaviour overall. Some matings with flanged males were even resisted resulting in forced matings. Furthermore, the results showed a correlation between food availability and time of associations. Low food availability in Tuanan does not allow a single flanged male to form long-lasting consortships with females. The latter causes the unstable male dominance ranks, and the reduced social protection of the females in Borneo, which in turn explains the absence of strong female preferences and the absence of a tendency of females to remain within earshot of the dominant flanged male. We conclude that variation in ecology is the driving factor for geographic variation in orangutan social organization.

Visual Cognition in Baboons: Assessment with Innovative Self-Testing Procedures

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Key Words: Baboon · Operant conditioning · Visual cognition

My laboratory has developed an innovative self-testing procedure to study visual cognition in non-human primates. The general design of this method is that the monkeys (baboons in our laboratory) are maintained in their social group and have a permanent access to operant conditioning test systems provided ad libitum in their enclosure. This setup has, so far, been used in a large number of experiments testing several aspects of baboons' cognition. Findings indicate a positive impact of the test systems on animal welfare. They further demonstrate some unrevealed cognitive capacities in this species, but also highlight some influences of the social context on individual performance. We propose that several key questions might be addressed more efficiently with this procedure, such as the interplay between social and non-social cognition, or between associative and cognitive processes.

Challenges of Primate Rehabilitation and Reintroduction

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Key Words: Rehabilitation · Sanctuaries · Displaced · Primates

Since the first primate sanctuary was set up in the early 1970s, sanctuaries have served as a refuge for all those primates rescued from the illegal pet trade. More than 40 years have passed and while sanctuaries are overcrowded, primate populations in the wild keep declining at an alarming rate. The illegal pet trade is still an issue today and, together with deforestation and poaching, is one of the main factors that contributes to the decline of primate populations in the wild. Relocation, translocation and reintroduction are today feasible options taken by many sanctuaries to make space in their facilities and to, of course, restock primate populations in their historical geographical range. However, releasing primates back into the wild is a complex task that needs very accurate planning. Success depends on several factors such as the availability of an adequate and protected release site, long-term habitat assessment and a very precise selection of healthy individuals able to establish viable wild populations in their natural habitats. Selected candidates for potential reintroduction, lacking the experience of living in the wild, require an extensive rehabilitation programme before being ready to be released. In order to improve their chances of survival, they need to obtain the necessary skill-set to function as part of a social community as well as learning about dangers and foraging in the wild. High quality sanctuaries with good behaviourists offer a unique environment where those primates, used for the illegal pet trade, can be taught the necessary natural skills to restock former primate areas and give primate populations a chance to recover.

Sociality and Communicative Complexity in Malagasy Primates

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Key Words: Communication · Lemurs · Sociality

The social complexity hypothesis predicts that animals engaging in many and varied social interactions should evolve more diverse signals. However, signal diversity may also be a result of the signalling environment or selection to avoid heterospecific matings. The relative importance of these factors on the evolution of signal diversity in primates is still poorly understood. Lemurs are an excellent model to study the influence of sociality and ecology on the evolution of signal diversity because they are organized into solitary, pair-living and group-living species, and occur in different habitats with different compositions of heterospecific congeners. In addition, lemurs produce a variety of signals in the three main sensory modalities: acoustic, visual and olfactory communication. Repertoire sizes of vocal and acoustic signals were available for 25 species and visual signal repertoire size was available for 13 species. Phylogenetic least-squares regressions revealed that communicative diversity correlates with group size, but not ecological factors, in all three communicative channels, suggesting that sociality is a prerequisite for the evolution of signal diversity in lemurs.

Relationships in Common Marmoset Families: Oxytocin Synchronicity Is Linked to Dyadic Bond Strength

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Key Words: Oxytocin · Bonding · Monogamy · Common marmoset

The establishment and maintenance of social bonds are crucial elements of group living and cooperation. Oxytocin has been identified to play a major role in pair-bonding, especially in monogamous species. Groups of monogamous common marmosets (*Callithrix jacchus*) are composed of a dominant breeding pair, its independent offspring and adult, reproductively inactive helpers. Whereas, strong and stable bonds are of high biological relevance between breeders, they are possibly less important for other group members. Hence, non-sexual relationships in marmosets might be rather balanced and may not require specific bonding with particular partners. The aim of this study was to assess the role of oxytocin in social behaviour and bonding in common marmosets, comparing breeding pairs and non-sexual dyads. We measured urinary baseline oxytocin levels and affiliative behaviour of 17 individuals in four captive marmoset family groups over a period of 6 weeks. Overall affiliative behaviour was not linked to individual oxytocin levels, even when controlling for sex and status. However, dyads varied with regard to bond quality (estimated based on mutual affiliation), and strongly bonded dyads showed high synchronization of longitudinal changes in basal oxytocin. Such a relationship between bond strength and oxytocin synchronicity was found in both breeding pairs and other dyad types. Our results show that in common marmosets (i) hormonal synchronization is an indicator of relationship quality and (ii) striking parallels exist in the hormonal correlates of breeders, breeder-helper and helper-helper dyads. This suggests that specific bonding is not only relevant for marmoset breeding pairs, but also for non-sexual partners and that it occurs independently of sex and social status.

Vervet Alarm Calls Revisited: A Fresh Look at a Classic Story

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Key Words: Alarm calls · Cognition · Playback experiments · Referential communication · Vervet monkeys

According to the text book story, vervet monkeys (*Chlorocebus pygerythrus*) give three distinct alarm calls in response to their three main predator classes, and the calls alone are sufficient to elicit different escape strategies. The calls were thus deemed as being 'functionally referential', and assumed to provide important insights into the evolution of speech. We used comprehensive quantitative analysis to re-assess the structural variation within vervet vocalizations. In contrast to the common notion, we found that the vervet alarm calls constitute a relatively graded continuum, with higher context specificity in female than male vocalizations. Importantly, both female and male alarm calls overlap in acoustic structure with calls produced in non-alarm contexts. Furthermore, we explored the alarm calls of the West African green monkeys, *C. sabaenus*. In response to snake and leopard models, female green monkeys produced chirp calls that revealed only graded variation in relation to predator type. Playback experiments paired with pre-exposure to a predator model showed that irrespective of context, subjects were more likely to respond to leopard chirps with a leopard-typical response. Predator priming did not have a sig-

nificant effect on the type of response, but, together with call type, did affect response duration. Conceivably, the immediate attribution of meaning was influenced by acoustic cues, while receiver's prior knowledge was incorporated to guide subsequent behaviour. Taken together, these results suggest that the vervet alarm calls do not fulfil one of the classic criteria for referential communication, and that listeners' refined cognitive abilities support adaptive responses.

The Nature of the Bonobo Society: A Case Study on the Learning Process of Primatologists

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Key Words: Bonobo · Socio-ecology · Captive · Wild

Behavioural research generates images of the nature of societies that can be related to theoretical concepts of evolutionary processes. Information from non-human primates has been crucial in developing and refining concepts on how environmental parameters trigger social relationships, the mode of mediating conflicts, individual strategies and, from these, behavioural traits that ultimately contribute to survival and reproduction. In addition, considerable methodological improvements in disciplines such as genetics and endocrinology are providing a growing body of reference data from non-invasively collected material leading to a better understanding of the proximate mechanisms of the observed behaviours. Research on bonobos has often been conducted with the notion that the species violates a number of biological paradigms, a puzzle that is neither expected in terms of its phylogenetic background, nor plausible in terms of its ecology. Compared to the remarkable discoveries obtained during the 1980s from studies in captivity, where dynamics of environmental and social conditions are artificially narrow, observations from the wild have lagged behind, creating a biased view of what bonobos can or cannot do. As a consequence, our knowledge about the socioecology of *Pan paniscus* was fragmentary and biased for a long time. However, the past two decades of long-term field studies conducted at multiple sites by independent research teams offer new insights into a social world that is diverse and dynamic. Research from captivity and from the wild seems to have found a balance that is mutually inspiring and leads to a more holistic picture of the bonobo. Reviewing the achievements of a growing community of researchers, we will identify the changes in our perception of the nature of an ape that – as some feel – is more human than any other primate.

Primates of the Caribbean: Using Historical Era Introductions of Monkeys in the Lesser Antilles to Understand Rates of Island Evolution

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Key Words: *Chlorocebus* · Island · Evolution · Morphometrics · Molecular

In response to the special characteristics of island environments, mammals often undergo evolutionary changes that are of fundamental importance for evolutionary biologists and ecologists.

gists. The introduction of African green monkeys (*Chlorocebus sabaues*) to the Caribbean approximately 450 years ago provides the opportunity to investigate the tempo and dynamics of primate evolution on islands following a dated colonization event and to understand better how populations respond to change. Combining morphometric and genetic analyses of the introduced Caribbean green monkey populations provides fundamental insight into evolutionary processes, most notably through the comparison of morphological and molecular differences across insular groups and between insular lineages and their mainland sister groups. In recent studies, it has been proposed that island taxa may experience accelerated rates of morphological adaptation over much-reduced 'micro'-evolutionary or ecological time-scales, suggesting that it may be possible to observe the evolution of quantitative characters in island populations over relatively short time periods.

Savanna Chimpanzees in Bandafassi Arrondissement, Senegal: The Past and the Future of Sympatry with Humans

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Key Words: Savanna chimpanzees · Senegal · Conservation status · Human impact · Evolution

The West African chimpanzee (*Pan troglodytes verus*) is listed as Endangered, facing a drastic decline. The apes in Senegal are limited to Kédougou region and are close to extinction. Most communities are isolated and live in sympatry with expanding human populations. Chimpanzees here compete with people over habitat, water and food, although traditional taboos prevent hunting. Further, apes of the Mandingue plateau live at the northern edge of the species' distribution, in a savanna landscape that was essential in human evolution. Thus, this research bears implications for understanding the context of early hominin behaviour, particularly habitat-use, foraging and material culture. The main objective of the project was to identify conflicts with humans in Bandafassi arrondissement and provide the initiative for chimpanzee conservation. Data on habitat use, nesting, feeding ecology and demography come from three priority sites and two periphery zones. From April 2010 through December 2011, 257 feeding records and 230 nesting sites were analysed, while apes were observed during 352 episodes. The average party-size was 8.3 (SD 5.2), the main activity was feeding (71.6%) and the dominant reaction to observers was retreat (48.1%). Chimpanzees used >55 tree species for nesting, but preferred *Pterocarpus erinaceus* (27.4% nests), which is most often pruned by nomadic shepherds. Their food repertoire was dominated by fruit (72.3%), but it included rare items such as soil, mushrooms, tubers, prosimians and bats. The apes regularly used tools in foraging for insects, baobab and tubers. From 63 plant resources, 21 are consumed by people and five key foods are commercially exploited. Sustainable harvesting of resources (for fair-trade), bio-horticulture and ecotourism are suggested as conservation alternatives.

Visitors' Effect on the Behaviour of Three Great Apes Species in Antwerp Zoo, Belgium

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Key Words: Visitor effect · Great ape · Zoo · Reaction · Public

The effect of visitors on the behaviour of 9 chimpanzees, 4 gorillas and 3 siamangs was observed in the Great Ape House of Antwerp Zoo (Belgium). The behaviours scored were 'animal ignores visitor', 'animal ignores visitor who is trying to elicit a reaction', 'animal looks at visitor' and 'reaction to visitor other than looking'. Of the three species studied, chimpanzees showed the least interest in the public. In 95% of the observations (233 of 246), they ignored visitors and in only 5% (13 of 246 observations) they looked directly at them. Siamangs looked at the visitors for 15% of the observations (19 of 126) and ignored them for 85% (107 of 126 observations), while gorillas looked at the visitors in 23% of the observations (22 of 97) and ignored them in 77% (75 of 97 observations). Gorillas thus paid the most attention to the public. When visitors were only watching, none of the animals responded in any way other than looking back or ignoring. Only three people tried to provoke a reaction (by knocking on the window or behaving in an abnormal manner) and only one ape (a siamang) responded. Nevertheless, the caretakers did report arousal of the animals in similar instances, indicative of behavioural stress. In summary, the great apes in Antwerp Zoo do not seem to react strongly to visitors watching them. They mainly ignore these visitors or look at them. Watching visitors can possibly be an enriching activity for these animals, but care should be taken to give the animals the choice to hide from the public. Provocative behaviour by the public should be discouraged.

Kin Matters: Effects of Male Relatives on Residence and Tenure Length and Thus Reproductive Success in Wild Long-Tailed Macaques

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Key Words: *Macaca fascicularis* · Kin selection · Reproductive success · Residence · Tenure

In primate species with female philopatry, the presence of maternal relatives has been shown to affect female reproductive success. For males, the dispersing sex, little is known about the effect of the presence of relatives, other than parallel first dispersal in the company of peers. Here, we report the effects of the presence of male kin on dispersal and mating success of male long-tailed macaques (*Macaca fascicularis*) in the Ketambe (Sumatra) population, using blood samples collected between 1986–1989 and analysed using 18 autosomal microsatellites. Using demographic (1976–1992) and genetic information, we identified maternal and paternal relatives (half-sibs, full sibs and father-son dyads) among males already dispersed from their natal groups. After immigration into a group, males with at least one close relative in the same group ($n = 20$) stayed in a group longer than males without relatives ($n = 18$). In addition, high-ranking males living in a group with male relatives retained higher ranks for longer. Thus, in addition to dominance rank and age, association with male relatives may affect a male's reproductive success, even in a species in which males are the dispersing sex.

Play in Mature Bonobos: Differences between the Sexes and Differences between Zoos

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Key Words: *Pan paniscus* · Social behaviour · Play · Captivity

Recent studies in play behaviour have found that female bonobos are more playful than males, and this has been linked to various aspects of bonobo society, including their egalitarian and female bonded society. Here, we investigate play behaviour in a large sample of zoo housed bonobos, housed at 6 different European zoos (Planckendael, Wuppertal, Apenheul, Frankfurt, Stuttgart, Twycross), totalling 15 males and 27 females older than 6 years. We discriminate between (1) play including juveniles and (2) play including only mature individuals. Play behaviour was recorded by focal animal sampling (mean/animal = 16.25 h) as well as 15 min group scan sampling. We studied play on an individual level and used both scoring methods. When considering only play with mature partners or individual play, we did not find a difference between time spent playing between male and female bonobos in those two play contexts, and results did not differ between focal sampling and scan sampling. Surprisingly, we found that male bonobos spent significantly more time playing with infants, compared to female-infant play – but this was only true for focal animal sampling and not for scan sampling. Interestingly, we found an effect of group on the amount of social play between adults, but no group effects on play including infants or on individual play. These results suggest that female bonobos do not play more than male bonobos, but that levels of playfulness can differ between groups and that care should be taken to generalise about the playful nature of bonobo society.

Walking Gorillas

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Key Words: Western lowland gorilla · Environmental enrichment · Bipedalism · Locomotion

In the wild, western lowland gorillas live in complex environments, impossible to fully represent in a zoo, which may lead to health problems (Hosey, 2004). Environmental enrichment, strongly related to cage complexity, can be enhanced by structural changes to cage furniture (Hosey, 2004). Western lowland gorillas exhibit bipedalism arboreally in the wild, and studies (Thorpe and Crompton, 2005) suggest that orangutan-like straight-legged arboreal bipedalism is an adaptation for negotiating flexible branches in the peripheral canopy, where the majority of fruits are found. Their hip extension levels exceed all other apes except humans and orangutans (Crompton et al., 2008), and foot proportions are more similar to those of humans than of any other great ape (Schultz, 1963). We hypothesize that the early hominin foot was mechanically effective on compliant arboreal supports using light-touch hand assisted bipedalism. Our study investigated if enclosure furniture allowed the gorillas to exploit this adaptation and display normal behaviour profiles. The gorillas in Twycross Zoo spent 54.3, 13.7 and 10.8% of their time being inactive, feeding and exhibiting abnormal and self-directed behaviours, respectively. Males spent significantly less time and females spent significantly more time above 1 m ($\chi^2 = 417.257$, d.f. = 1, $p = 0.000$), similar to wild gorillas (Inouye, 2003). Males used significantly less but females used significantly more multiple supports ($\chi^2 = 12.626$, d.f. = 1, $p = 0.000$). Given that the females were

more arboreal than males, multiple supports may have been used by females for stability in an arboreal context. Bipedal locomotion was exhibited significantly more than expected arboreally (>1 m) ($\chi^2 = 50.886$, d.f. = 4, $p = 0.000$), supporting our hypothesis that bipedalism has arboreal origins.

The Ability of Primates to Generalize

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Key Words: Chimpanzee · Macaques · Generalization · Matching-to-sample

It is known that primates can generalize information, but there is no clear idea about the difference in this between lower (Cercopithecidae) and higher (Hominidae) primates. The laboratory research of higher nervous activity at the Pavlov Institute of Physiology in Koltushi focuses on comparative cognitive development in children and chimpanzees. Using the matching-to-sample method, we have conducted a comparative study of generalization ability of macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*). In the first series of the study, the subjects had to match the real coloured geometrical figures to samples: real colour figure, to sample-its colour image, real colourless figure, its colourless picture and the sample-colour. Tasks were presented consecutively after reaching the 75% level of correct answers to each task. Macaques were trained at the first task for 100–150 trials and chimpanzees for 30–50 trials. Each following task in the sequence was solved by primates faster than the previous one. After solving the first three tasks (macaques) or first two tasks (chimpanzees), the primates understood the principle and performed the new tasks at the first presentation, without training. In the second part of the study, the primates had to transfer the formed generalized principle to new objects – the images of silhouettes of animals («specific») and the images of hieroglyphs (abstract). Macaques managed with matching-to-sample «specific» images on the first day; however, on the second and third day, their success decreased. Macaques could not manage tasks involving abstract images. This can be attributed to their high impulsivity and frontal and temporal-parietal structures level of development. Chimpanzees solved these problems at the level of 90% correct answers. This is probably explained by the fact the apes are able to grasp and retain in working memory the entire image, transferring internalized principle to complex images due to more advanced associative zones and well-developed eidetic memory.

Plio-Pleistocene Non-Human Primates of Bolt's Farm (Cradle of Humankind, South Africa): New Discoveries

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Key Words: Cercopithecoids · Plio-Pleistocene · Bolt's Farm · South Africa

Bolt's Farm has often been considered to be a single site of limited time span. However, it is a fossiliferous area which contains more than 30 loci of diverse ages. Most of the localities have

been discovered since the South African and French members of the HRU [Hope (Human Origins and Past Environments programme) Research Unit] started surveys in 2001. R. Broom was the first to prospect at Bolt's Farm between 1936 and 1950. He found the first cercopithecoid fossils. Later, the University of California expedition led by C.M. Camp between 1947 and 1948 amassed a significant collection of primate remains, e.g. BF 42 (skull and mandible of an extinct colobine monkey, *Cercopithecoides williamsi*) and BF 43 (complete skull of an extinct baboon-like primate, *Parapapio broomi/whitei*). While the different loci are undoubtedly Plio-Pleistocene in age, no more precise information about the age of the deposits was proposed until the surveys by the HRU team. Our preliminary studies on the fauna suggest that the loci of Bolt's Farm are of diverse ages, ranging from about 4.5 Ma to about 0.9 Ma. Bolt's Farm thus presents the longest chronological sequence within the Cradle of Humankind. The most significant discoveries made by the HRU team are: the oldest primate from the Cradle of Humankind (at Waypoint 160 aged about 4.5 to 4 Ma) and the new loci BPB (aged between about 4 and 3.5 Ma) and AC (aged between about 3.3 and 2.5 Ma). The primates found in these newly discovered sites are important for throwing light on the evolution of the cercopithecoid faunas of South Africa. The palaeoenvironmental context of the fossil sites provides information concerning the milieu in which the cercopithecoids evolved.

Chimpanzees' Behavioural Reactions at Different Subjective Value of Aim Achievement

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Key Words: Chimpanzee · Behaviour · Movement rate · Object value

A method known as 'Aim Approaching' (patent 1410948) was developed in the I.P. Pavlov Institute of Physiology in 1984 to investigate the mechanisms underlying purposeful behaviour in humans and chimpanzees. It was established that while 'aim speeds' close to or in excess of 250–400 mm/s activate positive emotional systems in subjects, low speeds (25 to 1 mm/s) activate negative emotional systems, while intermediate speeds activate an orientation response. However, although Pavlov first discussed the Aim Reflex in 1916, the role of subjective effects of aiming in organizing its achievement still remains unclear. Four adult chimpanzees were investigated. Using an 'Aim Approaching' method with reinforcement values set individually, we estimated the action of targets approaching at from 250 to 5 mm/s. Two control units were set at either end of a 1 m conveyor belt, one unit in front of the researcher and the other in front of the subject. The subject was able to activate the belt at speeds determined by the researcher. It was apparent that target speeds are linked to distinctions in organization of purposeful behaviour, emotion and reactions, apparently governed by unconditioned reflexes. Decreasing target approach speeds results in reduced efficiency of belt activation, reduced active target tracking time, and changed tactics in managing by the conveyor belt device.

Which Features Predispose Species to Evolve into More Complex Niches?

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Key Words: Niche complexity · Development · Provisioning · Brain size

Humans are known to occupy by far the most complex foraging niche of all primates. At the same time, we are characterized by slow development and large adult brain size. We recently showed that both slow development and extended provisioning allow for extended periods of skill learning (proxied by the relative age at adult-level skill competence, Schuppli et al. 2012). Here, we ask whether the same two factors ultimately allow species to evolve into more complex niches and how this is related to relative brain size. Using a comparative phylogenetic approach, we examined the links between different life history parameters, brain size and niche complexity in two taxa: 78 primate and 140 bird species. We divided niche complexity into knowledge-learning and motor-learning components. Our results suggest that two pathways allow species to evolve into complex niches: first slow, conservative development and second provisioning over extended periods of time. Primates seem to make use of the first pathway, whereas for birds the second pathway seems to be more important: in primates, we found a significant correlation between niche complexity and pace of development, whereas in birds we found a significant effect of the length of provisioning on niche complexity. This was found for both knowledge and the motor complexity of the niche. Interestingly, knowledge niche complexity is highly correlated with brain size in both taxa, whereas for motor complexity much weaker correlations are found. With this study, we are able to explain which life history and lifestyle features allow a species to evolve into a more complex niche. The results also shed light on important aspects of the evolution of human development and brain size.

