

# **Abstracts of Talks**

## **Nothing endures but change: contingency as the architect of primate behaviour**

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Primate social life and behaviour might be expected to be resilient in the face of contingency at a number of levels – phylogenetic, functional and proximate. Although this contingency is often acknowledged, at least theoretically, variability in behaviour is still commonly viewed as “noise” around a central tendency, rather than as a source of information in its own right. Allied to this is a tendency to assume that a species’ response profile is adequately reflected by the behaviour observed in any single social group at any one time. An alternative view is that selection has acted on social reaction norms that encompass demographic variation both between and within populations and demes. Here, using data from baboons and vervet monkeys, we illustrate how this alternative approach can provide a more nuanced account of social structure and its relation to contingent events at the ecological, demographic and phylogenetic level. More specifically, we consider the idea that variability selection is as important to other primates as it has been to hominins.

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## **External and internal constraints in socioecology**

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The predictive value of current models designed to explain the diversity of social organizations in non-human primates is questionable. It appears necessary to reappraise the assumptions on which they are based. Evolutionary transformation depends on a balance between the respective strength of environmental pressures, i.e. external constraints, and stabilizing processes, i.e. internal constraints. The latter arise from the need of individuals to preserve the state of adaptation of their organisms and societies against potentially disruptive factors. However, socioecological models to date have focused on the action of factors such as food distribution and predation risk, thus overlooking the role of internal constraints. I will take examples from the comparative study of macaques to illustrate how internal constraints have had a pervasive influence in the evolution of their societies. These constraints can exert strong stabilizing selection, thus opposing the adaptive changes possibly required by the ecological milieu. Further theories will have to integrate both type of constraints if we hope to attain a comprehensive understanding of how primate social organization evolves.

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## **Variation in grouping patterns, agonism, and social structure: what socioecological models attempt to explain**

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Socioecological models intend to explain variation in social systems by linking ecological conditions with behavioral patterns and resulting organizational structures. Beginning with crude ecological categorizations in the 1960s these verbal models initially attempted to explain general patterns of gregariousness and mating systems. In the 1980s and 1990s predictions were added concerning food distribution, agonistic behavior, feeding competition, and resulting female social relationships and dispersal. Although a formal test across multiple species and conditions has yet to be performed, this latter model, also called the “synthetic socioecological model”, has often been considered successful. More recently, however, it has come under increased criticism suggesting that its explanatory power is limited. Here, we review available evidence for variation in primate grouping patterns and its links to ecology and compare frequency of agonism as well as female dominance relationships across primate species. One goal of this presentation is to clarify how patterns actually vary across nonhuman primates and how they are constrained phylogenetically. In addition, we test how the observed variation in agonistic behavior and social relationships fits to some of the predictions of socioecological models. Although some crucial predictor variables are (still) unavailable, these comparisons are intended to scrutinize the predictive power of the synthetic model and to search for explanations for mismatches between the model and the behavior of living primates.

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## Evolution, ecology and physiology of social flexibility

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The resilience of an individual to environmental change depends on its ability to respond adaptively. Social flexibility is such an adaptive response, whereby individuals of both sexes change their reproductive tactics facultatively in response to fluctuating environmental conditions, which can change the social system of an entire population. Few species exhibit social flexibility where individuals can switch between group- and solitary living and both sexes have alternative tactics, leading to the question why social flexibility does not occur more often. A trade-off exists between benefitting from being specialised versus benefitting from being flexible. Thus, very stable conditions favour specialisation with the costs of low flexibility, while unstable conditions favour flexibility with the cost of not achieving the highest adaptation to the specific current environmental conditions. Most species live in an environment between these two extremes. I predict that social flexibility evolves in unpredictable environments with repeated similar changes, selecting for genotypes that enable a broad reaction norm for social behaviour. Direct costs of phenotypic plasticity seem to be surprisingly low, and mechanistic constraints of social flexibility are not well understood. Physiological mechanisms of social flexibility can differ in their temporal impact: neuronal mechanisms can lead to very quick and short lasting responses, endocrine changes take longer but might also last longer, while neuro-endocrine changes are predicted to be the slowest and longest lasting mechanisms. Because hormones also have important physiological effects, this could constrain their possibilities to constrain social flexibility. Importantly, much research has not focused on endocrine regulation of social behaviour because hormones can be expected to be the most important mechanism, but because it is very easy to measure hormones. Neuroendocrine changes have been demonstrated to be very important, too, but only in a few species, as these methods are more difficult to apply. Finally, neuronal mechanisms can be expected to be very important, but are at the same time very difficult to study and poorly understood. In sum, social flexibility is regulated by physiological mechanisms and predicted to maximize individual reproductive success under changing environmental conditions.