Flower Power: Flowers as a Fallback Food for a Population of Black-Handed Spider Monkeys (*Ateles geoffroyi yucatanensis*) in Central Belize

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Key Words: Spider monkeys · Fallback foods · Flowers · Feeding ecology

As a consequence of living in seasonal environments, many non-human primate species face regular periods of relative food scarcity. During these time periods, species may rely heavily on fallback foods. Fallback foods are often lower in nutritional quality, or more difficult to process, than preferred foods, and so their use may require specialized morphological or behavioural adaptations. Spider monkeys are known to be reliant on ripe fruit, but in the seasonal forests of Central America, ripe fruit availability varies. Previous research suggests that during times of low fruit availability, spider monkeys use leaves as a fallback food. However, other research on frugivorous primates suggests that flowers are used as a fallback food. Our research had two goals: to examine explicitly the use of fallback foods in a population of spider monkeys, and to examine the behavioural consequences of using fallback foods. Using a multinomial logistic model and 2 years of scan data, we modelled how the food selection of a population of spider monkeys varied by individual age and sex, and the availability of ripe fruit. We found that flowers, not leaves, met the criteria for a fallback food. Using general linear models, we then examined how activity

budgets and grouping behaviour changed with flower consumption, and found that increased flower consumption led to increased feeding, decreased travelling, and reduced subgroup size. These behaviours were interpreted as a response to the nutritional characteristics of flowers. Flowers contain less per capita energy than fruit, and relying on them may cause spider monkeys to adopt more energy-minimizing foraging strategies. This research highlights the importance of considering minor food items in a species' behavioural ecology.

Changes in Food Availability in Relation to Ape Cultural Behaviour: A Historical Biogeographic Approach

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Key Words: Ecology · Culture · Chimpanzee · *Pan troglodytes* · Human impact

The influence of ecology as a cause of community-specific behavioural differences in animals, namely cultures, is controversial, particularly for chimpanzees. Data collected on food availability, diet and cultural behaviour in Ugandan chimpanzee (*Pan troglodytes schweinfurthii*) communities found in the Budongo and Kibale forests, a distance of only 180 km, suggest that current ecological conditions are poor predictors of chimpanzee cultural diversity. The two forests were connected up to about 10,000 years ago, suggesting that cultural transmission between communities could occur up to that point. To explain the current differences in cultural behaviour, and notably tool use, between these genetically close communities, it is necessary to study the evolutionary history of chimpanzee populations in this area and the changes that have occurred between the two forests since they became separated. The biogeographic model states that environmental conditions have changed drastically over the last 300,000 years and that genetic fluctuations in a given taxon are connected to the ecological variations it faces. A potential scenario for Eastern chimpanzees sees an originally small chimpanzee population subsisting in a harsh environment and colonizing the post-Ice Age re-growing forests, when facing more favourable conditions. However, depending on the colonized forests, the environmental pressure to maintain some food-related tool-use behaviour in a community's cultural repertoire may have been eased, leading in some cases to the disappearance of certain behaviour, such as stick use. Finally, the continuous human impact on the forests over the last thousands of years may also lead to drastic changes in the ecology of the forests, and thus potentially to changes in chimpanzee cultural behaviour.

Common Marmosets Preferentially Share Difficult to Obtain Food Items

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Key Words: Food sharing · Provisioning · Independent foraging · Food extraction

Callitrichids are remarkable among non-human primates because they systematically provision their offspring by proactively offering food. Food items are shared mostly from adults to infants. Provisioning is of particular importance in post-weaning periods and shows a decreasing tendency to the point of independent foraging. However, some food items are more difficult to

acquire than others, and immatures reach independence for difficult to obtain items later. In this study, we tested if adult common marmosets (*Callithrix jacchus*) take the difficulty of food extraction into account in food sharing. If so, we expected a faster decline of food sharing for easy to obtain items but a slower decline for items that are more difficult to extract. We conducted two different test types, in which (i) food items were handed over directly to specific individuals of the group (easy access to food), or (ii) the same individuals had to extract the same type of food item from a puzzle box (difficult access to food). We tested 17 individuals during the juvenile period of new offspring (from first independent feeding until the birth of the next offspring), and conducted 1–2 tests of each type per week. With difficult to obtain food items, subjects continued to share food for a longer time period, started later to refuse begging by immatures, and stopped later to emit food calls to attract immatures to the food. These results suggest that common marmosets are able to adjust their behaviour according to the difficulty of food extraction. This adaptation can lead to indirect benefits for the adults, since they provide an adequate context for the infants to learn how to extract food, lead them towards efficient independent foraging and, therefore, reduce future provisioning of the young.

Is Scan Sampling a Valid and Effective Method to Estimate Allogrooming in Chimpanzees (*Pan troglodytes*)?

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Key Words: Observational methods · Scan and focal sampling · Grooming behaviour

Allogrooming is a behavioural pattern in which an animal grooms the fur or skin of another animal of the same species. In primates, this behaviour has gone beyond the mere function of cleaning and hygiene as it serves to establish new relationships, strengthen family ties, reinforce social structures or even solve the conflicts arisen within the group members. Given its important social role, knowledge of the time spent by animals practicing allogrooming and their directionality is essential to evaluate basic social aspects in a group, such as social structure or dominance hierarchies. The study of allogrooming is usually carried out by focal animal sampling that provides data on the duration of each episode of grooming, the identity of the animals involved and the directionality of the interaction. This observational protocol provides fairly accurate estimates for allogrooming but as it cannot be applied simultaneously to all members of the group, it is time-consuming and requires prolonged observation periods. Our goal was to test whether it would be possible to obtain equally accurate estimates of allogrooming through scan sampling, an alternative protocol that allows the observer to record data from several animals simultaneously. Thus, we compared data collected by two observers who recorded simultaneously the allogrooming behaviour of a group of six chimpanzees (2 males and 4 females) by means of both observational protocols: focal animal sampling and scan sampling. The study was carried out at the zoo Bioparc (Valencia, Spain) in July and November 2011. We gathered 80 h of observation grouped into two periods of 10 days each. Our results show that both methods produce similar estimates for the allogrooming exchanged within the group.

Tradition Formation in Wild Common Marmosets

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Key Words: Social learning · Common marmosets · Foraging techniques · Tradition spread · Tradition stability

Experimental studies on the formation of traditions have so far focused almost entirely on captive populations. We present an open diffusion field experiment conducted with wild common marmosets (*Callithrix jacchus*) in a fragment of Atlantic Forest in Brazil. We confronted 13 family groups (n = 119) with an artificial fruit that led to a reward by using one of two alternative techniques. Six groups were naïve to the task, but seven groups contained individuals that participated in a pilot study and were therefore already familiar with this experiment. Hence, we could use these experienced subjects as potential models for naïve individuals. Furthermore, four additional groups with one trained individual and two control groups with no experienced or trained individuals were also tested. The aim of this study was to investigate (i) whether the experienced individuals would remember how to solve the problem even after 2 years without exposure to the task and if so, whether they would still have their preference for a technique, (ii) whether naïve individuals would use the social information to learn from their skilled family members to solve the task and more importantly, whether they would use the same technique, and (iii) whether the individual and/or group behaviour would persist over time or whether the preference for a technique is fading and the distribution of the two alternative techniques becomes random. Our results show that wild common marmosets are able to memorize, learn socially and maintain preferences of foraging techniques over an extended period of time. This field experiment thus reveals a promising approach to studying social learning in the wild and provides the basis for long-term studies on tradition formation.

Ultrasonic Vocalizations by Spectral Tarsiers

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Key Words: Indonesia · Sulawesi · *Tarsius spectrum* · Ultrasonic · Vocalizations

Although the vocalizations of spectral tarsiers, *Tarsius spectrum*, have been studied for over three decades by numerous primatologists, the data in this study represent the first evidence that this species communicates in the ultrasonic range. In addition, this study characterizes the types of ultrasonic vocalizations given by spectral tarsiers. Data were collected at Tangkoko Nature Reserve in Sulawesi, Indonesia, from January through April 2013. Recordings were made on a Wildlife Acoustics Ultrasonic Song Meter BAT2 from ten groups of varying sizes and compositions. The ultrasonic recorder was placed at the base of the groups' sleeping trees and recorded from 0500 to 0700 using an omnidirectional microphone. The recorder sampled data at a rate of 192 kHz and recorded with 16 bit resolution. A total of 143,898 vocalizations were recorded above 20,000 Hz. These vocalizations fell into six main categories: chirps, twitters, choruses, doubles, high intensity calls and then whistles. While previous studies of the spectral tarsiers' choruses indicated that the frequency range of the calls is between 0–20,000 Hz, this study found that the choruses regularly range upwards of 80,000 Hz. Given that the vocalizations reported in this study were exclusively recorded at the groups' sleeping trees, it is likely that these vocalizations function as a form of territory and/or mate defence.

Do Captive Bonobos (*Pan paniscus*) Use Distance to a Food Goal in Selection and Planning of Routes?

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Key Words: *Pan paniscus* · Captivity · Support use · Route planning

For large arboreal primates moving around a complex three-dimensional environment is risky due to branch instability and deformation and the threat of falling. Careful choice of supports based on an understanding of the physical environment is vital to safe and energetically efficient arboreal locomotion. When using tools, primates have been shown to possess an understanding of the physical properties of tools and to have the ability to select a suitable tool for a particular task. Cognitive abilities similar to those needed for tool use may also be required when choosing supports for locomotion. This study investigated how bonobos determine which supports to use when accessing an out-of-reach food goal, as an analogue for the decision-making process during natural canopy locomotion. Do they plan a route in advance or do they test supports as they go? An out of reach food goal was positioned between two vertical ropes, such that only one of the ropes (balanced between left and right) could be used to gain access to the food goal. The ropes were connected vertically so that they were taut and provided little movement towards the goal, meaning the bonobos had to choose and climb a rope then reach for the goal whilst maintaining an active posture. In this experiment, distance to the food goal was manipulated with the aim of determining whether this influences bonobos decision-making when choosing a support. The influence of other support properties on decision-making, such as flexibility and connectivity, were also investigated. These experiments shed light on whether bonobos select supports based on certain properties and whether this implies similar cognitive abilities to those employed during tool use.

Impacts of Western Lowland Gorillas on the Regeneration of Logged Forests: Preliminary Insights in a Gabonese Logging Concession

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Key Words: Western lowland gorilla · Timber exploitation · Forest regeneration · Seed dispersal

Timber exploitation is expanding within the forests of the Congo Basin. In Gabon, the timber industry is currently the second largest working sector, and logging concessions cover 45% of the country's forest area, largely overlapping with the range of the western lowland gorilla (*Gorilla gorilla gorilla*, WLG). With respect to its large body size, long gut retention time and extended daily path length, WLG presents a great potential for seed dispersal compared to other African primates. As this species disperses seeds of variable size preferentially into open canopy habitats such as old logging roads and gaps, WLG may contribute significantly to the recovery of logged forests. However, its effectiveness in ecological processes governing logged forest dynamics and forest regeneration is still poorly known. In the present study, seed dispersal by WLG was studied in a 617,000-ha logging concession located in Central Gabon. WLG-dispersed seeds were identified through faecal analysis followed by germination trials to assess seed viability after gut passage. For the most abundant species, impact of gut passage on seed germination was assessed through comparative germination trials. Our 10-month study revealed that WLG dispersed seeds

of 45 plant species. Seed viability was assessed for 36 taxa, with germination success ranging from 0 to 100%. For the most represented taxon, *Santiria trimera*, in gorilla faeces in the period January to March, seeds passed in gorilla gut displayed significantly higher germination success than those extracted from fresh fruit or sown surrounded by pulp. The preliminary results of this long-term study suggest that gorillas disperse many different plant species and could be effective dispersers for most of them.

Primates Manipulating the World: A Comparative Study of Manipulation Complexity across 20 Species

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Key Words: Manipulation complexity · Brain size · Evolution of cognition · Comparative approach

Primates manipulate food and objects in a variety of contexts and in various manners. Presumably, more complex manipulations are a prerequisite for cognitively demanding activities such as extractive foraging, tool use and innovation. Thus, the degree of manipulation complexity of which a species is capable is expected to increase with brain size, which has been shown to proxy general intelligence in primates. However, manipulation complexity has never been compared in detail across primate species. In the present study, we assessed manipulation complexity in three different contexts (food, non-food objects and social) among 20 species of captive primates, including species from all five primate grades. Complexity levels of manipulations were identified with a Guttman scale. The resulting scale was consistent with earlier approaches to identify manipulation complexity. We found a positive correlation between absolute brain size and our measure of overall manipulation complexity, which was robust after controlling for phylogenetic relatedness. This result was particularly strong for the food context. These results shed light on the current discussion of the factors that shaped primate brain size evolution. Whereas much recent work highlights the importance of the social environment in selecting for intelligence, our results instead support a, not necessarily mutually exclusive, ecological explanation. Given that complex manipulations are primarily used in ecological rather than social contexts, the pressures imposed by the ecological environment may have been a major selective force in the evolution of primate cognition.

Captive Pygmy Marmosets (*Cebuella pygmaea*) Hunt and Consume Free-Living Birds

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Key Words: Pygmy marmosets · Hunting · Bird of prey

Pygmy marmosets (*Cebuella pygmaea*) eat arthropods and occasionally lizards and frogs. There is only one published report of a pygmy marmoset killing a bird (Townsend and Wallace, 1999): the marmoset was a pet and the bird was motionless because it had just crashed into a

window, the owner removed the monkey seconds after the killing and thus the eating of the prey was interrupted. Here, we report that pygmy marmosets in the Kristiansand Zoo in Norway regularly kill and eat different species of healthy, free-living birds. We present what, to our knowledge, are the first systematic data collected on this behaviour. We describe the patterns of bird consumption by the monkeys. Pygmy marmosets are the smallest monkey species and thus their bird hunting behaviour is especially interesting since they are about the same size as the birds they prey upon. It has been proposed that humans are unique among primates for their ability to hunt prey that equals or exceeds their own body size. We discuss the implications that hunting of prey of equal body size by pygmy marmosets has for human evolution.

Bonobos and Chimpanzees: How Similar Is Their Cognition and Temperament?

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Key Words: Cognition · Temperament · Chimpanzees · Bonobos

Despite the evolutionary closeness of bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), the behaviour of these two *Pan* species differs in crucial ways. A few key differences were revealed when both species were compared on a wide range of cognitive problems testing their understanding of the physical and social world (Herrmann et al., 2010). The tests of physical cognition consisted of problems concerning space, quantity, tools and causality, while those of social cognition covered social learning, communication, and Theory of Mind tasks. A further comparison of bonobos and chimpanzees in two main temperamental components, reactivity and self-regulation (Rothbart and Derryberry, 1981), was conducted to investigate other possible species differences. Subjects were presented with five temperamental tasks. The first two tasks investigated subjects' approach-avoidance behaviour in novel or uncertain situations. A third task tested subjects' inhibitory control skills: apes were required to inhibit a prepotent response for a just-learned successful action and had to find a new solution to a problem. Tasks four and five investigated subjects' attentional control. Apes were either tested for how well they remained focused on a problem despite a sudden distracting noise, or how persistent they were in solving a task in the face of failure. In addition, I will discuss the results in light of socio-ecological differences across the two species and what role temperamental factors might play in explaining any differences we might find across the species with regard to their cognitive performances.

A Large, Continuous, and Stable Population of Eastern Chimpanzees Inhabits the Forests of Northern DR Congo

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Key Words: Eastern chimpanzees · *Pan troglodytes schweinfurthii*

In 2005, we collected data on encounters with chimpanzees and made counts of their nests on 160 km of line transects and 2,277 km of recce walks across a 55,163 km² area in the Central

Uele Region of DR Congo. Our transect data collected in the Bili-Gangu area revealed a nest encounter rate of 2.43 nests per km (CL = 1.79–3.28), higher than at any other site in the DR Congo and comparable to encounter rates at East African sites. On these transects, we found a higher nest encounter rate in the remote forest [3.85 nests per km (CL = 2.51–5.87)] than in the area closer to the road [1.56 nests per km, CL = 1.07–2.26]. On our recce walks across the region, we encountered chimpanzee nests within 13 km of the largest population centres. Finally, when we re-surveyed 27 km of our earlier transects in 2012, we found no decrease in nest encounter rates. Our results suggest that the Central Uele and neighbouring regions are home to one of the largest remaining continuous populations of Eastern chimpanzees, and that in at least some forests the population remains stable as of 2012.

Gestural Communication in Great Apes: Intentionality, Syntax, and Semantics

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Key Words: Chimpanzee · Gestural communication · Great ape · Language origins

We will describe the communication of great apes with particular attention to the development and use of the rich repertoire of gestures employed in intentional communication. We will focus on the gesturing of the free-ranging wild chimpanzees of the Budongo rainforest in Uganda, and will discuss the evidence that gestures are used intentionally by individuals of all ages across a range of contexts, including 'evolutionarily urgent' ones. We will examine the possible explanations for the combination of gestures into sequences, including any evidence for syntactic like structures, persistence following failed communication, and the refinement, through experience, of a large repertoire of available gesture forms to a focused repertoire of regular use. Finally, we will examine the case for meaning in gestural communication, whether individual gesture forms can be said to have specific meanings and, if so, whether these are consistent across signalers. We will discuss whether or not the high levels of flexibility regularly reported in previous studies remain valid in the light of evidence from a wild population, and to what extent any flexible use involves the use of several gesture forms for a single meaning, or a single gesture form for several meanings.

Cultivar Feeding by Chimpanzees: From Community Variation to Conflict Mitigation

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Key Words: Cultivar · Chimpanzee · Human-primate conflict · Feeding traditions

With the large-scale conversion of natural habitats to other land-uses such as farming, numerous wildlife species are increasingly exposed to novel food sources – cultivated foods. Cultivar feeding by primates is a major source of conflict globally, impacting local livelihoods and impeding conservation. Although endangered, chimpanzees (*Pan troglodytes*) occur in areas of anthropogenic influence throughout tropical Africa. Here, we explore species-wide patterns of cultivar consumption by chimpanzees, and take an in-depth look at differences in cultivar selection in two chimpanzee communities living in forest-farm mosaics in East and West Africa. The avail-

ability of cultivars to many wild chimpanzee populations has occurred relatively recently in their evolutionary history, and we suggest this provides a novel mechanism to explore the acquisition and establishment of feeding traditions. However, from an applied conservation perspective, human-primate conflict mitigation requires evidence-based management that is founded on a good understanding of species' ecology and cultivar feeding habits.

Hair Cortisol Levels in Hair Samples of Non-Human Primates

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Key Words: Cortisol · Hair · Macaques · Common marmoset

Serum and urine are used to assess short-term changes in glucocorticoid. Values from such samples are specific for a single (or short) time-point. Recently, methods were developed to determine cortisol levels in hair. Cortisol from the circulation is incorporated into the hair shaft during growth, enabling determination of chronic hormone levels. We analysed the hormone levels in hair samples of a colony of 150 long-tailed macaques, *Macaca fascicularis*, that were moved from their original location to a new location at the BPRC. Hair samples were obtained by shaving a small part of the neck area during their regular health checks before, during and after moving, over a total follow-up period of more than 2 years. In addition, hair samples were taken from rhesus macaques, *Macaca mulatta*, and common marmosets, *Callithrix jacchus*, from the BPRC colony to determine hair cortisol levels in these colonies and to compare the different species. This study did not require invasive procedures and hair samples were obtained only when the animals had to be sedated for their routine health checks. In long-tailed macaques, cortisol levels in the hair samples increased when they moved to a new area. Two months after settling at the new location, cortisol levels showed a significant decline and significantly decreased in the new housing situation compared to pre-move levels. Rhesus and long-tailed macaques showed comparable levels of hair cortisol. Cortisol levels in hair from marmosets were much higher. In addition, very young animals from all three species tested showed extremely high cortisol levels. We conclude that hair samples of non-human primates can be used to determine cortisol levels reflecting prolonged stress levels. This can be used to monitor individuals and, where needed, improve the welfare of the animals.

New Perspectives on the Transmission of Malaria between Macaques and Humans: The Case of Vietnam

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Key Words: *Plasmodium* spp. · Zoonoses · Rhesus monkey · Non-invasive · Molecular typing

Increasing contact between humans and other primates in the wild, due to expansion of agriculture and development, pet trade, eco-tourism and research, is of concern to both conservationists and health officials. One important impact of this intensified contact is the transmis-

sion of zoonotic disease such as metapneumovirus, herpesvirus and Ebola virus. One emerging zoonose gaining attention in Asia is monkey malaria (*Plasmodium knowlesi*, Pk). A malaria parasite of long-tailed macaques (*Macaca fascicularis*) and pigtailed macaques (*M. nemestrina leonine*), its presence has been noted in people working at the forest fringe or inside the forest, as well as in an increasing number of domestic and foreign tourists. As part of a long-term epidemiological study of malaria in humans and a local effort to eradicate this disease from one of the last remaining endemic areas in Vietnam, we present results from an on-going study to identify the non-primate vector of monkey malaria in the surrounding forests of Khanh Phu Commune, a mountainous farming area in south central Vietnam's Khanh Vinh District of Khanh Hoa Province. Using a molecular technique developed to identify Pk from experimentally infected captive Japanese macaques (*M. fuscata*), we analysed faecal samples, collected opportunistically from wild monkeys in the forests surrounding hillside farmsteads, for the presence of Pk. Due to high levels of human-monkey conflict in the area, we were unable to observe the monkeys directly, necessitating the need to identify the malaria host species molecularly. Confirming molecular results of Pk isolated from the human population over-nighting in the forest for subsistence purposes, Pk was confirmed to be present in macaques identified as *M. mulatta* or possibly an *M. mulatta* X *M. fascicularis* hybrids.

The Bootstrapping Dimensions of Culture in Chimpanzees

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Key Words: Chimpanzee · Material culture · Innovation · Tool use · Cultural evolution

Stick or stalk-using behaviours are some of the most prominent and diversified forms of tool use among chimpanzees (*Pan troglodytes*) in their natural habitat. For example, using a wand or a probe for catching social insects on the ground and/or in trees or for harvesting honey is common to chimpanzees throughout their range with rare exceptions. However, the prevalence of each type of behaviour and its form differ by locality, implying cultural differences across chimpanzee communities. We employed reports of stick- or stalk-using behaviours across wild chimpanzee study sites to investigate the relationship between the material cultural repertoire of a community and its propensity to innovate. Upon controlling for field research presence, climate, habitat and subspecies and social variables, we tested the relationship between the habitual or customary probing repertoire of communities and instances of innovations using probes reported within these communities. We provide here preliminary evidence of a 'cultural bootstrapping effect'. We discuss the potential relationship between the cultural repertoire of a community and its propensity for innovation and, thus, invention, shedding possible light on cultural evolution in one of our closest living relatives.

Energetic Aspects of Primate Brain Size Evolution

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Key Words: Encephalisation · Energetics · Scaling · Diet

Primates are among the most encephalised animals, which is reflected in their considerable behavioural flexibility and problem solving abilities. However, within primates, brain size varies

considerably between species for any given body size. Numerous hypotheses have been put forward to explain this variation. In recent years, we have tested predictions that flow from a framework focusing on the energetic aspects of having a large amount of the metabolically expensive brain tissue. In this talk, I will give an overview of our findings from broad comparative phylogenetic studies in mammals, and their implications for our understanding of non-human and human primate evolution. In sum, we found evidence for two pathways to increase relative brain size compared to the ancestral state. First, a species may change its lifestyle to allow for a stable increase in its total energy budget, e.g. by changing its diet. Alternatively, or in combination with the first pathway, a species may allocate more energy to the brain and less to other expensive functions such as offspring production. Ultimately, this option results in very low population growth rates even in good conditions, as found in great apes. A further increase in brain size would not be compatible with demographically viable populations in these large-brained primates. However, using comparative evidence from mammals, we demonstrate that help from non-mothers can alleviate this trade-off between reproductive effort and brain size. Nevertheless, the energetic constraints on brain size evolution will only be overcome in species that can actually benefit from enhanced cognitive abilities. While such benefits are potentially ubiquitous, we would expect them to be undermined by unavoidable mortality in some socioecological conditions, and by the difficulty of transferring knowledge across generations in some social systems. A combined test of all these considerations remains a challenge, largely due to the shortcomings of the distinct datasets, but I will present the newest data and results from our current projects.

Do Wild Chimpanzees Have Functionally Referential Food Calls?

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Key Words: Food calls · Functionally referential · *Pan troglodytes* · Vocal communication

Vocal research on non-human primates has revealed little flexibility in production and usage, as well as limited referential capabilities. We investigated the variation present in chimpanzee food calls, a graded yet context-specific vocalization. Our aim was to elucidate to what extent these calls are referential in the wild since evidence for functional reference has been recently supported in captivity. Additionally, we investigated whether nearby conspecifics could potentially use any differences in food call structure to guide their foraging effort, as has been proposed in the ‘information sharing hypothesis’ for the function of food calls. We recorded and analysed food calls of chimpanzees from one habituated group living in Taï National Park. Vocalizations were recorded during continuous focal follows conducted over an 11-month field season, with measurements of tree species, size and fruit amount noted for every feeding event. We use robust mixed model analyses to investigate whether the acoustic structure of chimpanzee food calls are specific to food type and quantity. Preliminary results suggest that signallers may indeed be producing calls more specifically, with regards to fruit species and amount, than has been previously shown in the wild. We address the various motivational and cognitive factors that may contribute to the patterns observed in food call production. Furthermore, we are analysing responses of nearby individuals to these food calls, namely if others arrive. On-going analysis suggests food calls may also elicit specific responses. We discuss our results in the light of different theories proposed for the evolution of language in general, and more specifically concerning vocal communication systems in non-human primates.

Social Interactions in an All-Male Group of Hamadryas Baboons (*Papio hamadryas hamadryas*)

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Key Words: Hamadryas baboons · Bachelor group · Social behaviour

In captive primates, the formation of bachelor groups is a successful long-term solution that provides social housing for surplus males. However, in captive hamadryas baboons, culling of surplus males seems to be an acceptable management strategy to reduce group size and social tension, and subsequently increase the welfare of the remaining group. No studies have investigated if bachelor groups of hamadryas baboons provide an alternative for surplus males. Therefore, this pilot study focused on social interactions in a previously formed bachelor group of hamadryas baboons of seven individuals, three intact males and four castrated males. This group was housed at a rescue centre for exotic animals in The Netherlands and the last individuals were introduced in March 2011, 5 months prior to the start of this study. Social interactions were studied for a period of 8 months. Preliminary results indicated that a stable group had been formed in which little agonistic interactions occurred. Therefore, the formation of a bachelor group seems an appropriate long-term solution for male hamadryas baboons in captivity. Intact males received more submissive and affiliative behaviour from others, and were groomed more often compared to castrated males. On the other hand, castrated males showed more submissive and affiliative behaviour and were mounted more often compared to intact males. This indicates that there were behavioural differences between castrated and intact males which might have positively influenced the social compatibility of this group. Affiliative interactions such as grooming were primarily directed from castrated males towards intact males, this seems to resemble female-male interactions within a unit in wild hamadryas baboons.

The Interaction of Social and Ecological Parameters on Foetal and Infant Survival in Wild Crested Macaques

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Key Words: Offspring loss · Proportional hazards model · Socio-ecology · *Macaca nigra* · Female reproductive success

Premature loss of offspring can severely limit direct fitness of parents. In gregarious mammals, both ecological and social variables impact offspring survival and may interact with each other in this regard. Although a number of studies have investigated factors influencing offspring loss in mammals, we still know very little about the underlying causes and, in particular, how different factors interact with one another. We therefore investigated foetal and infant mortality in three large groups of wild crested macaques (*Macaca nigra*) over a period of 5 years by including potential social and ecological causes in a multivariate survival analysis. Infant, but not foetal, survival was most impaired after a recent take-over of the alpha-male position by an immigrant male. Infant survival was furthermore affected by the interaction between the number of group

females and food availability. This interaction also influenced foetal survival, but was additionally a function of maternal rank. Foetal survival probability also contrasted that of infants through its sensitivity to inter-group encounter rates. Our study thus stresses the importance of survival analyses using a multivariate approach and encompassing more than a single offspring stage for investigations of the determinants of female direct fitness. We further provide the first evidence for fitness costs deriving from high pressures of both within- and between-group competition in a Resident-Nepotistic-Tolerant primate species.

Does a Female Chimpanzee's Personality Determine Her Maternal Style?

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Key Words: Personality · Maternal style · Parenting · Chimpanzee

Within a species, individual mothers differ consistently from each other in their maternal behaviour towards their offspring. These individual differences between mothers have been termed maternal styles and are consistent over infant age periods and with successive infants. This consistency implies that factors other than social and demographical ones have a crucial impact on maternal styles. Personality may be an important factor determining these individual differences in maternal style. In humans, the association between maternal personality and parenting is well-described, while in other primates such evidence is scarce. Therefore, the aim of this study was to assess if maternal styles depend on mothers' personality in chimpanzees. Using established observational methods, we assessed the personality and maternal style characteristics of 11 chimpanzee mothers with dependent offspring in two different zoos (Abenteuerland Walter Zoo, Switzerland, and Chester Zoo, UK). Based on focal observations of 31 h/ind in Walter Zoo and 4 h/ind in Chester Zoo, we first assessed the characteristics of maternal styles. Then, we extracted the females' personality traits based on Koski (2011). Finally, we assessed whether several personality characteristics of the mothers, together with the mothers' age and parity, and the infants' age, influenced their maternal style. We will discuss the results in the framework of constraints to maternal behaviour and investment in primates, and the evolutionary history of maternal behaviour of humans.

The Role of Ecology in Shaping Chimpanzee Material Culture

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Key Words: Chimpanzee · Culture · Necessity hypothesis · Opportunity hypothesis · Tool use

Geographic variation in behaviour may be best explained in terms of culture if ecological and genetic explanations can be excluded. However, ecological conditions may in turn also affect cultural processes. We examined the influence of environmental factors on foraging tool use among chimpanzees (*Pan troglodytes verus*) at the Seringbara study site in the Nimba Mountains, Guinea. At Seringbara, nut-cracking and termite-fishing are absent, but ant-dipping is present.

We tested two ecological hypotheses to explain foraging tool use prevalence. The opportunity hypothesis states that encounter rates with nuts, insects or tools explain tool use patterns. We measured the density and distribution of nut trees, nuts, army ants and termites in relation to the chimpanzees' ranging patterns. The necessity hypothesis states that tool use is a response to scarcity of preferred foods (i.e. ripe fruit). We measured the temporal availability of nuts, army ants and termites in relation to preferred food sources. Our findings support the opportunity hypothesis: nut trees and *Macrotermes* mounds were rare and peripheral to the chimpanzees' range, whereas army ants were abundant and widespread. The necessity hypothesis did not explain tool-assisted insectivory, as neither ant-dipping nor termite-fishing functioned as a fallback strategy. Nuts were absent at times of fruit scarcity and thus not available as fallback foods. Our findings highlight the importance of considering environmental conditions in explaining foraging tool use by wild chimpanzees and emphasize the interplay between environment and culture. The next step will be to investigate the role of both ecological and social factors in shaping the opportunities for social learning of tool use skills across ape species.

Common Marmoset Personality Assessed with Behavioural Experiments and Observations

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Key Words: Personality · *Callithrix* · Exploration · Social role

Personality, i.e. individually consistent behaviour patterns that vary among individuals, appears ubiquitous in animals. Most personality variation is described in traits expressed in non-social situations. Yet, most animals interact with others, and many live permanently in social groups. Social environment may place additional constraints on behaviour, and influence the expression of behavioural dispositions. Such effects may be especially influential in species with clearly defined social roles, such as cooperative breeders. We assessed personality in 17 adult captive common marmosets, *Callithrix jacchus*, housed in 4 family groups. We used focal observations of the daily activities and targeted experiments to quantify consistent variation in a broad range of traits. The non-experimental focal data were collected at two time periods separated by 6 months, yielding individual scores of social behaviour variables (play, grooming, proximity, scratching). The experimental battery consisted of 8 exploration, predator-model and problem-solving experiments conducted in the group setting and repeated after 6 months. They yielded individual scores of non-social variables (boldness, exploration, persistence). We assessed the repeatability of all behavioural variables, and thereafter their cross-contextual consistency. Repeatability was also assessed separately among breeders and helpers. Finally, we assessed the trait structure with a factor analysis, and tested the sex and role differences of the factor scores. The results indicate that marmosets exhibit several personality traits, while the role and group place additional constraints on marmoset behaviour. We will discuss the findings in relation to personality in other primates and non-primate vertebrates.

Gestural and Vocal Communication in Great Apes: Evidence for the Multimodal Origins of Language?

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Key Words: Language origins · Communication · Gestures · Calls · Great apes

Historically, gestural communication has been viewed as a mere adjunct to speech. Recently, however, some theorists have re-cast gestural communication as an aspect of an integrated language system, i.e., as an inherently multimodal, embodied phenomenon. In studies on the communication of the other primates, researchers have coalesced around two competing, modality-specific theoretical positions: the vocal origins theory and the gestural origins theory. Proponents of vocal origins theories have emphasized the semantic content and syntactic features of primate calls, and more recently have revealed surprising flexibilities in primate call systems, including social influences on calling. Proponents of gestural origins theories have emphasised the flexibility of gestural production, and downplayed the flexibility of calls. Here, we will review evidence, from laboratory and field studies, involving hundreds of subjects, pertaining to a third possibility, that visual and auditory communication might be part of an integrated, multimodal system of intentional communication among great apes. In particular, two characteristics of communication will be highlighted: (a) intentionality (or ‘aboutness’) and (b) intentional action (or goal-directedness). Taken together, these studies reveal some surprising relationships between visual and auditory communicative behaviours in our nearest living relatives. Both modalities of communication are tailored to an audience’s characteristics, and are integrated with visual orientation to salient targets and social agents. Moreover, there is evidence of group-specific patterns in both modes of communication. We conclude that intentional communication among great apes, including humans, may be a modality-independent phenomenon.

Social Network Plasticity in Barbary Macaques (*Macaca sylvanus*)

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Key Words: Barbary macaques · Social networks · Plasticity · Behaviour · Node removal

Primates are very social, forming highly non-random and differentiated social networks with their group members. These networks, however, are expected to be plastic and flexible, depending on circumstances. To date, very few studies have looked at the flexibility of social networks, instead, networks are perceived to be stable and long-lasting. Here, we investigate how the disappearance of individuals affects social networks, making use of a ‘natural experiment’, i.e. the death of several group members in two groups of Barbary macaques (*Macaca sylvanus*). We compare the newly established networks (post-death) to those from before the disappearance of group members as well as to simulated networks, where we simulate the removal of individuals by simply removing the nodes from the network. This enables us to assess (i) the plasticity of primate social networks and (ii) the reliability with which networks can be predicted through removal simulations for highly cognitive and socially flexible species, such as primates. Preliminary results suggest that some of the new (post-death) networks differ significantly from those predicted by the removal of nodes from the pre-death networks, suggesting that Barbary

macaques do not simply follow the old network structure but re-build their social networks when circumstances change. The implications this has for the interpretability of network node removal studies will be discussed.

Distribution of the Javan Slow Loris (*Nycticebus javanicus*): Assessing the Presence in East Java, Indonesia

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Key Words: Javan slow loris · Distribution · East Java · Habitat

The Javan slow loris (*Nycticebus javanicus*) is a nocturnal primate restricted to the island of Java. Its range is highly fragmented, and it is unsustainably hunted for illegal pet and traditional medicine trades. Currently *N. javanicus* is listed as Endangered on the IUCN Red List, although on the basis of habitat loss alone, Critically Endangered would be more appropriate. The geographical range of *N. javanicus* is reported to be restricted to West Java, but habitat suitability analysis, based on a predictive ecological niche model, includes East Java within its range. To resolve the ambiguity regarding slow loris distribution, we visited East Java on three separate expeditions in 2012–2013 to resolve the presence of *N. javanicus*. We visited four localities, including Meru Betiri and Alas Purwo, walking along transects in them, and independently verified the species' existence at all of them. Other slow loris species are commonly found in deciduous forests throughout Indochina, thus it is not surprising that *N. javanicus* inhabits the moist deciduous forests of East Java, even though strikingly different from the evergreen rainforests of West Java. We used the maximum entropy modelling (MAXENT v. 3.3.3k) for species distribution modelling. Our model predicts further suitable habitats in East Java for *N. javanicus*. These habitats are similar to those surveyed; and we believe the species is likely to be present in these additional areas. Only 17% of the predicted distribution of *N. javanicus* is within the protected area network. Although lorises can persist in unprotected areas such as agroforests, they are exceptionally subject to poaching. New populations are already imperilled by threats when only just 'discovered' and are reliant on the actions of local people to protect them.

Socially-Guided Vocal Flexibility in Captive and Forest-Dwelling Guenons

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Key Words: Vocal communication · Human language · Acoustic flexibility · Semantic combination · Conversational rules

Non-human primate vocal communication is primarily a social act, as is human language. It is therefore legitimate to argue in favour of a coevolution between sociality and vocal complexity. However, in contrast to human language, vocal communication in monkeys and apes, our closest living relatives, has long been described as rigid and strongly genetically determined. We review recent evidences of vocal flexibility under social influences in captive and forest-dwelling guenons. First, a multi-level (i.e. sound unit, call type, vocal sequence) approach of the organizational structure of vocal repertoires reveals a complex encoding of social messages in vocal signals. Second, the analysis of the social context of communicative interaction demonstrates its role in the emergence of vocal variability in juveniles and adults, both in terms of production and us-

age. Third, a comparative study confirmed the influence of the characteristics of social system on the degree of communicative complexity observed at the species level. From there, parallels with different human language properties (e.g. semantic, syntax, accommodation, conversation) can be drawn. The debate is now open: are guenons' vocal properties precursors to language or consequences of socially-guided convergent evolution?

Grooming Network in a Group of Captive Chimpanzees: Effect of the Wild or Captive Origin of Members

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Key Words: *Pan troglodytes* · Social network analysis · Grooming

Many chimpanzees are housed in captive settings, with an increasing effort made to recreate social groups, where the members may be captive or wild born. A captive origin may mean restricted rearing conditions during early infant life: no mother rearing, social life missing. This has been linked with differences in tool-using behaviour between captive and wild born chimpanzees (Morimura and Mori, 2010). If physical cognition can be impaired by non-natural rearing, what might be the consequences on social cognition? To investigate this topic, we analysed the grooming network of a captive chimpanzees group (*Pan troglodytes*), composed of 7 wild-born and 8 captive-born individuals, using social network analysis (SNA). Grooming is a complex social activity in which chimpanzees spend up to 25% of their waking time (Nakamura, 2003), and it is known to play a role in the emergence and maintenance of social relationships (Fedurek and Dunbar, 2009). We derived the HWI matrix of body contacts from behavioural observations and conducted SNA centrality measures. We simulated removal of captive-born versus wild-born animals in the network, from the highest betweenness coefficient to the lowest one, in order to assess group cohesion. We found that the positions of members in the network did not differ in centrality. Changes in the network during removals of wild-born or captive-born members were not different: cohesion was maintained equally whatever the origin of group members. Contrary to long-term effects on physical cognition, living in social groups compensates for the negative effects of non-natural early rearing conditions and this rearing apparently did not impair social cognition. Here, again the use of social network analysis proves to be useful in management of captive groups (Shel et al., 2013).

Who Is Calling? Variation in Reliability of Individual Signatures in Bonobo's Calls

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Key Words: Vocal communication · Individual signature · Emission contexts · *Pan paniscus*

This study focuses on the potential information changes in calls according to emission contexts. Social interactions are complex in great apes and rely on a great array of communication signals. However, their forest life may favour the acoustic channel. Here, we investigate the encoding of individual signature in bonobo's (*Pan paniscus*) calls and test its reliability among their

vocal repertoire. About 330 calls have been recorded in four different emission contexts – from peaceful to tense situations – in a captive group of nine individuals in La Vallée des Singes, France. To assess which of the spectral, amplitude and temporal cues could support individual identity coding, we define a set of six parameters describing the acoustic structure of calls. To quantify the reliability of the individual signature, we took a multivariate approach using a cross-validated and permuted discriminant function analysis. We expected that even if all types of calls produced in any contexts might convey information about individual identity, the degree of reliability may vary among call types resulting from emotional status of the emitter and social stakes. This study contributes to a better understanding of the bonobo communication system which mediates their complex social relationship under the specific constraints of living in a closed habitat.

What Gestures of Non-Human Primates Can (and Cannot) Tell Us about Language Evolution

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Key Words: Gesture · Facial expression · Vocalization · Language evolution

Many theories of language evolution are based on comparative evidence of the communicative abilities of our closest relatives, the non-human primates. The majority of these theoretical approaches propose a unimodal origin, usually gestural or vocal, and aim at identifying the corresponding precursors to human language in other primate species. The aim of this presentation is to summarize the main results of a systematic review of research on gestures of great apes and monkeys published over the last 50 years and to compare them with studies on facial expressions and vocalizations, with focus on their methodological approaches. The main findings are that most gesture research is conducted on great apes, while vocal and facial studies mostly focus on monkeys. Furthermore, gestures are investigated in captive settings, mostly by using observational methods, while the majority of studies on vocalizations are conducted in natural settings by using experimental approaches. Thus, research into vocal, gestural and facial behaviours has very different methodological, but also different theoretical approaches and as a result, comparisons of communicative patterns across modalities are problematic. Therefore, based on our current knowledge about primate communication, any conclusions about possible origins of human language seem to be premature, and we suggest that a multimodal approach to primate communication is essential to understand the complexity of their communicative systems and to identify phylogenetic precursors to human language as part of a multimodal system.

Is There ‘Meaning’ in Great Ape Gestural Communication?

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Key Words: Gestures · Meaning · Flexibility · Language evolution

Many theories on language evolution – regardless of whether they suggest a vocal or gestural origin – rely on comparative evidence of the communicative abilities of our closest relatives, the non-human primates, to identify potential precursors to language in these species. Gesture

researchers usually argue that one of the distinguishing features of non-human primates' gestures is their high degree of flexibility, which can be considered in different ways: (1) 'means-end dissociation', which refers to the use of a particular gesture in different functional contexts and/or several gestures for one specific context, and (2) gesture sequences which consist of combinations of two or more gestural signals. Both strategies enable non-human primates to adjust their gesture use to their partner's behaviour and to increase the range of potential meanings that can be conveyed by combining the components of a more or less limited gestural repertoire. Because of their flexible use, however, very few gestures have a specific meaning, but their meaning is defined by the context in which they occur. Thus, in contrast to many vocalizations of non-human primates, their gestures are (1) less context-specific and do not represent functionally referential signals and, related to this, (2) gesture sequences do not represent meaningful combinations used for other functions than their single components. Therefore, I will first provide an overview of recent research on the flexible use of gestures in great apes to demonstrate how they create meaning in their interactions with others. I will then discuss how these findings relate to evidence from vocal studies with the aim to identify 'blind spots' and biases that currently constrain a fruitful debate about the origins of human language.

Conformity to Group Specific Tool Use Behaviour among Three Neighbouring Chimpanzee (*Pan troglodytes verus*) Communities in Côte d'Ivoire

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Key Words: Chimpanzee · Tool use · Conformity · Côte d'Ivoire · Nut cracking

Tool use is a very important part of everyday life in wild chimpanzees and allows them to exploit more diverse food sources. Tool expertise is suggested to be acquired mainly through social learning as young chimpanzees spend a lot of time observing tool handling by their mothers and other fellow group members. Through nut cracking behaviour of three neighbouring chimpanzee communities in the Taï National Park in Côte d'Ivoire, we can examine how group specific tool selection is manifested in three chimpanzee communities. We first investigated tool choice for nut-cracking over the course of 27 years and found that group dependent tool selection persists over time despite changing role models and immigration. We further were able to show that there are no differences in fidelity to group norm behaviour between females and philopatric males, supporting the hypothesis that immigrants tend to adopt the cultural behaviour of their new group, which would lead to persisting behaviour in one community over time. Additionally, we describe a study case where one immigrating female adopted the group behaviour of her new community. Community dependent conformity in tool selection in neighbouring populations suggests a cultural transmission process even in adult group members as an adaptation to group specific behaviour. This is the first time that this level of conformity to a cultural trait over generations can be shown in wild chimpanzees.

The Effect of Between-Group Competition on Within-Group Grooming

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Key Words: Aggression · Competition · Grooming · Network · Socioecology

When between-group competition is high, more cohesive groups (where group members have a larger and stronger network of social bonds with one another) should be more capable to co-operatively defend resources from less cohesive groups, other things being equal (e.g. group size differences). There is convincing evidence of the effect of between-group competition on within-group cohesion in humans but scarce data exist on other mammals. We collected data (from the literature and through a questionnaire sent to colleagues) on the level of aggressive between-group competition and within-group grooming on 28 social groups from 17 primate species. We used network analysis to measure within-group grooming distribution. We ran a series of phylogenetically controlled generalised least square regression models independently for males and females. The frequency of aggressive inter-group encounters a social group had experienced was positively related to within-group grooming distribution. In populations with more frequent between-group aggressive encounters, females maintained denser and more equally distributed grooming networks. We found scarce evidence for a relationship between aggressive between-group competition and within-group grooming in males. Our findings indicate that grooming distribution can be modulated by the level of aggressive between-group competition in females but less so in males. Such sex difference could be due to the fact that, in many primate species, males rarely groom each other. Moreover, the effect of an aggressive between-group encounter on grooming distribution could be short-term in males and may not translate in a stronger and larger network of social bonds in the long-term.

The Role of Primate Conservation to Fight the Illegal Trade in Primates: The Case of the Owl Monkeys in the Colombian-Peruvian Amazon

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Key Words: CITES · Primate conservation · Colombian-Peruvian Amazon · Malaria research

This study reports on impacts of illegal trade in owl monkeys (*Aotus nancymaae*, *A. vociferans*) for the biomedical research market in the Colombian-Peruvian Amazonian border. Through right of information requests and interviews, we found 912 owl monkeys, including *A. nancymaae* sourced from Peru, trapped over a 3-month period in 2012 to supply a Colombian laboratory. This malaria research facility had permits for use of only 800 *A. vociferans* annually yet experimentation took place using *A. nancymaae*. High levels of extraction in Peru have had population-level impacts with significantly lower densities of *Aotus* spp. (3–24 individuals/km²) compared to Colombian sites with low hunting pressure (26–44 individuals/km²). Post-experimental release of this species in Colombian territory has created a new distribution, and the status and impact of this on resident populations of *A. vociferans* remain unclear. The trapping method has also had environmental impact, with loss of over 65,000 adult nesting trees, annually. *Aotus* species are registered under CITES Appendix II, however, no official records exist and CITES legislation has failed, due principally to a lack of appropriate monitoring by responsible organisations resulting

in non-compliance. Of further concern is that we had previously documented the illegal trade and reported to the appropriate governmental authorities yet still no action was taken. Enforcement occurred only when an NGO undertook legal action against organisations responsible. A successful first instance ruling in 2012 resulted in temporary closure of the laboratory. Using the trade in night monkeys as a case study we consider implementation and enforcement of CITES to address weaknesses and identify mechanisms to improve law enforcement.

Orangutan Locomotion: Forest Structure and Inter-Specific Differences

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Key Words: Orangutan · Locomotion · Habitat · Species · Support use

This is the first study to undertake a full comparison of interspecific differences in orangutan locomotion using rigorous statistical testing. We examined locomotor behaviour in three study sites in Indonesia, two on Sumatra (*Pongo abelii*): Ketambe (dry lowland forest) and Suaq Balimbing (peat-swamp forest); and one on Borneo (*Pongo pygmaeus wurmbii*): Sabangau (peat-swamp forest). Log-linear modelling was used to examine how the different species interacted with their environment in terms of the number, size and types of arboreal supports used during locomotion, and whether these differences were greater at the habitat or species level; or whether differences existed between all study sites. The results revealed that orangutan locomotion and support use was strongly influenced by habitat type. The strongest association was between habitat, support type and support diameter (incorporating the number of supports used for weight bearing), although this may merely signify differences in support availability between forest types. Orangutans in dry lowland forest generally use larger branches and boughs for locomotion than in peat-swamp forest, whereas in peat-swamp forest orangutans use both single and multiple trunks and mixed support more frequently. Log-linear modelling revealed that orangutan locomotion is best explained in simple terms based on the orientation of the torso, rather than differentiating between more distinct forms of locomotor behaviour, or in terms of suspensory or compressive locomotion. Orangutan locomotion had a stronger association with support characteristics than any influence of habitat, indicating that similarities in orangutan locomotion are more important than differences imposed by forest structure.

How Do Barbary Macaques Cope with Tourism?

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Key Words: Primate tourism · Barbary macaques · Behavioural coping mechanism

Primate tourism is a growing industry and it offers significant potential benefits for conservation. Concerns have recently been raised, however, about the impacts of such tourism on the welfare of the animals involved. Previously, we studied adult male Barbary macaques (*Macaca sylvanus*) in a tourist exposed group in the Middle Atlas Mountains of Morocco; these males showed an increase in anxiety and physiological stress levels when physically interacting with tourists, but surprisingly showed no such negative responses when simply in the presence of very high tourist numbers, or when tourists were present for long periods. The lack of impact of tourist numbers or exposure time was proposed to be due to these animals using behavioural mechanisms to cope effectively with the associated stress. Here, we tested this idea, investigating wheth-

er adult Barbary macaques in this group use behavioural coping strategies to deal with tourism pressure. Five behaviours thought to function as coping strategies were analysed: escape, displacement, affiliation, aggression and restlessness (defined as the rate of change between behaviours). Understanding how primates might cope with anthropogenic disturbance such as tourism is crucial for better understanding the complex human-primate interconnection. Such work will also help to inform the management of primate tourism, in order to maximise its conservation benefits and minimise the welfare costs to the animals involved.

Primate Behaviour and Parasite Transmission in the Ecuadorian Amazon

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Key Words: Social network analysis · Parasites · Ecuador

Social network analysis allows us to identify the role and the cohesion of individuals within a group of primates. It can also be useful in order to study parasites and disease transmission within that group. In this study, we have observed the social relations of two groups of *Lagothrix* sp. in two different habitats: captivity and semi-captivity in the Ecuadorian Amazon, from February to June 2011 and from February to June 2012. We carried out focal sampling every minute and performed scan sampling every 5 min. The first group (GA), of six individuals (three females and three males) is the captive group. The second group (GB), of eight individuals (six females and two males), is the group in semi-captivity. We calculated the clustering coefficient (GA = 0.155 and GB = 0.348), the average degree (GA = 1.429 and GB = 2.778), and the average path length (GA = 1.647 and GB = 1.859). We also calculated parasite richness for each individual of each group. Individuals in the captive group had between 4 and 7 parasite species, while the animals in semi-captivity had a range of between 1 and 3 parasite species. Several studies have suggested a quicker transfer of diseases with a shorter average path length, and a higher clustering coefficient would mean a slower transfer for the entire group. In this study, the semi-captive group was less stable but had fewer parasites. The captive condition is more suitable for parasite transmission due not only to the difference of paths among the individuals but also to the area of contact. We hope that Social Network Analysis will provide an important contribution for primate management at a zoo or sanctuary.

Chimps of a Feather: Chimpanzee Friends Have a Similar Personality

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Key Words: Chimpanzees · Personality · Homophily · Friendship

Recent studies have revealed that many primates have stable long-lasting social bonds with particular individuals in their group. Moreover, several studies show that having such strong social bonds is adaptive. However, apart from some, sometimes contradictory, patterns among kin, peers and dominance relationships, it still remains unclear what determines these friendships. In humans, friendships are partly determined by similarity in personality. Although the study of personality in animals has received considerable attention recently, the effect of similarity of person-

ality traits on friendships has not yet been studied in animals. Here, we investigate how similarity in six different personality traits influences the friendships of 38 captive chimpanzees. We find that chimpanzee friends are indeed more similar than non-friends in three of the six personality traits and that this effect is particularly strong among unrelated individuals. Thus, we show that among chimpanzees non-kin friendships are related to similarity in personality. We suggest that similarity in personality increases the predictability of your partner in cooperation in particular, and as such may be adaptive. Moreover, we suggest that the 'choosing' of similar friends with regard to personality is an evolutionary old mechanism that may be shared with other primates too.

'Abnormal' Behaviours in Zoo-Living Bonobos: A Preliminary Study

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Key Words: *Pan paniscus* · Zoos · Welfare · Abnormal behaviour

A recent study by Birkett and Newton Fisher (2011) reports on the occurrence of abnormal behaviour in a sample of 40 zoo-housed chimpanzees. The authors found that all chimpanzees in the study displayed at least two abnormal behaviours and concluded that abnormal behaviour is endemic in captive chimpanzees. Here, we report on a preliminary study of 26 female and 17 male bonobos, all older than 6 years of age, living in six zoos. Each of the bonobos was studied by focal animal sampling, totalling between 13 h and 20 h of focal observation per individual. We present data on prevalence (proportion of individuals in a group that show behaviour), diversity (number of types of behaviour), frequency and duration of behaviours that were listed as abnormal in the literature. We recorded a total of 22 abnormal behaviours. The number of abnormal behaviours in each group ranged from 5 to 12 (median = 8) and was not correlated with group size. The individual repertoire varied from 1 to 8 (median = 3). There was no significant difference in repertoire size between males and females. Age did not have a significant effect on repertoire size or proportion of time spent in abnormal behaviour. Wild-born bonobos had a higher repertoire size, but did not spend more time in abnormal behaviour than mother-reared or hand-reared individuals. In conclusion, the bonobos in our sample showed less abnormal behaviours compared to the chimpanzees in the study by Birkett and Newton-Fisher. This may be a consequence of the different background of the individuals (no bonobos in our study had laboratory backgrounds) or past and/or current management practices: including more naturalistic group sizes and group dynamics.

What Lateralization and the Brain Substrate of Primate Vocal and Gestural Communication Can Tell Us about the Origins of Language: A Review of Behavioural and Neuronal Findings

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Key Words: Gestures · Vocalizations · Communication · Hemispheric specialization · Language evolution

Most language functions are under the dominance of the left cerebral hemisphere and involve a complex neural network in which some cerebral regions play a key-role, such as Broca's

and Wernicke areas within the frontal and the temporal lobes respectively. Thus, the question of the lateralization and the localization of the neural substrate involved in gestural and vocal communication in non-human primates is essential for evaluating the potential continuities with such hemispheric specialization for human language and thus for determining the best candidate for direct precursors of speech. In the present paper, in distinguishing the perceptive system from the production system, we review the findings related to behavioural lateralization and brain correlates of both vocal and gestural systems in non-human primates. Behavioural asymmetries for vocal perception (using the head orientation paradigm toward a source of sound) and neurobiological studies frequently showed that perception of conspecifics' vocalizations involved a left-hemispheric dominance and some cerebral areas within the temporal lobe that might be related to Wernicke's area in humans. The production of species-typical vocalizations by both apes and monkeys has been shown to be mostly related to right-hemisphere dominance and to involve subcortical areas and the limbic system (related to emotions in humans) but not homologous language areas. In contrast, intentional communication, including attention-getting atypical vocal sounds in chimpanzees and gestural communication in baboons and chimpanzees, has been shown to elicit rightward oro-facial and manual lateralization and to be related to leftward neuroanatomical and neurofunctional asymmetries within language's area homologues in chimpanzees.

How Ecology May Affect Orangutan Innovation and Culture

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Key Words: Innovation · Culture · Technology · Orangutans

Geographic variation in behavioural variants across wild populations is often used to infer cultural processes. However, this geographic method must ignore cultural variants that have a clear link to ecology. As a result, we know relatively little about the role played by ecology in the nature and complexity of the variants and the size of the overall repertoire. Here, we focus on technology, and also include zoo-living and free-living ex-captive orangutans in the comparison. Among wild populations, we find that Sumatran *Pongo abelii* populations have more technological variants (and also more insect-feeding techniques and extractive-foraging variants) in their repertoire than the Bornean *Pongo pygmaeus wurmbii*, which have larger repertoires than Bornean *Pongo pygmaeus morio* populations, whereas this contrast is smaller for cultural tool repertoires. Captive and ex-captive populations have larger technological repertoires and more complex variants. The overall pattern of variation is consistent with an effect of terrestriality and sociality on skill acquisition through their impact on (socially-facilitated) affordance learning, and an effect of exposure to human role models and provisioning on novelty response and exploration tendency. This broad comparison of technological repertoires thus supports a general model for the evolution of cumulative technology in which a central role is played by opportunities for innovation and social transmission linked to ecology, either directly (terrestriality) or indirectly (association patterns and opportunities for social learning, exposure to human role models and provisioning).

Hand Preferences in Human and Non-Human Primates for Motor versus Communicative Gestures in the Same Experimental Setup

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Key Words: Communicative gesture · Handedness · Hemispheric specialization · Human infant · Non-human primates

Language origin and its lateralization have been debated for more than one century but are still very controverted. Two main hypotheses are currently proposed. On the one hand, the theory of a vocal origin states that language results from a progressive evolution of animals' vocal communication. On the other hand, the hypothesis of a gestural origin considers that language evolved from gestures. According to this latter perspective, left-hemispheric control would have initially been present in manual gestures, and later would have come to include vocalizations. To test the role of gestures in the origin of language, we present here four studies investigating hand preferences for grasping (motor gesture) versus pointing (communicative gesture) to objects at several spatial positions in human infants and three species of non-human primates using the same experimental setup. We expected that human infants and non-human primates would show a comparable difference in their pattern of laterality according to the task. We tested six capuchins, six macaques, twelve baboons and ten human infants. Those studies are the first of their kind to examine both human infants and non-human primate species with the same communicative task. Our results show remarkable convergence in the distribution of hand biases of human infants, baboons and macaques on the two kinds of tasks and an interesting divergence between capuchins' and other species' hand preferences in the pointing task. They support the hypothesis that left-lateralized language may be derived from a gestural communication system that was present in the common ancestor of macaques, baboons and humans.

Linking Studies of Behaviour, Habitat and Morphology in the Non-Human Great Apes: What Can We Learn?

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Key Words: Primates · Anatomy · Ecology · Positional behaviour

We often study parts of the morphology-behaviour-habitat interface in isolation from one another, sometimes relating one to the other, but rarely taking a broad view of the whole. A primate's behaviour, be it related to feeding, travelling or social interactions, will be influenced by both the ecology of their environment and their morphology and therefore should not be studied in isolation. In an attempt to understand some of these relationships more fully, I will apply an ecomorphological framework to our understanding of non-human great ape behaviour, in particular their locomotion and posture. Such behaviours are a key component of all others and provide insight into the adaptations required for success in different species. The non-human great apes themselves have a closely shared evolutionary history, yet each has also become further specialised to their own niche. Broadly, the muscle architecture of the non-human great apes appears to be very similar at a whole muscle level, pointing to their shared ancestry and the com-

monalities of their behaviour. Variation, however, may be present at a finer level in the more plastic muscle fibres of chimpanzees and orangutans. This may reflect some of the differences in their behaviour and use of the arboreal habitat, and hints at more subtle adaptations in these species. By using our knowledge of the ecological relevance of the behaviours they perform we could be more targeted in our approach and maybe begin to uncover some of the more subtle, but vital, adaptations present in our closest-living relatives.

Non-Sagittal Shank and Foot Movements in the Kinematic Articular Chain during the Swing Phase of Gait

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Key Words: Foot · Gait · Swing · Metatherians · Eutherians

Foot movements involved in the kinematic articular chain of the gait in metatherians (e.g., marsupials) may be analysed to unravel eutherian (e.g., primate) gait. We thus analysed videos (from the public domain) of a walking wombat, *Lasiornhinus latifrons*. From take-off, its foot's lateral side stays continuously lifted, causing everted foot positions during most of the swing phase, as also observed in the opossum, *Didelphis marsupialis*. Here the cardan-like ankle joint transmits shank axial rotation to foot-eversion or foot-inversion (Narain and van Zwieten, 2009). Only recently, have measurements from primates, viz. man, allowed extrapolation of these data to bipedal gait. At the onset of swing, foot eversion clears the human foot from the ground (Legault-Moore et al., 2012). Also recently, sophisticated technology captured foot eversion at the end of swing in the running cheetah *Acinonyx jubatus* (National Geographic video: Hubbard et al., 2012). While doing so, this eutherian shows lower leg internal axial rotation with simultaneous heel-abduction, toe-extension and toe-abduction. The latter phenomenon might be universal, as was described in metatherians (van Zwieten et al., 1991).

Reassessing Slow Loris Reintroductions: Why Aren't Reintroduced Slow Lorises Surviving and How Can Success Be Improved?

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Key Words: Slow loris · Reintroduction · Translocation · Compassionate conservation

Javan slow lorises have three times been considered amongst the world's top 25 most endangered primates. The illegal animal trade on Java results in 100s of lorises being culled annually from the wild for pets. We analyse data from one rescue centre, and compare these data to the first wild field study of slow lorises in Cipaganti, Garut, to examine why reintroductions so far have failed. Of 180 animals entering the rescue centre between 2008–2011, 64% had damaged teeth and were thus unsuitable for release to the wild. Of 12 animals released, 6 died and the fate

of 4 others remains unknown. When comparing released animals to wild animals, released animals had home ranges an order of magnitude larger than wild ones (averages: released = 33.1 ha, wild = 3.3 ha), and path lengths measured over 10 days were significantly longer (averages: released = 15.76 km, wild = 4.24 km). No released animal's incremental area curve showed that an animal had settled within its home range, whereas all wild animals' incremental area curves reached an asymptote within 10 days. Released lorises ate no gum, which comprises not only 70% of the diet of wild Javan slow lorises, but also of the diet of all other slow lorises studied so far. Causes of death included 'visible weakness' and unexplained infection. These data combined suggest that the released animals found themselves in a period of hyper-dispersal, running themselves to death. We make several suggestions for further release on the basis of our new understanding of Javan slow loris behavioural ecology: longer pre-release period, release into caged one-hectare enclosures, careful choice of sites containing gum trees and no release into areas containing native lorises of this highly territorial species.

Densities, Distribution and Detectability of a Small Nocturnal Primate (Javan Slow Loris *Nycticebus javanicus*) in a Montane Rainforest

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Key Words: Indonesia · Survey methods · Lunar phobia · Nocturnal mammal · Conservation

Nocturnal mammals can be challenging to survey and, especially for many species that live in dense forest habitats, limited information is available on densities and distributions. We surveyed the endemic Javan slow loris *Nycticebus javanicus* in the montane forests of Mt Gede Pangrango, West Java, Indonesia. Surveys were conducted on 23 transects (260 h covering some 93 km) using variable speeds between 200–800 m/h. Densities on individual transects varied from 0 to 52 individuals/km², with an overall density of 15.6 individuals/km² [95% CI 9.7–25.2 individuals/km²]. Encounter rates per km were strongly influenced by the speed at which transects were walked with fewer lorises detected at higher speeds. This effect was absent when considering encounter rates per hour. Detectability of Javan slow lorises was not affected by the amount of lunar light and we found no obvious differences in slow loris behaviour and moonlight. Part of the study area comprised disturbed forest but encounter rates did not differ between disturbed and primary forest. Our study shows that slow lorises are not homogeneously distributed in their montane habitat and that they occur at relatively low densities. Unlike in some of their congeners, we found no evidence for lunar phobia or lunar phillia. A comparison with other surveys of Lorisiformes revealed no statistically significant relationship between survey effort or the speed at which transects were walked and estimated densities, but speed was positively correlated with encounter rates.

Hand Use during Non-Locomotor Behaviours in the Wild African Apes

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Key Words: Gorilla · Chimpanzee · Manipulation · Grasping · Hand use

Comparative studies of primate grasping and manipulative behaviours in captivity are numerous but there has been little research on hand use in the wild. Hand use during wild non-locomotor behaviours may reveal increased ranges of joint mobility or manipulative behaviours that have been previously ignored or underestimated. Manipulative behaviours in apes can strongly correlate with different habitats at the species and population level. Chimpanzees more often use tools in the wild and thus are thought to be more manipulative than gorillas. However, captive studies have demonstrated high dexterity in both taxa. We investigate hand use during manipulation (e.g. food processing, tool-use) in wild mountain gorillas (*Gorilla beringei*, Bwindi Impenetrable National Park, Uganda) and wild chimpanzees (*Pan troglodytes verus*, Tai National Park, Cote d'Ivoire). We used video data collected in the wild that included 32 gorilla (n = 9 individuals) and 53 chimpanzee (n = 11 individuals) instances of manipulative tasks. Digital images were extracted and analysed frame by frame. Preliminary results show that hand grips are similar between gorillas and chimpanzees during the manipulation of common food objects, such as long plant stems or branches. During the manipulation of species-specific food objects, gorillas use variable thumb-index grips during the manipulation of thistles and small plant stems, while chimpanzees use similar grips during nut-cracking. These preliminary results suggest that dexterity shown by Bwindi mountain gorillas is as high as that of Tai chimpanzees despite the former not being tool-users. Gorillas frequently use precision grasping to obtain small rather than large food items, which is similar to chimpanzees and other non-human primates.

Assessing Conflict between Humans and Commensal Non-Human Primates in Sri Lanka following an Ethnoprimateological Approach

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Key Words: Ethnoprimateology · Conservation · Human-primate interactions · Asia

Sri Lanka is an excellent area to study the relationships between humans and commensal primates: the island is home to slender lorises, macaques and langurs and, for the last 40,000 years or so, humans. The widespread existence of homegardens, mimicking the forest structure by adopting different layers, allows primates to come into close contact with humans, and the predominant religions adopted by Sri Lankans may facilitate a peaceful co-existence. Repeated crop-raiding and conflict over space may cause people to become increasingly intolerant of primates. Adopting an ethnographic perspective allows mitigation policy to be defined with regard to a local cultural context in which traditions and religious parameters often exist for the preservation or to the detriment of wildlife. We draw from three case studies from the southwest where, following an ethnoprimateological approach, we assessed levels of conflict between humans and primates in both an agricultural and urban context. Direct observation of primates (for 182 days and

339 nights) and large-scale interview surveys (1,036 interviewees) revealed generally high levels of tolerance in both settings. Macaques and langurs were observed to be able to live commensally with humans; slender lorises were not. High levels of crop-raiding along the forest edge by macaques and langurs and frequent use of roofs as part of arboreal pathways by langurs are prime examples of causes for discontent. Heavy reliance on fruit by otherwise folivorous langurs compromises their dietary needs and parasite loads of commensal primates are suspected to be unhealthily high. The relationship between humans and slender lorises is less direct and their persistence is fully dependent on adequate forest protection.

The Chimpanzees of Ifon Forest: Could Populations in Southwest Nigeria Survive?

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Key Words: Chimpanzee · Flagship · Nigeria · Extinction

We carried out a survey of the chimpanzee population in Osse River Park (Formerly Ifon Forest Reserve), Ondo State, Nigeria, with the aim of proposing it as the park flagship species for the newly established project. We conducted focus group discussions in December 2011 to collect information about the presence and distribution of chimpanzees from the local hunters, farmers and gatherers of non-timber forest products. We conducted a direct field survey for 5 months from February to May 2012 in the park, carefully searching through the forest fragments for direct sighting/indirect signs of chimpanzees' activities. We recorded the waypoints, sample points and tracks geo-referenced with the Global Positioning System (GPS). We downloaded the map into professional 5.0 software and plotted the map of the study area, acquired and generated from the satellite imagery using Arcview 3.3a to depict the ground-truthed data from our observations. We saw no recent evidence of chimpanzees (direct or indirect) in the park: a location where the animal was known to have been present until the year 2007. The situation in the park illustrates the accelerated rate of chimpanzee population decline/loss in the region and raises the question: can the remnant population of chimpanzees in south western Nigeria survive imminent extinction?

The Caring Ape: Evidence for Empathy in Bonobos

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Key Words: *Pan paniscus* · Empathic gradient · Comforting gestures · Perception-action mechanism

Empathy is essential for successful social interactions. In humans, it steadily increases according to the subjects' emotional closeness (empathic gradient), being lower between weakly bonded individuals and higher between tightly bonded ones. Consolation and yawn contagion, considered to be empathy-driven phenomena in humans, have also been studied in bonobos, a prosocial and tolerant ape. In bonobos, consolation seems to be prosocial as it plays a role in pro-

tecting the victim against renewed attacks and works in reducing its anxiety. Moreover, in bonobos consolation follows the human empathic gradient, as spontaneous comfort is mostly offered to kin, then friends, then acquaintances. A similar trend is also true for bonobo yawn contagion, which increases with social closeness, thus mirroring what is found in humans, in which emotional bonding modulates the phenomenon as well. A further hint supporting the common roots of empathy derives from a direct comparison of human and bonobo yawn contagion. The frequency of yawn contagion in these species does not differ when weakly bonded subjects are involved. The difference arises when friends and kin are involved, with humans showing higher levels of yawn contagion than bonobos. It seems that when a stronger emotional connection ties two subjects, the human empathic intensity strikingly emerges. Hence, is it legitimate to hypothesize that in *Homo* and *Pan* (the last ape lines to have separated around 5–7 mya) consolation and yawn contagion arise from different proximate factors thus resulting from a phenomenon of convergent evolution? Applying Darwin's parsimony principle to consolation and yawn contagion, we can state that if we accept that such phenomena are empathy-based in humans, we must accept the same for non-human apes.

Not Only a Human Affair: Embracing Behaviour in *Theropithecus gelada*

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Key Words: *Theropithecus gelada* · Hugs · Social closeness · Biological roots · Comparative approach

Embracing, one of the most widespread forms of human affiliation, plays important roles in other primates as well. Human embracing occurs in a great variety of social contexts. It can be a greeting display to announce the recognition of one another, it can provide comfort to others (e.g. consolation) and reduce anxiety in the receiver. Human embraces favour subsequent social contacts and are generally preceded by affiliative facial displays (e.g. smiling). Moreover, embracing morphology can be predictive of the intimacy of the relationship between subjects. To explore the biological roots and test some hypotheses on the function of embracing at an evolutionary level, a comparative approach is necessary. To reach the goal, we selected *Theropithecus gelada* as a model species. Geladas live in a one-male society whose components (especially females!) show high levels of affiliation and cohesion. In geladas, embraces are performed in four different ways, two involving frontal contact and two directed to the posterior. Our data show that, as in humans, gelada embraces are mainly associated with a positive facial expression (lip-smacking) and favour the onset of social interactions (grooming). It is performed almost exclusively by adult females especially when they share a good relationship. Moreover, the most intimate forms of embraces, the frontal ones, highly reflect the strength of the bond between subjects thus suggesting that morphology of embraces can be predictive of their function. Finally, a linkage between embracing and other-oriented behaviours seems to exist: the best embracers were also the best consolers. In conclusion, even though the 'embracing issue' remains open, some features of this behaviour seem to be shared between human and non-human primates.

Morphological and Immunohistochemical Characterisation of Cutaneous Meissner and Pacinian Corpuscles from *Macaca fascicularis*

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Key Words: *Macaca fascicularis* · Meissner corpuscles · Pacinian corpuscles · Morphology

The mammalian glabrous skin contains specialized sensory organs known collectively as mechanoreceptors responsible for the detection of different types of mechanosensation such as touch, vibration or pressure. Recently, these sensory formations have been analysed in humans and some animal models looking for structural or immunohistochemical changes due to neurological or systemic diseases. Detailed studies looking at the species-specific morphological structures and protein pattern expressions in animal models are of considerable importance to obtain experimentally accurate conclusions. Monkeys of the *Macaca* genus are currently used in studies of the peripheral nervous system because of the similarities with man in the structure and protein expression of most peripheral nervous system structures. Here we report detailed morphological and immunohistochemical findings in the study of Meissner and Pacinian corpuscles obtained from the palmar side of *M. fascicularis* fingers. Preliminary ultrastructural study show that Meissner and Pacinian corpuscles are smaller compared to human ones, and shows the occurrence of numerous paciniiform corpuscles. An additional morphological feature was the presence of abundant blood vessels surrounding them, and more within the outer lamellae of the capsule. The immunohistochemical profile of both kinds of mechanoreceptors matched that reported in humans, with the exception of the expression of some putative mechanoproteins. Data from this study reveal structural and protein-composition differences of *M. fascicularis* cutaneous mechanoreceptors compared to human glabrous skin mechanoreceptors. We conclude that particular features from skin sensory innervation in *Macaca fascicularis* must be considered to set conclusions from pathological conditions designed experimental assays.

The Primate Skeletal Collection Curated at the Universidad de Valladolid (Spain): A Research Resource

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Key Words: Bone collections · Primate osteology

Primate skeletal collections are not very common. The most important in terms of species representation and number of specimens are located in Switzerland (Anthropology Department, Universität Zurich-Irchel, Zurich), Germany (Zoologisches Museum A. Humboldt, Berlin), The Netherlands (Rijksmuseum van Natuurlijke Historie, Leiden), England (Natural History Museum, London) and USA (National Museum of Natural History, Washington; American Museum of Natural History, New York). In Spain, the largest and most diverse collection of primate skeletons is curated at the Anatomical Museum, Faculty of Medicine, University of Valladolid. This museum dates back to 1861, but the preparation of animal skeletons begun in 1986. Specimens come from zoological parks, rescue centres, transfer of animals confiscated at customs and exchange with other research institutions. Currently, the section of primates is composed of 801 specimens covering 132 species, from *Microcebus* to *Gorilla*. Sex and provenience is known for all specimens, which are classified into four age groups: foetuses, juveniles, immatures and adults.

Before skeletisation, specimens that arrive in a good state of preservation are frozen in order to carry out dissection of the muscular system, and musculo-skeletal atlases of *Gorilla*, *Pongo*, *Pan* and *Hylobates* have already been published. Species diversity and sample sizes offer potential research opportunities in diverse areas of primatology, and since most are specimens from captivity, a high frequency of degenerative conditions is observed, which makes the collection a valuable resource for pathology and gerontology. With a policy of free access to the collection to applicant researchers, the number of visiting scholars has increased considerably in recent years.

Social Structure of a Semi-Free Ranging Group of Mandrills *Mandrillus sphinx*: What Role for Central Individuals?

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Key Words: Associations · Social network analysis · Betweenness · Eigenvector centrality · *Mandrillus sphinx*

Most studies initially considered mandrill groups to be an aggregation of one-male-multifemale units, with males occupying central positions in a structure similar to that observed in baboon species. However, a recent study hypothesized that mandrills form stable groups with few permanent males, and suggested that females occupy more central positions than males within these groups. In this study, we used social network analysis to investigate the identity and the role of central individuals in a semi-free ranging group of mandrills. The betweenness and the eigenvector centrality for each individual were correlated to kinship, age and dominance. Our results showed that the cumulative distribution of betweenness followed a power function. This property showed that some group members, mostly females, occupied a high central position. Moreover, we found that these central females were also high-ranking individuals. Finally, a resilience analysis showed that the simulated removal of individuals displaying the highest betweenness values splits the network into small subgroups and increases the average number of isolated subgroups. Critically, this study confirms that females appear to occupy more central positions than males in mandrill groups. These females also seem to be crucial for group cohesion and probably play a pivotal role in this species.

The Enhancement of Secondary Succession by Western Lowland Gorillas (*Gorilla gorilla gorilla*) in a Moist Tropical Forest of Southeast Cameroon

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Key Words: Forest dynamics · *Gorilla gorilla gorilla* · Seed dispersal · Tropical forests

Among animal seed dispersers in tropical ecosystems, the contribution of primates is recognized to be of paramount importance. However, the role played by the largest species of the Congo Basin, the western lowland gorilla (*Gorilla gorilla gorilla*) has received little attention. Here, we provide the first long-term study describing all aspects of the ecology of seed dispersal

by gorillas at a single site. Over 3 years of investigation in the forests of Mimpala, southeast Cameroon, we have identified 55 species whose seeds were found undamaged in 1,030 faecal samples. On average, one faecal clump contained 2.4 seed species and 51.8 seeds. Gut passage, of a mean rate of 54.7 h, does not affect viability of seeds and may even enhance germination success in some cases by separating the seed from the fruit pulp and/or by abrading the seed coat. As a result of habitat preference, seed deposition is biased towards open canopied environments, namely light gaps and young secondary forests. Monitoring of seedlings suggested that this directed-dispersal is an effective method of dispersal, as a significantly higher number of marked faeces still contained viable seedlings after 1–2 years in these habitats compared to the others. Quantitatively, this may be of benefit primarily to the tree genus *Uapaca*, as its seeds were found in almost half of all faecal clumps and its seedlings constituted the majority of the seedling cohort established in faeces. Furthermore, as a consequence of their heliophilous temperament, *Uapaca* seedlings were among those that developed the best at these seed deposition sites. We conclude that the western lowland gorilla may be a highly effective seed disperser within areas of secondary succession and its extirpation would likely have implications for forest dynamics.

The Schedule of Savannah Sounds: Chimpanzee Pant Hoots and the Sound Environment in an Open Habitat, Issa Valley, Ugalla, Western Tanzania

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Key Words: Chimpanzee · Pant hoot · Long call · Savannah · Tanzania

Chimpanzee loud calls, or pant hoots, have been studied extensively in closed-forest habitats, with attention being paid almost exclusively to call meaning and function. However, the logistical limitations of using traditional means of study to simultaneously monitor both caller and receiver have meant situating vocalization behaviour in a social context which has been almost impossible. With chimpanzees in dry, open habitats living at dramatically lower densities, and yet ranging over areas >10× greater than those in tropical forests, vocal communication may be a critical element to their maintenance of a fission-fusion social system. In the current study, conducted over 15 months in the Issa Valley, Ugalla, western Tanzania, I designed and deployed a remote acoustic monitoring system that transmits data in real-time to a central location to study chimpanzee use of sound across a large landscape. I report here on the temporal patterns associated with pant hoots and describe to what extent chimpanzees vocalize when environmental conditions are optimal for loud call transmission. The implications of long calls in the maintenance of savannah chimpanzee sociality in a marginal habitat are discussed.

Referential Gestural Signalling: New Insights from Chimpanzees (*Pan troglodytes*) and Ravens (*Corvus corax*)

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Key Words: Communication · Language · Reference · Non-human primates · Corvids

Referential acts play a crucial part in our every-day communication since human language is, in its essence, a referential system. Reference can be made via icons, indices and signs but

also via ostensive/inferential communication, in which the behaviour of the actor directs the attention of the recipient to particular aspects of the environment. The earliest uses of ostensive/inferential communication can be observed in human children around the age of 9–12 months. However, what about comparable gestures in our closest living relatives, the non-human primates or in other animal taxa? The present paper aims to provide a brief overview of the state of the art to encourage future research into the evolutionary origins and uses of referential gestural signalling. Social bonds may be a key factor in understanding this form of communication.

Comparing Affiliative Relationships of *Cebus* and *Sapajus* Species: A Social Networking Approach

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Key Words: *Cebus* · *Sapajus* · Grooming · Social network · Clustering coefficient

Capuchin monkeys (*Sapajus* and *Cebus* spp.) are characterized by male dispersal and female philopatry, with highly differentiated social relationships especially among females. Yet, still little is known about how social dynamics differ between these two clades. Here we used social network analysis (SNA) to explore variability in the structure of capuchin monkeys' affiliative network. Analyses were run on female-female grooming data extracted from 14 wild groups. 6 groups were *Sapajus* spp. (4 *S. nigritus* and 2 *S. libidinosus*, formerly *C. apella*) and 8 were *Cebus* spp. (*C. capucinus*). No significant difference was found in the comparison of group network metrics (i.e., eigenvector, clustering coefficient and group density) between *Cebus* and *Sapajus*. However, the levels of inter-individual variability of clustering coefficient, a metric of a group's level of cohesion, were significantly different. In *Sapajus* spp. grooming was more likely to be exchanged between individuals that were well connected (high clustering coefficient values), while individuals with low clustering coefficient values were more likely to make the links between different subgroups. By contrast, in *Cebus* spp. grooming was more homogeneously distributed. Moreover, the exchange of grooming appeared to be less reciprocal in *Sapajus* than in *Cebus* spp. It is possible that a different role played by kinship and dominance hierarchy in the two clades account for the variations in grooming distribution. Taken together, our results suggest that although *Sapajus* and *Cebus* spp. do not differ in the overall feature of their social structure, the former species are characterized by more differentiated and heterogeneous relationships than the latter.

Eco-Ethological and Kinematical Approaches to Grasping in Primates

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Key Words: Grasping · Prehension · Evolution · Kinematic · Eco-ethology

Grasping is a vital function involved in a larger ecological context integrating food acquisition, locomotion and social interaction. Among primates, this function is associated with a great diversity of morphology, diet, environment and locomotor strategies. From a comparative evolutionary perspective, several questions arise: What favoured the use of the hand by the first primates? What favoured the diversity of prehensile capacities in primates? What are human specificities? To understand the evolution of grasping in primates, the ecological and functional constraints associated with grasping is extremely insightful. First, an eco-ethological approach was used to look at many strepsirrhine, platyrrhine and catarrhine primate species, showing that the use of the mouth versus one or two hands depends on the properties of the food (i.e. size, fruit versus prey, embedded food) and on the locomotor substrate. Second, a kinematic approach revealed different upper limb strategies (i.e. joint amplitudes) according to species and mode of locomotion (terrestrial versus arboreal). Together, these analyses revealed that many parameters such as digit contact strategies, wrist velocity and joint amplitudes are shared by humans and many other primate species. Future research needs to focus on a broader comparative perspective by (1) further exploring the existence of correlations between anatomical and behavioural parameters linked to grasping, (2) tracing the evolution of these parameters in the order Primates with more informed interpretations of fossil remains, and (3) renew our understanding of the evolution of grasping in primates by analysing this function in other tetrapods.

Prevalence and Richness of Gastrointestinal Parasites of Capuchins (*Cebus albifrons*) Interacting with Humans in the Ecuadorian Amazon

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Key Words: Parasites · Ecuador · *Cebus albifrons*

Zoonotic parasites have affected non-human primate populations for millennia. Currently, anthropogenic disturbances to primate habitat have tipped the balance of these delicate relationships to a point where parasites are negatively affecting primate populations. The exchange of disease is a concern for host populations, humans, sympatric organisms, and wildlife conservation in general. Furthermore, the close phylogenetic relationship between humans and non-human primates results in high potential for pathogen exchange. Here we examine the prevalence and richness of gastrointestinal parasites in relation to host intrinsic (age, and sex) and extrinsic (habitat, altitude, soil pH and slope) factors. We collected 45 fresh faecal samples from a group

of 15 free-ranging white-fronted capuchins (*Cebus albifrons*) in the Ecuadorian Amazon town of Misahualli. This group interacts daily with humans, including sharing food and frequent touching. Samples were analysed via Ritchie's sedimentation technique and the hyper saturated sugar solution for the flotation technique. We detected the prevalence of two taxa of nematodes (*Strongylus* sp., *Capillaria* sp.) and one cestode (*Hymenolepis* sp.). These taxa are known to be zoonotic, being passed between humans and non-human primates. Further analysis will determine the degree of pathogen exchange between these closely related species.

Chimpanzees Open Hard-Shelled Fruits Differently across Communities

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Key Words: Chimpanzee · Social · Learning · Culture · Foraging

Researchers investigating the evolutionary roots of human culture have naturally turned to comparing behaviours across non-human primate communities, with tool-based foraging in particular receiving much attention. This study examined if the behaviours underlying natural extractive foraging differ across non-human primates communities that have the same foods available. Specifically, the behaviours applied to open the hard-shelled fruits of *Strychnos* spp. were examined in three socially separate, semi-wild chimpanzee (*Pan troglodytes*) colonies that lived under shared ecological conditions at Chimfunshi Wildlife Orphanage and that were comparable in their genetic makeup. The chimpanzees (n = 56) consistently applied six techniques to open these fruits. Analyses revealed differences across three measurements of the application of fruit-opening techniques. One colony was found to combine more techniques than the other colonies, and there were differences in the application of three specific techniques, with full biting and fruit cracking entirely absent in some colonies. Further, cross-colony differences were found for the number of fruit opening events required per fruit. This study provides empirical evidence that the behaviours underlying natural extractive foraging show differences across non-human primate communities that likely cannot result from ecological and genetic grounds, thus contributing to evidence of animal culture. In addition, the hard-shelled fruits were occasionally observed being used as 'hammers' to crack open other hard-shelled fruits (fruit cracking). This is, to the authors' knowledge the first reported case of this behaviour in chimpanzees.

Sexual Dimorphism and Intra- and Interspecific Variability in the Size of the Foramen Magnum in Primates

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Key Words: Foramen magnum · Sexual dimorphism · Body size

We present results of a study of sexual dimorphism in the size of the foramen magnum in human and non-human primates. Sagittal and transverse maximum diameters of the foramen magnum, as well as a set of postcranial measurements related to body size, were recorded to the

nearest mm in several species of non-human primates ($n = 300$) from the collection curated at the Faculty of Medical Sciences (Valladolid, Spain), and in 140 human skeletons from the documented collection curated at the Lisbon National Natural History Museum (Portugal). At the intraspecific level, the study of sexual dimorphism using the Student's t test indicates the presence of sexual differences in some species including humans, but in most cases a discriminant analysis indicated a low discriminatory power of the foramen magnum dimensions. At the intraspecific level, low to moderate correlations were observed between foramen magnum dimensions and postcranial measurements. However, at the interspecific level, a strong correlation was observed between the size of the foramen magnum and postcranial size. The well-known early fusion of the primary centres of ossification that form the foramen magnum (pars basilaris, pars lateralis and squama occipitalis) could explain the low sexual dimorphism in adult specimens of the order Primates. The explanation of the correlation at the interspecific level between foramen magnum and body size is discussed with data related to the evolution of the size of the spinal cord and vertebral foramen in primates.

Preliminary Behaviour of the Endangered Javan Slow Loris (*Nycticebus javanicus*) in West Java, and Implications for Conservation

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Key Words: Nocturnal primates · Prosimian · Activity budget · Habitat protection · Reintroduction · *Nycticebus javanicus*

Javan slow lorises (*Nycticebus javanicus*) are Red-Listed as Endangered, with key threats being habitat destruction and the illegal pet trade. Despite some studies about captive or rescued/released animals, not much is known about the behaviour and ecology of wild animals. We present preliminary behaviour data of the first-ever study of wild *N. javanicus*. The study population persists in a mosaic-like habitat with agriculture fields and interspersed trees and patches of bamboo, bushes or abandoned fields. We directly observed animals for 165.75 h during the onset of the dry season between April and June 2012. Animals spent 28.7% of their time foraging and feeding, 35.1% sleeping and resting, 13.6% travelling, 9% alert and 7.4% grooming. They fed mainly on gum of *Acacia decurrens* (55.9%) and nectar of *Calliandra catothyrsus* (32.2%). We found that animals were very social, spending 13% of observations within sighting distance, 37% of which they were in body contact. Including allo-grooming, they spent 7.8% of the observations socialising. Animals preferred bamboo and *Acacia decurrens* over other tree species. If slow lorises are held in captivity, whether in zoos or in rescue centres, we stress the importance of social partners, including gum in the diet and offering gouging opportunities, especially when preparing rescued animals for release. The importance of certain tree species can help in conservation planning and protection of habitat and has to be considered when selecting release sites. Javan slow lorises seem to cope well with a human-modified mosaic-like landscape as described for this study site. Accordingly, we recommend recognising unprotected, human-modified landscapes in conservation schemes and emphasise the importance of community-based conservation.

Locomotion and Support Use in Captive Western Lowland Gorillas (*Gorilla gorilla gorilla*)

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Key Words: Gorilla · Locomotion · Positional behaviour · Arborealism

The locomotor behaviour of lowland gorillas is one of the least known among the apes. Despite gorillas being labelled 'the terrestrial ape', studies have found western lowland gorillas to be surprisingly arboreal, often climbing 30 m into the forest canopy during foraging. These studies report quadrupedal walking, climbing and scrambling, and occasional use of bipedalism and suspension, in the arboreal locomotor repertoire of semi-habituated lowland gorillas. However, the relationship between their habitat and locomotor behaviour remains poorly understood. It has been suggested that lowland gorillas are more similar in their arboreal locomotion to orangutans than to the more closely related chimpanzee. Orangutans use complex locomotor strategies to negotiate the forest canopy, including weight distribution among multiple supports, and using branch compliance to reduce the energetic cost of locomotion. Lowland gorillas may therefore be more adept at arboreal locomotion than is generally reflected in zoos. This study aims to provide a profile of locomotion, posture and support use in a captive group of adult western lowland gorillas, and assess whether they emulate the natural positional behaviours reported in previous research. Promoting natural physical behaviour in captive individuals by creating enclosures that imitate the functionality of the wild habitat not only aids health problems such as obesity, but could enhance the efficacy of reintroduction programmes. Focal animal sampling allowed individual physical behaviour profiles to be constructed, which were then combined to produce a captive locomotor repertoire. This was compared with data on wild lowland gorillas, and we give suggestions for supports that promote natural locomotor profiles in captive groups.

Measuring Social Tolerance in Lemurs: An Experimental Approach

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Key Words: Social tolerance · Malagasy primates · Co-feeding · Cross-species comparisons

Social tolerance crucially influences the life of group-living animals. It affects food accessibility, number of grooming partners and spread of information within social groups. However, social tolerance is difficult to operationalize and difficult to compare across species. Observational studies allow the behavioural traits underlying social tolerance to be identified for species comparisons, but experimental approaches, in which individuals are, for example, allowed to co-feed on a feeding platform, are less cumbersome. The aim of this study was to establish a standardized co-feeding task to obtain comparable and straightforward measurements of social tolerance across species. We studied two wild species of Malagasy primates; relatively egalitarian red-fronted lemurs (*Eulemur rufifrons*) and more hierarchically organized ring-tailed lemurs (*Lemur catta*). The experimental setup consisted of one or two arenas placed on the ground with one food bowl each in the centre. Based on video-recordings of feeding animals, we determined how many individuals were in the arena and how many individuals were simultaneously feeding. We found that red-fronted lemurs scored higher values for the number of individuals in the arena as well as

for the number of individuals co-feeding compared to ring-tailed lemurs, indicating that they are more socially tolerant. This simple set-up is therefore suitable for measuring social tolerance in terrestrial species in the field for direct cross-species comparisons. Moreover, social tolerance appears to have a direct relationship with a species' dominance style.

Looking for Individual-Level Differences in Cognitive Abilities: Is There a Marmoset 'g'?

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Key Words: General intelligence · G factor · Individual differences · Cognitive test battery · Common marmoset

The general intelligence factor 'g' is well established in humans: a person who performs well in one cognitive test will very likely do so in many others too. It is only recently that researchers have started to develop test batteries to assess individual-level differences in the cognitive abilities of non-human primate species. However, the only test battery explicitly designed to measure g in a New World monkey species, the cotton-top tamarin (*Saguinus oedipus*), has not yet been validated. We are currently evaluating this series of tests to determine its potential to differentiate reliably between individuals and provide repeatable results. A slightly adapted version that takes into account smaller body size and progress in the field is used to examine whether g is found in a very closely related species, the common marmoset (*Callithrix jacchus*). Fifteen captive marmosets were tested by the same experimenter with tests such as reversal learning, perceptual speed and memory to explore if some subjects perform consistently better than others across several cognitive tests that presumably measure independent abilities. Results obtained so far support the notion of a marmoset g, but we are also testing various alternative explanations.

The Introduction of Artificial Habitat Structures in Two Troops of Lemur Species (*Eulemur sanfordi*) in Semi-Free Ranging Enclosures

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Key Words: Artificial habitat structures · Conservation · Lemur locomotion

This study investigated the introduction of artificial habitat structures to a strata level that did not contain many structural supports. This structure was predicted to increase the use of that strata level in two troops of semi-free-ranging Malagasy lemurs- *Eulemur sanfordi* (Sanford's brown lemur) – at the Lemur Conservation Foundation, south central Florida. According to White et al., (1995), and Dagosto (1995) the lemurs within the genus *Eulemur* are arboreal quadrupeds. Rose (1973) categorized the genus *Lemur* as a medium sized arboreal quadruped whose positional behaviour may vary from species to species. Medium sized arboreal quadrupeds use diagonal sequences, galloping gaits, and preparatory and recovery stages when leaping and locomoting. This project took place in two different phases: before introduction of artificial habitat structures and after artificial habitat introduction. The artificial habitat structures were in the form of artificial vines made to replicate natural vines and approved for primate use by Disney

and the LCF's Scientific Advisory Counsel. The primary investigator (PI) collected 60 h of data before and 60 h of data after introduction, on each troop, distributed evenly over daylight hours. The PI used group scan sampling to record the troops' behaviours, location and direction of travel. *Eulemur sanfordi* increased its use of horizontal and vertical structures and began to take advantage of the horizontal spaces provided by the artificial vines. This study on the introduction of artificial habitat structures provides documentation of successful ways to supplement these forests and aid in wild lemur conservation.

Do Wild Orangutans Learn from Each Other? Evidence for Observational Learning from Two Populations of Wild Orangutans

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Key Words: Observational learning · Orangutans · Skill acquisition · Social transmission

Numerous lab experiments have shown that several primate species are capable of observational learning in captivity. Studies on observational learning in the wild are, however, more scarce. Here, we present evidence of observational learning by peering (i.e. attentive close-range watching for over 5 s) from two populations of wild orangutans, *Pongo abelii* at Suaq Balimbing (Sumatra) and *Pongo pygmaeus wurmbii* at Tuanan (Borneo). Our results indicate that in the feeding context infants peer more with increasing complexity of the food item or with increasing rarity of the food item in the mother's diet. With increasing skill level infants' peering rates decrease. We, moreover, found that infant peering is followed by increased rates of try-feeding, exploration and object play. For complex behaviours such as nest building and extractive foraging, peering is often directly followed by the so called 'peering-practicing cycle' during which the immatures seem to try to replicate the observed behaviour. Older immatures, additionally, show a preference for peering at role models other than the mother that potentially exhibit new behavioural variants. Direct comparison of the two study populations indicates that immature orangutans at Suaq Balimbing not only have more opportunities for social learning from role models other than the mother, but also, in general, peer more frequently than immatures at Tuanan. In sum, our results suggest that social learning in the form of observational learning seems to play a major role in orangutan development. The difference in the opportunities and reliance on social learning, especially for vertical transmission, most likely influence how easily innovations spread within a population and how easily they are maintained.

Origin of Modern African Hominoids: Influence of Climate?

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Key Words: Hominoidea · Old World · Neogene · Palaeoenvironments · Climates

For several decades, the origin of the African apes and humans has been debated: did their ancestors originate in Eurasia or Africa? Is the 'Back to Africa' hypothesis tenable? Is a strictly African origin acceptable? A high diversity of hominoids in the Middle and Late Miocene of Europe does not imply that Africa was devoid of them. Fossils collected in Africa over the last decade suggest that none of these scenarios may be correct. In addition, molecular dates of di-

vergence seldom agree with the fossil evidence. Modern hominoid lineages are known from the Upper Miocene, indicating that their history was probably more ancient than previously thought. Palaeoenvironmental evidence suggests a different scenario. Non-human hominoids are basically tropical animals and all through their 25 My long history they inhabited tropical areas, as indicated by palaeobiological analyses. In the Early Miocene, most of Africa was tropical and the distribution of hominoids was Panafrican. When the Antarctic Ice Cap expanded to cover the entire continent about 17 Ma, the Earth's climatic belts shifted northwards, such that mid-latitude Eurasia became subtropical, allowing hominoids to disperse into vast tracts of the Old World from Spain in the west to China in the east. Although they were widely distributed in Eurasia, they still occurred in Africa where they are represented by ten lineages. For several million years, faunal interchanges were possible between Eurasia and Africa and hominoids could probably move freely between the continents, palaeogeography and the position of the tropical zones permitting. This is why it is not possible to propose a precise geographic origin for African apes and humans, although the palaeoenvironment and palaeoclimatic zone can be predicted with confidence.

Optimizing Scale Search in Species Distribution Models

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Key Words: Scale optimization · Species distribution model · Bonobo · Habitat fragmentation

The influence of spatial scale on ecological processes and pattern formation, such as species distribution has been a major research topic for decades. It has become even more relevant in the context of global change. In many studies, the influence of a predictor on a response derived over multiple and discrete spatial scales is evaluated. Due to the inherent issue of multiple testing, this approach can be problematic. In this study on the distribution of bonobos, we suggest a 3-step procedure that overcomes this problem. It takes into account the decay of a predictor by using a weighting function of distance to the observation of interest. We use variables to account for human pressure, food availability, patchy structure of the forest and re-use of nesting sites. Firstly, we ran a model with a fixed scale for every predictor based on expert opinion. For significant variables, we then derived the distance weighted influence over a range of scales. This helps to narrow down the search for the final model parameter estimates. Findings indicate that bonobo distribution is driven on the intermediate scale by forest patch structure. Food availability explains their abundance only at smaller scales. These results demonstrate the sadly well-known influence of habitat fragmentation on animals' density and distribution but also highlight the importance of understanding the influences of scale and the animals' perceptions of their environment by using appropriate statistical procedures. Our method can be particularly useful for formulating specific management hypotheses for conservation. Furthermore, its principles can be of use to other types of studies, such as behaviour.

Behavioural and Ecological Responses to Anthropogenic Food Use and Implications for Conflict Management – A Case Study of Long-Tailed Macaques (*Macaca fascicularis*) in Singapore

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Key Words: *Macaca fascicularis* · Food-enhancement · Human-macaque conflict · Ecology · Singapore

The core population of long-tailed macaques (*Macaca fascicularis*) in Singapore is found along the perimeter areas of the forest reserves system, which is bordered by residential and recreational areas. This close interface between macaques and humans has resulted in conflict situations. The diet, activity, ranging and habitat use of two overlapping groups of food-enhanced macaques were examined in relation to their use of natural and anthropogenic food resources. The group that consumed more anthropogenic food spent less time feeding on wild fruits and flowers, less time resting and more time locomoting. They used forest habitats less often and had a larger total home range and mean monthly home range. Dietary composition was correlated with natural fruit availability but activity budget, habitat use and ranging patterns were correlated more with food availability from refuse sites and provisioning. These results were likely due to anthropogenic foods being spatially dispersed and unpredictable, mainly from a few refuse sites where they had limited access and from dispersed and irregular human provisioning, requiring the macaques to adapt their foraging strategies to exploit these resources. They showed small scale variability in feeding and ranging behaviour, contributing to the complexity of their adaptive variability in a human altered habitat. Behaviours and ranging patterns associated with anthropogenic food resource exploitation by macaques amplifies opportunities for undesirable interactions between macaques and humans. Measures applied to mitigate human-macaque conflict may achieve highly inconsistent results, intensifying the challenges for wildlife managers.

Personality Traits in Common Marmosets (*Callithrix jacchus*)

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Key Words: Animal personality · Common marmosets · Boldness-shyness · Activity · Exploration-avoidance

Originating in human psychology, research on personality has recently broadened its focus on non-human animals. By definition, animal personalities (or behavioural syndromes, tendencies, constructs, temperaments) are groups of correlated behaviours; i.e. a consistent way in which different animals of the same species behave throughout time, contexts and situations, and are, to some extent, heritable. Although studies on most non-human animals are based on behavioural and/or physiological data, those on non-human primates are often based on questionnaires. In this study, we tested 21 individuals from three family groups of common marmosets (*Callithrix jacchus*) on a behavioural level. The animals were tested in five different tasks (general activity, novel food, novel object, predator and foraging under risk) on two occasions. All behaviours were digitally recorded, and parameters such as latencies, manipulation time, vocalisations, foraging, locomotion and focus were analysed. Four principal components were extract-

ed, explaining together 82.28% of variance. Three components consisted of traits related to boldness-shyness (39.53% of variance), activity (19.52% of variance) and exploration-avoidance (14.75% of variance); the fourth component consisted of the duration of calls given (8.48% of variance), possibly indicating a trait with a social character. The comparisons between sexes and among the three family groups served as additional illustrations of a complete behavioural repertoire of common marmosets. Taken together, our findings support the idea that personality traits are consistent within and between individuals across time and contexts.

Factors Affecting the Presence of the Critically Endangered Brown-Headed Spider Monkey (*Ateles fusciceps fusciceps*) in NW Ecuador

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Key Words: *Ateles* · Critically Endangered · Census

Ecuador has the highest rates of deforestation and population density in South America. Land conversion for agriculture has led to an 80% loss of habitat of the Critically Endangered Ecuadorian brown-headed spider monkey (*Ateles fusciceps fusciceps*). The lowlands and cloud forests of NW Ecuador, a biodiversity hotspot, are the last refuges of this species. The cooperative Tesoro Escondido harbours one of last healthy populations of *A. f. fusciceps*. This study aims to identify factors that affect the presence of *A. f. fusciceps* in Tesoro Escondido. Census' were carried out on 2 pre-existing trails, recording subgroup size and composition. Additionally, for each trail, data on tree density, tree height, altitude, canopy connectivity and climate were collected every 200 m. Data were collected with the help of parabiologists. The population at Tesoro Escondido was dominated by females, potentially due to Tesoro being located in a core area of the home range. Furthermore, spider monkey density was affected by tree density and altitude. These results indicate that primary forest at low altitude should be marked as areas of conservation priority for *A. f. fusciceps*. Future conservation action should focus on providing alternative livelihoods in areas where logging for land conversion is prominent.

Preserving Primates' Culture: An Ethnoprimateological Approach to Assess the Human-Non-Human Primate Interface in a Semi-Arid Habitat in North-Eastern Brazil

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Key Words: Conservation · Primate culture · Ethnoprimateology · *Sapajus libidinosus*

Uncontrolled fires and illegal logging are causing loss of biodiversity and consequent decrease of living conditions for primates. Non-human primates are part of human primates' ecosystem interacting with them in various ways, including crop-raiding. In order to preserve primate biodiversity and culture, this study aims to understand the dynamics of the human-non-

human primate interface in a semi-arid habitat in north-eastern Brazil, where a population of wild *Sapajus libidinosus* routinely uses stone tools to crack encased foods, a finding that has important implications for understanding human evolution. I show how an ethnoprimateological approach might be useful for evaluating the impact of long-term field research, building local awareness and promoting conservation of biodiversity. In December 2012 and in April 2013, I visited 46 resident families in a rural area 30 km from Gilbués (Piauí). I tested how a semi-structured interview was valuable in describing the life of the local community mainly in terms of environmental perception, especially of capuchin monkeys. Results indicated that the life of the local community is based on a subsistence economy. All interviewees knew capuchin monkeys; the degree of feelings towards the monkeys varied according to personal experiences and damage inflicted by the monkeys. Overall, residents complained about the lack of infrastructure in their region and noted that uncontrolled fire is the major threat to their natural resources. Results show that use of ethnographic methods enriches our knowledge of the culture of human populations and provide them with awareness about their own attitudes towards the monkeys. This approach is worthwhile for a long-term field research programme aiming at preserving the populations and cultures of both tool using capuchins and the local community.

Who Is Calling Out There?

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Key Words: Orangutan · Long call · Competition · Playback experiment

Long calls by flanged male orangutans (*Pongo pygmaeus wurmbii*) serve as a long-distance communication signal and allow individuals to adjust their ranging behaviour. Long calls can be heard up to circa 1 km in a dense rainforest and are emitted only by flanged males. They do so in two main contexts: (1) spontaneous long calls (which indicate the direction of subsequent travel) and (2) long calls given in response to a trigger such as another male's long call. Bornean flanged males are known to be more competitive among each other: males are more often challenged vocally or physically and therefore involved in more fights than those on Sumatra. The risk of getting injured in such fights is quite high and therefore needs to be represented in the decision to call. Here, we did playback experiments to test whether the response to a long call is based on the latter's acoustic features (which could indicate a male's strength) or on the history of social interactions (encounters, long call battles, or fights) with the caller. We tested the responses of different Bornean flanged males with different dominance status in Tuanan toward long calls of two unfamiliar flanged males from Sabangau, one a dominant and the other a subordinate. If response decisions are based on acoustic features, Tuanan flanged males should approach and respond more to the subordinate long call and less to the dominant flanged male. If, in contrast, social interactions are needed, Tuanan flanged males should challenge both long calls equally according to their own dominance status. The results suggested that response decision seems to be based on the history of social interactions, made possible by the fact that long calls are individually recognizable.

Vasopressin Receptor Gene Polymorphism Variability and Personality in Bonobos (*Pan paniscus*)

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Key Words: Vasopressin · Personality · *Pan paniscus* · Behavioural ratings

Many studies have shown an important role of genes coding for neurotransmitter receptors in the brain on both human behaviour and personality traits. Studying this association in bonobos and comparing these results with those found in humans might give us better insight into the evolution of human behaviour. In this study, we focus on the VNTR in the promoter region of the vasopressin receptor gene (*avpr1a*) named 'RS3'. In humans, this polymorphism is known to have an influence on behavioural traits, such as aggression, altruism and fear, and personality traits, such as novelty seeking and persistence. We collected DNA from 159 bonobos (of whom 32 were wild caught) in European and American zoos and analysed polymorphisms through PCR and fragment analysis. We determined personality profiles for 155 individuals, by using a 54 adjective questionnaire, filled out by zoo keepers. Using factor analysis, we found a six factor personality structure in bonobos, similar to the structure found in chimpanzees with the factors labelled 'Conscientiousness', 'Dominance', 'Extraversion', 'Agreeableness', 'Attentiveness' and 'Adjustment'. Our genetic analysis shows that, in contrast to chimpanzees but similar to humans, bonobos do not have the 360 bp deletion in the promoter region of *avpr1a*. We did find variation in length of RS3 ranging from 288 to 315 bp. In humans, normal variation lies between 310 and 341 bp and longer repeats are associated with increased mRNA levels in the brain, higher amygdala activation and an increase in altruistic behaviour. We will discuss the link between RS3 variation and differences in personality in bonobos for 119 individuals.

Is Bigger Really Better? Case Study – Behavioural Follow-Up of a Group of Bonobos (*Pan paniscus*) That Moves into a Bigger Enclosure

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Key Words: *Pan paniscus* · Captivity · Stress · Environments

Animals housed in captivity are known to be confronted with stressors specific to their confinement. Compared to being in their natural setting, they often have restricted movement due to space limitations and no retreat space and they are also often kept in abnormal social groups. These stressors frequently induce a higher prevalence of stress related behaviour, an increase in abnormal and agonistic behaviour and a general decrease in activity, although not all empirical studies show the same results. This case study is a follow-up of a move of an entire bonobo group into a new and bigger enclosure consisting of 3 adjacent, connected indoor cages and 2 outdoor areas. Their old enclosure was smaller and the group was housed in two subgroups in separate indoor cages with each cage having a small outdoor area. We focus on changes in general activity budgets and stress related and agonistic behaviour. We collected behavioural data through obser-

vations of 7 bonobos (older than 7 years old) using focal animal sampling in combination with all occurrences and scan sampling, 2 months before and after the move. As they were being moved into a new and more stimulating environment, we expected to see a decrease in abnormal behaviour and an increase in activity. Also, as bonobos normally live in what is called a 'fission-fusion society', we expected the new enclosure to allow them to show more naturalistic aggregation patterns that can change during the day and thereby a possible decrease in agonistic behaviour.

Inhibition and Tolerance in Rhesus Macaque Post-Conflict Interactions

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Key Words: Social tolerance · Post-conflict affiliation · Inhibition · Rhesus macaques

Social tolerance is considered an important capacity allowing social cohesion, where the tolerant individual inhibits its competitive impulses. Post-conflict affiliation (PCA) incorporates these elements and may reveal connections between these different capacities, since PCA promotes social cohesion. PCA is only possible when aggressive impulses are inhibited and will only occur when post-conflict approaches are tolerated. We tested the relationship between PCA, post-conflict inhibition of aggression and tolerance of approaches in three groups of captive rhesus macaques (*Macaca mulatta*) for individuals in their role as aggressor or as victim. We expect that individuals that are good at inhibiting aggression after a conflict will also accept the approaches of the former opponent. In addition, individuals good at inhibiting aggression will be more readily accepted by their former opponents. We discuss our findings and explore whether post-conflict aggression may result from a lack of inhibition or is based on inadequate processing of social signals from the opponent.

Behavioural Plasticity, Population Persistence, and the Adaptive Potential of Primates

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Key Words: Behavioural evolution · Adaptation · Life history · Muriqui

Comparative primate field studies have revealed high levels of inter- and intraspecific variation in behaviour patterns, which often deviate from phylogenetic or ecological-based predictions. Long-term studies have also exposed extensive evidence of phenotypic plasticity, which can lead to behavioural changes over an individual's lifetime. Considering the highly altered demographic and ecological conditions under which many primates now live, it is difficult to distinguish adaptive facultative responses that occur over ecological time from behaviour patterns that were selected over evolutionary time. Indeed, these altered conditions raise fundamental questions about whether behavioural adaptations to past selection pressures continue to be adaptive today. Thus, many underlying assumptions about behavioural evolution and its impact on species differences in resilience are increasingly being challenged. Tracing the behaviour and life histories of members of an expanding population of the critically endangered northern muriqui (*Brachyteles hypoxanthus*) over a 30-year period provides examples of some of the vital ways in

which behavioural plasticity and population persistence are inextricably linked. In addition to predictable shifts in their grouping patterns and habitat use, recent analyses of the demographic consequences of changes in the muriquis' reproductive patterns and life histories suggest that behavioural plasticity may not always be adaptive. These findings have implications for understanding the adaptive potentials of other primates in our rapidly changing world, and emphasize the necessity of incorporating these insights into conservation efforts on their behalf.

Explanations of Matriarchal Social Structures

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Key Words: Matriarchal social structure · Lemurs · Agent-based modelling · Life-history modelling · Hyenas

Matriarchal social orders are uncommon in mammals, thus there is much interest in understanding the Lemuriform infraorder of primates. Here, we focus on a comparative study between *Lemur catta* (ring-tailed lemur) and *Crocuta crocuta* (spotted hyena). The social order of these species seems similar, yet each contradicts many of the theories promoted to explain the other's sociality. Both species have only one or two offspring per litter, which may increase the importance of females, but this they share with other primates. Female hyenas show unusual masculinization and aggression, but in lemurs the greatest aggression is male-on-male (Ralls 1976). East et al. (1993) find that size difference also cannot explain dominance. We hypothesize that where reproduction is limited and food scarce, female dominance may benefit inclusive fitness by increasing the number of infants reaching reproductive age. This we explore in simulations based roughly on the life-history and resource constraints of lemurs and hyenas. Dependent juveniles travel with their mothers, and subordinate animals give way to superordinates when feeding. Agents of sufficient well-being seek opposite-sex members of the same species to reproduce. We show that female dominance outcompetes a system without gender structure, but if we augment neutral dominance with flexible social structuring such that females with dependent offspring are favoured, this outcompetes simple female dominance. Similar augmentation of the female-dominant system provides no cost or benefit over the basic augmented system, however, so our model does not in itself explain male dominance in 'higher' primates. An additional cost, such as risk of injury to dominants, may explain observed patterns of matriarchal social structure.

Intersexual Dominance Relationships and the Influence of Leverage on the Outcome of Conflicts in Wild Bonobos (*Pan paniscus*)

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Key Words: Female coalition formation · Female feeding priority · Winner-loser effect · Self-organisation hypothesis · Sexual coercion

Dominance relationships between females and males are characteristic traits of species and are usually associated with sexual dimorphism. Exploring the social and contextual circumstances in which females win conflicts against males allows one to study the conditions triggering shift-

ing power asymmetries between the sexes. This study investigates dominance relationships in bonobos (*Pan paniscus*), a species in which females are thought to display social but not physical dominance. To identify dominance relationships among females and males, we first explored how intrasexual dominance status affects the outcome of intersexual conflicts. Second, by incorporating social and behavioural information about the context of intersexual conflicts, we tested the extent to which different components of power are relevant for the observed asymmetries in the relationships. Post-hoc analyses indicate a sex-independent dominance hierarchy with several females occupying the top ranks. Our results also reveal that two factors – female leverage and motivation to help offspring – had a significant influence on the outcome of intersexual conflicts. The finding that male aggression toward offspring provoked counter-aggression and alliance formation by females may indicate that infanticide still poses an inherent threat to female bonobos. The results of our study do not indicate an overall reduction in male aggression against females but do show lower levels of this male aggression in the mating context, and an absence of male aggression towards those females displaying visual signs of elevated fecundity. This indicates that both female sexuality and male mating strategies are involved in the shifting dominance relationships between the sexes.

Femoral Condyle Curvature and Walking Midstance in Mammals

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Key Words: Femur · Kinematics · Locomotion · Knee

The articular surfaces of long bones reflect the habitual locomotion and posture of mammals because the size and shape of joints must meet requirements for strength, stability and mobility during normal activity and do so without suffering damage or dislocation. This project examines changes in curvature across the medial femoral condyles of mammals, including large-bodied African hominids, finding that regions of low curvature correlate with knee midstance angles during walking. Virtual surface models of femora representing 16 mammalian species were created using a white-light surface scanner. The profile of the medial condyle, relative to the axis of knee flexion-extension, was extracted as two-dimensional coordinate landmarks and these landmarks were treated as sliding semilandmarks in a geometric morphometric analysis. Species-average medial condyle profiles were created and a region of low curvature was identified on each profile. The position of the region of low curvature was quantified relative to the biomechanical axis of the femur using a novel metric termed the angle to low curvature. Kinematic knee angles across the gait cycle were collected from the literature and were regressed against the angle to low curvature metric at 1% increments of the gait cycle. The highest correlation between kinematic knee angles and the angle to low curvature values occurs at 29% of the total gait cycle, which is midstance for most mammals. Since peak ground reaction forces occur at midstance, the region of low curvature is thought to maximize midstance femorotibial contact, thereby accommodating peak forces. *Pan* and *Gorilla* do not deviate further from the general mammalian regression line than do other mammals in the sample.

Improving the Accuracy of Monitoring Great Apes in the Wild: A Case Study from Southeast Cameroon

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Key Words: Western lowland gorilla · Central chimpanzee · Monitoring · Nesting behaviour · Hunting

Monitoring populations of endangered species over time is crucial in guiding and evaluating conservation efforts. Monitoring non-habituated great apes is commonly achieved through counting nests, calculating density and extrapolating to individuals. Field methods and conversion factors to estimate density have potential errors which limit the power and accuracy of monitoring, particularly where chimpanzees and gorillas live in sympatry. The results of monthly nest count surveys (24 months, 2009–2011) in the 'La Belgique' field site, north of the Dja Biosphere Reserve in Cameroon, highlight problems and suggest improvements to site-specific and range-wide great ape monitoring. Bias in density estimates can arise from unreliable nest builder identification: western lowland gorillas (*Gorilla gorilla gorilla*), known to have flexible nesting behaviour, were found to sleep in tree nests 3.80% of the time; while sympatric central chimpanzees (*Pan troglodytes troglodytes*), traditionally assumed to be exclusive tree-nest builders, slept in ground nests 3.37% of the time. Inaccurate nest production and decay rates also lead to bias: site-specific rates are calculated and compared to those from other sites, which are commonly adopted in density estimate calculations when site-specific rates are not available. Finally, in non-protected forests the use of transects and forest trails by local people for hunting influences great ape nesting: we present lower density and encounter rates per kilometre on established transects compared to newly opened ones. We found no change in nesting behaviour as a result of monthly surveys; therefore supporting the use of repeated surveys for great ape monitoring, assuming precautions are taken to minimise or prevent the use of transects by hunters.

What Are the Ecological Drivers and Behavioural Preconditions for Behavioural Innovation?

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Key Words: Innovation · Tool use · Darwin's finches · Woodpecker finches · Flexible stem hypothesis

One precondition for animal culture is behavioural innovation. If innovations spread socially and are transmitted over generations, the scene for cultural phenomena is set. But what are the ecological drivers and behavioural preconditions for innovation? We will explore these questions using Darwin's finches as a model system. This species group is endemic to Galapagos where environmental conditions are harsh. Darwin's finches display an extraordinarily high number of behavioural innovations, such as using tools, drawing blood from seabirds or breaking seabird eggs. Our experimental data also show a high baseline of behavioural parameters that are proposed preconditions for innovation, namely reversal learning and operant learning. These preconditions for innovativeness could be driven by ecological factors, such as unpredictable

conditions and/ or depend on being descended from a flexible stem species. Our data support both hypotheses. Our data on social transmission is limited to tool use in the woodpecker finch. We found that, in this species, tool use does not depend on social transmission, but is based on a specific genetic predisposition. The ecological importance of tool use may be the key to understanding why this behaviour is genetically fixed: tools allow woodpecker finches to reach otherwise inaccessible prey that is rich in nutrients, an ability that is probably essential to survival in the coastal zones. If a new behaviour provides a selective advantage, genetic transmission may be favoured because it is more reliable. This is especially so when the cost of learning is high or the likelihood of encountering the necessary information is low. The latter is certainly true for the woodpecker finch, a solitary species with a short juvenile period.

Interspecific Variation of Social Tolerance in Macaques

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Key Words: Social style · Covariation · Tolerance · Macaque

Macaques are characterised by both the profound unity of their basic social organisation patterns and a wide range of interspecific variation in social tolerance. The study of their social relationships revealed that their social systems comprise sets of correlated behavioural traits, thus limiting them to a small number of social styles that evolve rather slowly through phylogeny. Some macaque species are portrayed by marked social intolerance and a steep dominance gradient whilst others display a higher level of social tolerance associated with relaxed dominance. Many behavioural traits appear to covary with these patterns: the degree of asymmetry in conflicts, the rate of conciliatory patterns, the intensity of aggression, the frequency of affiliative interactions, the degree of maternal permissiveness, the amount of alloparental care, the form of social play, the degree of kin preference among females and individual temperament. Temperament is a key variable that could link individual reactivity thresholds to environmental disturbance and to the amount of resources conceded by dominants to subordinates at the social level.

Sleeping Site Selection of Proboscis Monkeys, *Nasalis larvatus*, along the Kinabatangan River, in Sabah, Malaysia

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Key Words: Sleeping trees · Sleeping sites · Proboscis monkeys · Anti-predation strategies

We studied characteristics influencing sleeping site selection by proboscis monkeys, *Nasalis larvatus*, along the north riverbank of the Kinabatangan River, in Sabah, Malaysia. We identified 81 sleeping trees of one-male and multi-male groups from November 2011 to January 2012. 17 variables were recorded for each tree and more general data were collected for the entire site. We compared sleeping plots and control plots to determine if habitat has an impact on sleeping tree selection by proboscis monkeys. All sleeping trees were close to the river (<35 m). They were taller (27.402 ± 9.922 m), larger (159.324 ± 101.504 cm), with larger and higher first branches (11.732 ± 5.056 m) and had fewer vines. The selection of sleeping tree (and site) characteristics was likely to be related on the one hand to risks of predation and injuries of falling, and on the

other to social interactions and efficiency of locomotion. We noticed that global area also plays an important role. Seeds eaten by proboscis monkeys were studied by faecal analysis. Their abundance and specific diversity were inversely correlated. This analysis provided more information about fruit consumption by proboscis monkey. Finally, proboscis monkey behaviours were recorded by scan sampling method at sleeping sites, where resting accounted for the major part (53.6%) of the activity budget. We observed that members of different age-sex classes did not use sleeping sites in the same way. Differences primarily occurred between adult males and other more vulnerable individuals: adult females with infant and juveniles. The observed patterns seem to be explained by anti-predation strategies.

The Orangutan Enigma: 'King of the Swingers' or Morphologically and Ecologically Defunct?

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Key Words: Orangutan · Morphology · Ecology · Locomotion

The great apes are thought to have evolved to forage and move within the terminal branch niche, the flexible branches at the periphery of tropical forest trees where the majority of fruits and narrowest gaps between tree crowns are situated. But this is a particularly challenging environment since branches taper towards their ends, and will deflect substantially under the body weight of large apes, increasing the risk of falls. In theory, compliant branches may act as external springs adding momentum to locomotion, but most researchers have found that compliant supports increase the cost of arboreal locomotion in monkeys and lemurs. Orangutans are the only great ape to have remained exclusively in this great ape ancestral niche and they should, in theory, have evolved a particularly refined suite of adaptations to facilitate arboreal living. Yet, they are notable for being the largest habitually arboreal animal; have the longest interbirth-intervals of any mammal and many Bornean populations experience significant nutritional stress, requiring them to catabolise their fat reserves. Furthermore, approximately 75% have healed fractures, dislocations and contusions resulting from past falls. These factors suggest an animal operating at the limits of its locomotor, behavioural and energetic plasticity. In this presentation I will draw on our studies of functional morphology, locomotion and cognition in orangutans and other apes (including humans), to understand whether orangutans really are the King of the Swingers.

Female Sexual Signalling in Wild Tufted Capuchin Monkeys: Implications for the Graded-Signal Hypothesis in a New World Primate

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Key Words: Sexual signalling · Behavioural proceptivity · Faecal hormones · Ovulation

Research on primate sexual signals has largely focused on testing the adaptive significance of morphological signals of fertility against two main hypotheses, the graded signal hypothesis and the reliable indicator hypothesis. However, some primates lack these morphological signals

but produce behavioural displays of sexual proceptivity. Such behaviours in tufted capuchin monkey (*Cebus apella nigrurus*) females have been proposed to be functionally equivalent to morphological sexual signals in catarrhines. In this study, we examined the function of these behaviours by testing predictions derived from the two hypotheses. Specifically, we recorded proceptive behaviours and copulations on two wild groups of tufted capuchins. We observed eight cycling females over two mating seasons for a total of 15 ovulatory cycles. These behaviours were then related to the timing of ovulation as determined by analysis of faecal progesterone metabolites. Results indicate that proceptive behaviours are significantly associated with fertile phases. More importantly, within the fertile phase, proceptive behaviours varied according to the probability of ovulation. In contrast, female proceptivity did not vary with measures of female reproductive quality (e.g., fecundity and dominance rank). Finally, when considering male mating responses, copulations were synchronized in relation to female fertile phase and were intensified by dominant males during days with a high probability of ovulation. Therefore, proceptive behaviours in this species appear to be reliable signals of ovulation and resemble a graded signal system. Accordingly, males time their mating activity around the female's fertile phase, with dominant males gaining access to females during days in which ovulation is more likely.

Substrate Use and Grasping Strategies during Food Acquisition in *Microcebus murinus*: Insights for Understanding Primate Grasping Origins?

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Key Words: Grasping · Locomotion · Food acquisition · Mouse lemur

Grasping is a widespread behaviour among tetrapods. In primates, hands and feet are involved in many grasping tasks such as food acquisition or the grasping of the locomotor substrate. Associated with these behaviours are numerous grasping strategies. Many questions about the origin and the evolution of prehensile capacities, which are much diversified across this group, remain. Some suggest that grasping evolved in an arboreal habitat consisting of fine branches associated with insect predation and/or fruit and flower exploitation. However, few studies have tested the importance of arboreal conditions and diet (e.g. frugivorous, omnivorous) on the use of the hands in food grasping. Here, we studied a model often described as representative of the earliest primates: *Microcebus murinus*. Across two behavioural experiments of food acquisition we showed that (1) the substrate diameter influences food acquisition strategies (mouth versus one or both hands), (2) the food properties, particularly the mobility of the prey, had an impact on the use of the hands versus the mouth, (3) *M. murinus* seems to be more an opportunistic species rather than being adapted to a fine branch milieu as previously suggested. The predation and arboreal hypotheses should be explored more widely in tetrapods, in particular in groups having some terrestrial versus arboreal species and prehensile versus non prehensile species. Such studies could help us to understand the convergence of the evolution of grasping and may allow us to test the specificities of primate grasping abilities.

The Relevance of Animal Non-Linguistic Reference to Human Language

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Key Words: Functional reference · Animals · Vocalisations · Semantics · Language evolution

The functionally referential (FR) framework has acted as an important cornerstone to understanding the complexities underlying animal communication. Moreover, it has shed crucial light onto the differences and similarities that exist between animal communication systems and human language. Specifically, calls elicited by external events in animals can potentially act as homologous or analogous data points necessary for unravelling the emergence and uniqueness of semantic capabilities in human language (Zuberbühler 2005, Fitch et al., 2010). However, whilst informative, the framework actively avoids clarifying what cognitive capacities might accompany such signals (Macedonia and Evans, 1993). Recently, it has been suggested that the FR framework should be abandoned in favour of a more contextually-variable approach (context less-specific calls), particularly because this may require more sophisticated cognitive processing mechanisms and hence may represent a more fruitful field for future language evolution research (e.g. 'animal pragmatics'). I will argue that instead of abandoning the framework completely, one approach could be to place more focus on what cognitive mechanisms underlie the perception and production of these calls. I will review what evidence exists for flexible production and representation-like processing of FR calls in animals and the paradigms used to investigate this. Only by incorporating both surface level similarities and the associated cognitive mechanisms (e.g. nominal representations, Gallistel, 1990) between animal non-linguistic and human linguistic reference can we really get at the evolutionary path that culminated in full-blown human semanticity and hence the relevance of functional reference to human language.

Assessment of Orangutan (*Pongo* spp.) Rehabilitation Methods in Indonesia

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Key Words: Orangutan · Rehabilitation · Indonesia · Sanctuary · Release

The practice of orangutan (*Pongo* spp.) rehabilitation and reintroduction has been conducted in Indonesia for more than 40 years. Reintroduction is considered one conservation strategy for orangutans, but a lack of monitoring and standardisation between programmes has led to criticisms of the value of this approach. Rehabilitation methods used at four orangutan rehabilitation centres in Indonesia were assessed, in order to identify the key factors that contribute to the successes, and failures, of rehabilitation. This study was used to explore: (1) the epidemiology of stereotypical behaviours in rehabilitant orangutans, and (2) environmental challenges and opportunities for the development of positional behaviour in captive rehabilitant orangutans in Indonesia. Rehabilitant orangutans' behaviours were associated significantly with the captive rehabilitation environment; life history prior to rescue failed to account for all abnormal behaviours. Changes made to the physical habitat highlighted the importance of providing complex

environments for effective psychological and physiological rehabilitation. Stereotypic behaviours were prevalent in all sanctuaries with most (>90%) orangutans in the study showing signs of these behaviours. Positional behaviours observed during rehabilitation could be improved through appropriate housing conditions and enrichment. The absence of opportunity to practice energy-efficient modes of travel, such as sway and ride, may be detrimental to fitness after release, especially in times of a negative energy balance. Improving conditions and monitoring methods used for orangutans during rehabilitation is vital to improving, and determining correctly, results after release.

Could Bonobos, *Pan paniscus*, Influence the Dynamic of Forest (Re)Colonization in a Forest-Savanna Mosaic?

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Key Words: Bonobos · Seed dispersal · Forest regeneration · Mutualism · Forest-savanna mosaic

The forest-savanna mosaic of Western D.R. Congo is a particular ecotone with forest patches characterized by a high diversity of habitat types and a large proportion of transitional forests at edges. This ecosystem is highly disturbed by human activities, forests being degraded by slash-and-burn agriculture and savanna being used for cattle ranching, though it is inhabited by bonobos, *Pan paniscus*. We investigate how this large frugivore can participate in the natural regeneration of the forest in this fragmented ecosystem. We identified all seed species dispersed by faeces analysis (24 months, 1,977 faeces, 78 spp. identified). To assess the effect of gut transit on germination, we collected seeds in faeces and directly in fruits to conduct germination trials (1,391 seeds of 12 spp.). Habitat use by bonobos was identified with indirect signs over 180 km of transect inventories. Bonobos appear to disperse a large number of viable seeds by endozoochory. Seed transit in gut can have a harmful, neutral or positive effect on germination capacity. Species benefiting from endozoochory are characterized by varying light demands and shade tolerance. Percentage of germination and germination speed of the most important species in the diet (*Marantochloa leucantha*, *Aframomum* sp., *Musanga cecropioides*) is enhanced when ingested. Bonobos tend to avoid human activity and stay in more remote forested areas for sleeping, whereas direct observations and indirect signs indicate they are not restricted to primary forests but use forest edges and savanna matrix. Through the ingestion of a large number of seeds, the enhancement of germination and the deposition of those seeds to diverse habitats types, bonobos are likely to favour forest regeneration at early and late successional stages.

Identifying Behavioural Signals in Trabecular Bone Structure of the Hominoid Third Metacarpal

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Key Words: Cancellous bone · Locomotion · Hand use · Manipulation · Apes

The hand is a direct contact between the individual and the environment, thus differences in locomotor and manipulative behaviour across extant hominoids may be reflected in the bony morphology of the hand. Trabecular bone is capable of adapting during life in response to loading and therefore may hold a behavioural signal associated with hand use across hominoids. Here, we apply a novel, whole-bone methodology (AnthroMorph) to microCT scans of the hominoid third metacarpal to investigate whether trabecular structure reflects differences in hand posture and loading in knuckle-walking (*Gorilla*, *Pan*), suspensory (*Pongo*, *Hylobates* and *Symphalangus*) and manipulative (*Homo*) taxa. Results demonstrate a clear correlation between variation in trabecular structure and differences in hand loading and posture among hominoids. Trabecular bone volume distribution and regions of greatest stiffness correspond with predicted loading of the hand in each behavioural category. In suspensory and manipulative taxa, bone volume and greatest stiffness are concentrated on the palmar or distopalmar regions of the metacarpal head, whereas knuckle-walking taxa show greater bone volume and stiffness throughout, and particularly in the dorsal region; patterns that correspond with the highest predicted joint reaction forces. Trabecular structure is characterised by high bone volume fraction and a high degree of trabecular orientation in knuckle-walking taxa in contrast to the suspensory brachiators. Humans – in which the hand is used primarily for manipulation – have a low bone volume and a variable orientation. The correlation between behaviour and trabecular structure in extant hominoids demonstrates the potential contribution of this method to reconstructing behaviour in fossil primates.

On the Posture and Locomotion of *Micromys minutus*: A Living Model for Understanding Primate Origins

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Key Words: Positional behaviour · Substrate use · Rodent · Eurasian harvest mouse · Primate evolution

Multiple hypotheses have been proposed to explain primate origins. In doing so, different evolutionary scenarios tend to adopt modern living non-primate models that partly simulate the morphobehavioural apomorphies of primates. This work explores the positional behaviour and substrate use of Eurasian harvest mice (*Micromys minutus*) as living models for inferring the evo-

lution of versatile behaviour in early primate ancestors. Harvest mice are among the smallest rodents in the northern hemisphere, weighing 10 g. They are agile climbers, feed on stems and terminal twigs, and are almost exclusively arboreal. We provide a detailed quantitative analysis on how locomotion and postures relate to different behavioural contexts, substrate types and inclinations, in an enriched naturalistic environment with a variety of fine flexible arboreal substrates. This tiny rodent shows postural modes requiring secure pedal grasping, and a varied positional repertoire composed of clambering and climbing, making considerable use of fine flexible branches of different inclinations during travelling and feeding/foraging. This behaviour appears to fit in an intermediate phase between stage 2 (*Tupaia*-stage) and stage 3 (*Caluromys*-stage) in Sargis et al.'s (2007) scenario on primate evolution. Furthermore, these findings provide additional information on the role of tiny size in relation to flexible positional repertoire, an aspect that has been underappreciated in the primate evolution literature.

Genetic Relatedness, Spatial Association and Rates of Affiliation and Agonism in Adult Black Howler Monkeys (*Alouatta pigra*)

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Key Words: Kinship · Social relationships · Affiliation · Agonism · *Alouatta pigra*

The interplay between kinship and social interactions was examined in five multimale-multifemale groups of black howler monkeys (*Alouatta pigra*) in Palenque National Park, México. All adult males ($n = 15$) and females ($n = 13$) served as focal subjects for 12–16 months, resulting in 473–519 focal hours per group. Dyadic rates of affiliation and agonism were calculated as number of events divided by the sum of focal hours for both adults. Spatial proximity was calculated as percentage of time two adults spent within 2 m of each other. Pairwise relatedness (r) was estimated for all intragroup adult dyads based on 20 polymorphic microsatellite markers. Female-female (F-F) dyads spent 20% of their time in close proximity, while male-female (M-F) and male-male (M-M) dyads spent 9 and 4%, respectively, of their time in close proximity ($p < 0.001$). F-F dyads engaged in affiliation at roughly twice the rate than did M-F and M-M dyads ($p = 0.028$). Agonism was rare, but M-F dyads engaged in agonistic interactions at roughly twice the rate seen in F-F and M-M dyads ($p = 0.016$). Ten of 17 F-F intragroup dyads, 7 of 21 intragroup M-M dyads, and 11 of 57 intragroup M-F dyads were considered closely related. Kinship had no effect on the time spent in close association within M-M, F-F, and M-F dyads ($p > 0.05$). In addition, kinship was not correlated with affiliative rates in either M-M or F-F dyads ($p > 0.05$), but estimates of r were positively correlated with affiliative rate in M-F dyads ($p = 0.002$). Furthermore, closely related females engaged in agonistic interactions at lower rates compared to unrelated females ($p = 0.048$), but kinship had no effect of agonism among either M-M dyads or M-F dyads. These results suggest that kinship influences social relationships in *A. pigra*.

Conservation Efforts for the San Martin Titi Monkey (*Callicebus oenanthe*) in Ojos de Agua, Peru: Density Estimates and Habitat Suitability Modelling

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Key Words: *Callicebus oenanthe* · Density estimates · Habitat suitability

As of October 2012, the San Martin titi monkey (*Callicebus oenanthe*) is listed in the The World's 25 Most Endangered Primates list (Mittermeier et al., 2012). For this Critically Endangered primate (Veiga et al., 2011) and for Peruvian conservation NGO Proyecto Mono Tocón (PMT), there could not be a better time to focus the attention of the world's conservationists on this species. Now that research has determined the distribution of the species (Bovéda-Penalba et al., 2009; Mark, 2003; Rowe and Martinez, 2003; van Roosmalen et al., 2002; Vermeer et al., 2011), the next important step in the conservation of *C. oenanthe* is estimating the densities of the known populations in important conservation areas, creating protected areas and expanding existing ones. This study has focused on determining the density of *C. oenanthe* in locally managed conservation concession Ojos de Agua with the use of a triangulation method (Aldrich et al., 2008). As well as determining the density of the population within Ojos de Agua, we also examined the habitat of *C. oenanthe* within the dry forest of Ojos de Agua by measuring tree density, tree diameter at breast height and distance to forest edges, and we mapped sources of human disturbance. When combining this information with data from a similar study in Reserve Morro de Calzada, a few hours northwest of Ojos de Agua, we obtain a good idea of the habitat requirements for the species. This information is of vital importance to locate the areas around Ojos de Agua that are suitable for expansion of the conservation concession. This study is part of a larger umbrella project set up by PMT to study the habitat requirements of *C. oenanthe* and explore the possibility of creating corridors between the most important fragments for the survival of the species.

Advancing the Field of Primate Conservation Education: An Innovative Global Model for Collaboration

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Key Words: Primate · Education · Collaboration · Network · Global

Primate Education Network (PEN) is developing a scalable model to address the lack of information sharing and collaboration in primate conservation education. PEN is dedicated to connecting and empowering primate conservation educators worldwide. The network has established a global presence through an online platform and a growing team of Regional Coordinators and Advisors in Latin America, Europe, Africa and Asia. Regional Coordinators facilitate communication and collaboration among primate educators. They organize regional workshops and training and design action plans in primate education. We will discuss how educators can get involved with PEN to connect and collaborate with other educators, share resources and best practices, and receive the training and support needed to design and deliver successful primate education projects and programmes.

The Endangered Barbary Macaque (*Macaca sylvanus*): Conservation Efforts, Struggles and Success Stories in Morocco

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Key Words: Barbary · Macaques · Conservation action plan · Morocco

The Barbary macaque (*Macaca sylvanus*), a primate species that can only be found in Morocco and Algeria in the wild, has been classified as 'Endangered' on the IUCN Red List since 2008. The continuous over-exploitation of natural resources in the habitat areas in Morocco and the poaching of infants for the pet trade to Europe have resulted in a dramatic decline in numbers over the last decades. The Moroccan Primate Conservation Foundation (MPC) has been working on the conservation of the species since 2003. Although MPC works nationally, the main focus is on preserving and protecting the last large Barbary macaque population that can be found in the wild; the population of the Ifrane National Park in the Middle Atlas mountains. Conservation of Barbary macaques requires a multi-level approach as many stakeholders are involved; poachers, loggers, law-enforcement officers, customs, legislators, local communities, local and national governments, the EU, potential macaque buyers in Europe etc. Recently MPC organised a meeting with the Moroccan High Commission of Water and Forests to create a Conservation Action Plan (CAP) for the species in Morocco with help of experts. The first activities described in the CAP will take place in 2013, which can be seen as a major success as the Moroccan authorities are now supportive and motivated to conserve this unique species together with local and international NGOs.

Surviving Scarcity: How Do Nursing Orangutan Mothers Save Energy When Fruit Availability Is Extremely Low?

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Key Words: Energy budget · Fruit availability · Lactation · Sociality

Orangutans (*Pongo pygmaeus wurmbii*) in Bornean swamp forests endure huge intra- and inter-annual variation in fruit availability. With lactation and infants' nutritional dependence lasting around 6 years, reproduction cannot be timed so that increased energetic needs coincide with high food availability. Nevertheless, infant mortality is remarkably low. Even though orangutans are known for their conservative energy expenditure, periods of extreme fruit scarcity are expected to affect nursing mothers and their growing offspring. In addition to changes in the composition of the diet (more bark and leaves), we expect reduced intake of high quality fruit to elicit energy-conserving responses, not only in activity budget but also in social and other behaviour. Here, we present data on the Tuanan population collected since 2003, including more than 17,500 h of nest-to-nest focal follows on mother-offspring dyads. When fruit is extremely scarce, females tend to rest more. However, they also make day nests less frequently, suggesting they even conserve energy by reducing their nest-building efforts. They select abundant fallback foods and thus minimize travel. This reduces their chance of encountering other individuals and indeed they spend less time in close association with conspecifics. Fruit scarcity also affects the activity

budgets of the offspring, reducing exposure to role models other than the mother and their opportunities for social play. Overcoming periods with fruit scarcity by their successful fallback strategy may explain the extremely conservative level of sustained investment in lactation and thus infant growth rate over the extended period of infant dependency in this great ape.

Ecological Effects on Opportunities for Innovation and on Estimates of a Population's Cultural Repertoire

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Key Words: Innovation · Culture · Ethnographic method

There are two important reasons to study the impact of ecological conditions on culture in nature. First, most studies documenting animal culture have necessarily relied on the 'ethnographic method' (or 'method of exclusion'). This method involves conservative geographic comparisons, since population differences correlated with clear genetic or habitat differences are excluded. Especially the latter almost inevitably leads to serious underestimates of a population's cultural repertoire, and, more insidiously, may lead to a considerable bias in the documented content of culture. Second, ecological conditions also influence cultural processes, by affecting the probability that particular innovations arise. More broadly, ecological conditions also affect the spread of these innovations by affecting associations and tolerance. Here, I suggest an alternative to the ethnographic method: estimating a population's cultural repertoire by documenting its set of learned skills, with the latter defined as skills acquired gradually after social attention to practitioners and often after practice. I also illustrate the role of ecology in innovation, by showing that the geographic distribution of various forms of extracting seeds from *Neesia* fruits among orangutans is correlated with the frequency of opportunities for innovation, rather than genetic variation.

Separation-Training of Very Young Common Marmosets (*Callithrix jacchus*): Implications and Challenges

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Key Words: Common marmosets · PRT · Young

Animal welfare and its constant improvement is one of the key issues in animal research. Therefore, we have set up an extensive animal training programme, which is based on Positive Reinforcement Training (PRT) at the BPRC. For our breeding colony of common marmosets (*Callithrix jacchus*), we asked whether it was possible to train very young (15 weeks average) marmosets to check regular weight development and health. No invasive techniques were used and care was taken to avoid stress. The animals needed to be temporarily separated from their family-group to enable monthly health checks, without adding stress for the family-members. Initially, 8 twins were trained in this project. Later on, 3 younger twins (4 days average) were added. Previously, we had trained older offspring and parents to be separated from the group by means of an in-cage corridor-system. A similar training plan, making use of this corridor-system, was devised for this study, and training started two weeks before the first health check. While training, it appeared that group stability has a big effect on trainability. In the 'older-twin' group, we sepa-

rated individuals 60 out of 96 times by means of the corridor-system for health checks. For the 'younger-twin' group, training attempts started at the age of 4 days. Although training-success in this group was comparable to the 'older-twin' group (success rate 6 out of 12 times), training-time was much longer. This and additional data from this study suggests that common marmosets are not susceptible to training before the age of 14 weeks.

Improving the Golden-Headed Lion Tamarin Breeding Schemes by Establishing Founder Relatedness through Combined Microsatellite Marker and Pedigree Analysis

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Key Words: Captive breeding · Founder relatedness · Pedigree analysis · *Leontopithecus chrysomelas* · Microsatellites

Self-sustaining captive population must be genetically managed to minimize loss of genetic diversity, inbreeding and adaptation to captivity. Accurate genetic management of a captive population relies mostly on pedigree analysis. However, the majority of the pedigrees in captive breeding programmes are far from perfect for various reasons. Most importantly, founders are assumed to be unrelated, often resulting in an overestimation of the genetic diversity present in a population. The European captive breeding population of the golden-headed lion tamarin (GHLT), *L. chrysomelas*, which is endemic to the Atlantic Forest of South-Bahia and threatened with extinction, has grown from 46 founders to a size of approximately 220 animals in the last decades. The pedigree is known for about 98% of the primates and the genetic diversity retained is estimated to be 97% of the source population. However, GHLT founders were imported from Brazil in small groups for which mutual relatedness was unknown. The main objectives of this study were to estimate the genetic relationship between the GHLT founders and to resolve gaps in the pedigree of the captive GHLT population. We used 21 microsatellite marker loci to infer genetic relatedness among 95 captive individuals in the first generations. Tissue samples were collected post-mortem, and for live animals non-invasive hair samples were used for DNA extraction. Pedigree and molecular data were combined into one estimator of relatedness by a weighing method developed by Bomcke and Gengler (2009). Integration of the relatedness estimates was completed through the use of the PMx software. The changes in mean inbreeding, mean kinship, founder genome equivalents and GD were assessed, and these will be discussed in terms of improving the management of the captive population.

Tool Use Behaviour of Gorillas in Captivity: Qualitative and Quantitative Analysis

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Key Words: Gorilla · Tool · Lateralization

We have observed more than 1,500 cases of tool activities in the Prague Zoo. Gorillas used tools as weapons during aggressive behaviour, they drew food closer using sticks, and they used

plastic boxes to make steps and pyramids to acquire food which was placed too high to reach it simply by hand or by club. Special cases of tool using behaviour were recorded as comfort behaviour, when gorillas made primitive shoes from wooden shavings, to prevent their feet getting cold and/or wet, when walking across snow or a wet floor. All those cases have shown that gorillas' tool behaviour does not take place only in a food context. It can be detected frequently during social, play and agonistic behaviour and, in many cases, it cannot be interpreted as a simple imitation of human tool behaviour. An analysis of current hypotheses on the origin of tool behaviour in primates has demonstrated that more basic factors have played a role in the origin and evolution of tool behaviour. It is not possible to select just one of them, like play, aggression or presence of a specific object in the living environment. We suppose that this process had a more complex nature.

Assessment of the Consequences of Anthropogenic Pressures on *Alouatta palliata* and *Ateles geoffroyi* Physiology in Northern Costa Rica

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Key Words: Howler monkey · Spider monkey · Stress · Parasite · Caño Pama Biological Station

Previous studies have shown a positive relationship between proximity to humans or habitat fragmentation and parasite levels in non-human primates (NHPs). However, to date few have explicitly explored links between parasite load and stress conditions. To understand better the links between parasite prevalence and NHP immune system efficiency and stress levels, faecal samples of *Alouatta palliata* and the Critically Endangered *Ateles geoffroyi geoffroyi* were non-invasively collected in northern Costa Rica. We investigated whether the presence of gastrointestinal parasites was related to the abundance of hormones (cortisol and testosterone). Samples were gathered across three areas differing in the frequency and diversity of human presence, i.e. around the Caño Palma Biological Station, near villages and at ecotourism sites. Two grams of each faecal sample were stored in a sugar saturated solution with 10% formalin to conserve the parasites; the remaining matter was dried to preserve DNA and steroid hormones. The samples enabled the quantification of parasites as well as testosterone and cortisol levels using ELISA as proxies of general health status and stress levels. Data on parasite abundance and hormone levels were contrasted across the two species and the three different sampling areas. Furthermore, we assessed the genetic exchange among the different groups of primates sampled. We genetically analysed the samples using 12 microsatellites previously validated by the University of Costa Rica. We verified whether transmission of parasites among the groups could be possible concomitant to the genetic exchange. This study aimed to understand better and assess the impact of human factors on NHP health and across NHPs with different socio-ecological characteristics.

The Socio-Ecological Adaptation of Released Chimpanzees in Guinea, West Africa

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Key Words: Chimpanzee · Release · Adaptation · Chimpanzee Conservation Centre · Guinea

Throughout their range across Africa, chimpanzees (*Pan troglodytes*) are threatened with extinction due to habitat destruction, disease and unsustainable levels of hunting and capture, in spite of being protected by national and international laws. In recent years, the bush meat and the pet trade have resulted in a significant increase in the number confiscated orphan chimpanzees. The Chimpanzee Conservation Centre (CCC), located in the High Niger National Park (HNNP), is the only Pan African Sanctuary Alliance (PASA)-accredited sanctuary caring for chimpanzee orphans in Guinea, West Africa. This sanctuary has been rehabilitating confiscated chimpanzees since 1997. With the aim of reinforcing the wild chimpanzee population of the HNNP and to enhance park protection, the CCC, in 2008, released a first group of 12 chimpanzees into the Mafou core area of the park. Five of those individuals have since settled at the release site and continue to be monitored. In August 2011, the CCC was able to re-enforce this resident group with the successful addition of 2 adult females. Post-release monitoring of these individuals involved distance monitoring using simple VHF and/or ARGOS and GPS store-on-board radio collars. Here, we present data downloaded in 2011–2012 from the GPS store-on-board collars of 2 adult males and these 2 additional adult females. These data allowed us to analyse their social dynamics, party composition, habitat preferences, day range and home range use. Our results indicate that these females integrated successfully into the resident group and that the behaviour of these wild-born released orphan chimpanzees mirrors that of wild counterparts inhabiting similar savannah dominated landscapes, suggesting that they have adapted appropriately to their release conditions.

Risk Proneness in Capuchin Monkeys (*Sapajus apella*): Does Feeding Ecology Play a Role?

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Key Words: Risk · Ecology · Capuchin monkeys · Primates · *Sapajus apella*

Different fields of research have investigated the problem of how individuals respond to risk, defined as a situation with a known distribution of possible outcomes. Animals as diverse as fish, birds and bumblebees are usually risk averse. However, studies on non-human primates have revealed a more varied picture. When tested with the same paradigm, cotton-top tamarins and bonobos avoid risk, common marmosets are risk neutral, whereas chimpanzees are risk prone. Here, we presented six capuchins with choices between a 'safe' option (four food items) and a 'risky' option (one or seven food items) in three conditions: (1) Neutral (50% chance to receive seven food items); (2) Advantageous (66% chance to receive seven food items), and (3)

Disadvantageous (33% chance to receive seven food items). In the Neutral and in the Advantageous conditions capuchins were risk prone. In contrast, in the Disadvantageous condition they were risk neutral. When later presented with pairwise comparisons between all risky options, capuchins flexibly adjusted their choices, preferring the risky option more (i) in the Advantageous condition than in the other two conditions and (ii) in the Neutral condition than in the Disadvantageous condition. Thus, although capuchins adjusted their choices on the basis of the average pay-out of the risky option, they were overall highly risk prone. This result could be explained by taking into account that in the wild capuchins often cope with risky situations. In fact, they hunt vertebrates that can strike back, process and eat cashew nut despite its caustic protection, and use tools on the ground where the potential risk of being predated is high.

A New Tool to Study Primate Hand Biomechanics: Dynamic CT of Thumb Opposition

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Key Words: Functional morphology · Primate hands · Medical imaging

The unique dexterity of humans is largely determined by the opposability of the thumb. Humans are not the only primates to possess an opposable thumb, catarrhine primates also have an opposable thumb allowing precision and power grips. Yet, due to marked differences in the thumb anatomy of these primates, dexterity is lower than observed in humans. Despite the importance of the thumb in various gripping activities, the functional implications of its specific morphology are not fully understood. This is mainly due to the technical difficulties in visualizing and quantifying motion of the hand bones. The complex 3D arrangement of the small bones with multi-planar range of motion and skin motion artefacts means that state-of-the-art motion capture techniques have a limited applicability. To acquire an accurate characterization of the 3D kinematics of the bones involved in thumb opposition, a dynamic CT protocol was developed. A motion simulator was used to guide passive opposition of the thumb at a constant speed. During a full opposition/reposition cycle, a time series of 19 CT frames was collected (FOV: 12 cm, slice thickness: 0.625 mm, voxel size: 0.036 mm³). Post-processing software (Mimics 14.12) was used to segment the CT frames, resulting in a time series of 3D bone reconstructions, which were exported as STL-files and imported in Matlab to calculate kinematics of thumb opposition. Dynamic CT scanning is a valuable method to quantify movements of individual hand bones during manipulative tasks. Its main advantage is that it allows direct acquisition of bone geometry during thumb movement allowing real-time imaging of internal joint motion. This method is applicable in living subjects, due to the low radiation dose, but can also be applied using hands of primate cadavers.

Behavioural Ecology of Bonobos (*Pan paniscus*) in the Forest-Savannah Mosaics of Western Democratic Republic of Congo

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Key Words: Bonobo · Forest-savannah mosaic · Behavioural ecology · Conservation · Western DRC

The long-term survival of the Endangered bonobo (IUCN, 2012) will depend on well thought out conservation programmes that need to be built both upon the species' ecological requirements and local socio-economics realities. Yet there is still a lot to find out, including information on the species geographical distribution. In 2005, the presence of a western population was confirmed in the forest-savannah mosaic in the south-western part of the Lake Tumba Landscape. With the exception of an early study carried out in Lukuru, the species is mainly known from lowland rain-forest research sites in the Cuvette Centrale. The western forest-savannah mosaic is an ecotone with a marked seasonal pattern, a high variability of habitats and monthly variations in fruit production. All this leads to spatio-temporal variation of food availability. In order to increase studies and monitoring of this unique population, WWF initiated a habituation process of two groups of bonobos 6 years ago. The groups are now semi-habituated, making the collection of direct daily observations possible. Our objective is to describe the behavioural strategies developed by this population in order to cope with spatio-temporal variations of food availability. This will be approached by identifying daily activity, ranging and grouping patterns, in order to understand how they affect social structure. It should also allow us to define the use of savannahs. Our findings will help determine specific conservation measures for this endangered species.

The Ecology of Stone Tool Use: Insights from Wild Bearded Capuchins

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Key Words: Tool use · Culture · Innovation · Learning

Only recently has non-anecdotal use of tools been discovered in capuchin monkeys. These reports concern populations belonging to the genus *Sapajus* living in the north east of Brazil. In contrast, tool use seems absent in various types of forested habitats in South and Central America where several long term studies have been (and are still being) carried out. In the best-studied field sites where capuchins use tools they mostly use stones (to crack encased foods and excavate) and sticks (for various purposes, such as probing into holes). The majority of these activities occur when capuchins are on the ground. Moreover, systematic data coming from FBV field site, where I do my research, have shown that capuchins do not face food scarcity and that stone tool use occurs throughout the year, reflecting nuts availability. Here, I will speculate about the role of terrestrial habits on the emergence of stone tool use and illustrate data concerning the acquisition of stone tool use by youngsters living in a group where adults are proficient tool users. Finally, I will discuss possible factors affecting the presence and the absence of tool use in capuchin monkey populations.

Lessons Learned from Javan Gibbon and Langur Rehabilitation and Reintroduction Project in Java: Reinforcing the Isolated Javan Langur Population in the Coban Talun Protected Forest, East Java, Indonesia

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Key Words: Java · Primates · Rescue · Rehabilitation · Reinforcement

The Java Primates Project is a cooperation project between The Aspinall Foundation and the Directorate General for Forest Protection and Nature Conservation, Ministry of Forestry, Republic of Indonesia, aims to preserve Java's endemic primates and their habitat. The Javan gibbon (*Hylobates moloch*) is listed by IUCN (2012) as Endangered while the Javan langur (*Trachypithecus auratus*) is listed as Vulnerable, with the reasons for population decline identified as the illegal pet trade, hunting, and loss and fragmentation of habitat. This study will present our works on rescue and rehabilitation of those two most threatened primates in Java and focus on current reinforcement of the eastern subspecies of the Javan langur population into their former habitat. Populations of the subspecies of Javan langurs occurring in East Java, *Trachypithecus auratus auratus*, occur in isolated forest fragments, and in many of these appear to be at low densities or, in some cases, extinct. The aim of the Coban Talun langur reinforcement project is to re-establish a viable, self-sustaining population of the Javan langur in the Coban Talun Protected Forest, East Java, Indonesia. This is being undertaken through the release of langurs held at the Javan Langur Rehabilitation Centre (JLRC) in East Java, supplemented by langurs transferred from the captive breeding colony at Howletts and Port Lympne Wild Animal Park in the UK. The project will involve intensive pre-release preparation, long-term post-release monitoring and release site management. The first release of 13 langurs held at the JLRC occurred in September 2012, and all 13 were still alive 6 months post-release. Six langurs from the UK were transferred to Java in January 2013, for release later in the year.

Distinguishing Contextual Effects on Meaning Attribution versus Decision-Making in Primate Communication: An Example with Capuchin Monkeys (*Cebus apella nigrinus*)

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Key Words: Communication · Functional reference · Pragmatics · Alarm calls · Cognition

Context-specific signals such as predator-specific alarm calls are widely singled out as functionally referential and possible precursors to language. However, signals that are not context-specific appear also to be meaningful, although this seems to depend on the ability of receivers to ascribe different meanings across contexts. Understanding whether context truly affects meaning in these cases is difficult because context should also affect receiver decision-making. In contrast, because the meaning of context-specific signals is stable, contextual variation in responses to such

signals would seem attributable to decision-making. Tufted capuchins give different calls in response to aerial and terrestrial predators. While the aerial alarm is context-specific (elicited only by aerial stimuli), the terrestrial alarm is given in other contexts, including 'deceptive' uses during feeding, resulting in a decreased response rate to the latter in feeding contexts. To determine if variation in responses to terrestrial alarms is better explained by variation in either meaning attribution or decision-making, I conducted a playback experiment with wild capuchins in Iguazú, Argentina. Specifically, I played back aerial alarms in competitive contexts and non-competitive contexts to determine if responses vary similarly to those of the less specific terrestrial alarm. Preliminary results suggest that receivers respond less strongly to the aerial alarm in competitive contexts relative to non-competitive contexts. Given that such trends are better explained as variation in decision-making, the reduced response rate to terrestrial alarms likely also results from a decision to ignore signals during feeding, rather than from receivers attributing different meanings to deceptive signals.

Herbaceous Plant Availability and Use by Western Lowland Gorillas in South East Cameroon

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Key Words: Dja Reserve · Forest understory herbs · Nest building · Plant use · Western lowland gorilla

The ecological patterns and the use of herbs were studied in a forest site in south east Cameroon to assess the influence of ecological factors on these resources and establish a link between environmental variables and herb availability and use by gorillas. Herbs were monitored in 250 4-m² plots to investigate possible influences of environmental factors on their availability. Nests built by gorillas were monitored during an extended period to identify the plant species used in their construction and classify them in terms of preference. Herbs of the families Marantaceae and Zingiberaceae were preferentially used by gorillas, and light seemed to be the limiting factor to plants of these families. The spatial variability in the magnitude of abiotic factors translated to spatial variations in the community structure of herbs. Environmental gradients influenced gorilla ranging patterns, as they commonly built nests and harvested their herb foods in habitats with high herb species diversity, many large-sized herb stems, more pronounced herb clumps and high herb stem density. Recently, disturbed forest areas and less-accessible swamps which are characterised by a limited visibility and a high density of herbs can play a crucial role in the ecology and conservation of gorillas as they provide abundant and clumped nest-building materials, year-round nutrient-rich herbs and natural protection from hunters. Although light appears to be an important factor for herb availability, soil properties and climatic variables potentially represent important drivers. Conservation-applied research efforts should therefore focus on issues such as the effect of climate change on gorilla plant resources and the impact of logging-induced alterations of canopy and forest soil properties on herbs.

Early Colobine Adaptations: Functional Morphology of the Elbow in *Microcolobus* from Nakali, Kenya

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Key Words: Africa, Colobinae · *Microcolobus* · Miocene · Evolution · Locomotion

Microcolobus is the earliest colobine monkey (late Miocene) represented by rich postcranial elements from Nakali, Kenya. This material is important for inferring the evolution of habitat preferences and the radiation and dispersal of early colobines from Africa to their migration and proliferation in Eurasia. In this context, we studied 6 distal humeri, 3 proximal ulnae and 5 proximal radii of *Microcolobus* from the Nakali formation in Kenya. For comparative purposes, we also examined the respective elements of fossil *Victoriapithecus* and *Mesopithecus*, and of 154 extant colobines. The fossil material was qualitatively studied and quantitatively describe through 30 linear measurements. Morphologically, *Microcolobus* resembled *Colobus* spp. and multivariate analyses placed it closer to the arboreal colobines. All were distinguished by a low distal humeral articular surface with shallow and wide facets and a medially directed epicondyle, an anteriorly oriented olecranon and low and narrow sigmoid and radial notches, and a shallow and narrow radial head with equally narrow fovea. These features suggest a mobile mainly flexed elbow with ample forearm rotations suitable for negotiating arboreal substrates. Our results indicate that colobines were initially an arboreal radiation utilizing middle Miocene African forests. Throughout its evolutionary history, this radiation shifted into different degrees of terrestriality and arboreality that enabled the exploitation of more open habitats and migrating corridors, as well as the invasion of forested patches and the rapid diversification of colobines across Asia.