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## **A physiological mechanism enables social bonding between non-kin, promoting flexible bonding options**

*Crockford C<sup>1</sup>, Wittig R<sup>2</sup>, Ziegler T<sup>3</sup>, Zuberbühler K<sup>1</sup> & Deschner T<sup>2</sup>*

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Mammals that maintain close social bonds with certain other group members have more surviving offspring. Although such relationships are often with kin, they also exist between non-kin. The benefit of not restricting bond partners to kin members may be that a greater range of individuals gain enhanced fitness. However, the mechanisms of how close social bonds are formed and maintained are little understood, particularly in non-kin. We examine if a physiological mechanism may promote bonding between non-kin. The 'social bonding' hormone, oxytocin, plays a crucial role in kin bonding and pair bonding across mammals and as well, leads to feelings of increased generosity and trust in unrelated humans. Previous studies show that peripheral oxytocin levels excreted in the urine relate positively to social bond strength with an interaction partner, in humans (in kin), and marmosets (in pair bonds). Using this approach in 33 wild chimpanzees, we show that urinary oxytocin was higher after kin and non-kin social bond partners had groomed compared with non-bond partners grooming, and resting controls. Also, we show that food-sharing, a controversial act in chimpanzees, raised urinary oxytocin levels and is likely to act as a bonding mechanism in chimpanzees. We argue that oxytocin is likely to represent an important mechanism through which close social bonds have evolved in non-kin.

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## **Coping with social stress: flexible modulation of heart rate in greylag geese (*Anser anser*)**

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Social contexts are among the most potent stressors, affecting individual behaviour, physiology and the immune system. However, not all members of a population are equally affected and individuals differ in their responses to stressors according to their social embedding, personality, status, sex, age, etc. Especially in species living in a complex social system, such as the greylag goose, a flexible modulation of the physiological stress response in order to optimize the investment in the social domain is to be expected. Here, we investigated heart rate (HR) responses to various social and non-social events in 25 greylag geese fitted with fully implanted sensor-transmitter packages. HR was not only modulated by physical activity, but also by psychological factors, such as motivation and emotion. The relevance of specific events, e.g. the risk of being defeated, identity of the individuals involved had a significant effect on HR in both interactions in which an individual was actively involved and interactions an individual was watching as a “bystander”. In individuals actively involved in interactions, we found post-conflict shaking and preening to be affected by the HR response during the encounter. Also, unpaired individuals showed a higher HR modulation to agonistic interactions than paired individuals. In summary, we found social events to have pronounced effects on an individual’s physiology, which may have serious consequences with respect to energy expenditure, an animal’s health or even reproductive success. Still, individuals modulated their HR response according to the relevance of single events and a secure social embedding seemed to help in coping with social stressors. Therefore, living in social groups seems potentially energetically costly for greylag geese, but the individual investment is optimized by flexible modulation of the physiological stress response according to subsequent needs and requirements.

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## **The co-evolution of a division of labour and public-goods production**

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The division of labour remains largely unexplored in the context of evolutionary biology. This is in stark contrast to economics where has been studied for almost 300 years. Where division of labour is discussed, it is often assumed that there are clear reproductive and non-reproductive castes. Despite this, division of labour applies to a wide variety of biological situations, from obvious scenarios such as parental care, specialization in vigilance or foraging tasks or the germ-soma divide. There is clearly a strong need to tie these concepts together into a coherent framework in which the evolution of a division of labour may be studied in different biological systems. Here we define what we see as a division of labour in evolutionary biology as a behaviour where a discrete type, each potentially producing a different trait, exist in a locality, and where the production of such a trait confers a benefit on a different type of individual. We show that a division of labour can easily evolve without reproductive castes. We further illustrate key issues which need to be addressed to unify the currently disparate use of division of labour in the biological literature.

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## **Hyena sociality and behavior: flexibility and constraints**

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Like many primates, spotted hyenas are large-bodied, highly mobile animals that occupy a fantastically diverse array of habitats. Their societies far more closely resemble those of baboons and other cercopithecine primates than those of any other carnivore species; like many primates, spotted hyenas regularly need to solve social problems that require knowledge of kinship, rank or past history of give-and-take. These hyenas thus live in groups that impose the same types of cognitive demands as those imposed on primates. Furthermore, relative to those of other hyena species, the brains of spotted hyenas are large, and these animals also exhibit many primate-like abilities in the domain of social cognition. These facts suggest that there has been considerable convergence between primates and spotted hyenas with respect to the selection pressures favoring the evolution of social behavior and intelligence. However, whereas social rank and reproductive success are often only loosely correlated in most primates, this correlation is very strong in spotted hyenas, and low social rank clearly imposes severe constraints on behavioral flexibility. In addition, hyenas' ability to solve problems other than social ones appears to be constrained by tendencies to perseverate and other cognitive limitations. In contrast to that of primates, the behavioral flexibility of hyenas is also limited by morphological constraints imposed by demands of feeding and locomotion. Finally, recent work suggests that brain evolution in these and other mammalian carnivores is constrained by both phylogenetic relationships and recent history. Therefore, despite remarkable convergence between spotted hyenas and cercopithecine primates with respect to sociality and social decision-making, the hyenas appear to exhibit substantially less behavioral plasticity than do primates.

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## **Personality, fitness and life history**

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The study of personality has a long tradition in psychology, but has only recently attracted attention from evolutionary biologists and ecologists. This is surprising, given that two of the main questions related to personality are also central topics of interest in evolutionary biology. The first question is related to the variance within a population: why is there so much variation in personality within natural populations? The second question is related to the limit of phenotypic plasticity: why is a given individual not able to express all the variation present in a population? Here I explore the links between variation in personality and fitness in natural populations, and discuss the limited plasticity of personality traits within a more general life history strategies framework.

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## **Behavioural reaction norms: animal personality meets individual plasticity**

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Recent studies in the field of behavioural ecology have revealed intriguing variation in behaviour within single populations. Increasing evidence suggests that individuals differ not only in their average level of behaviour displayed across a range of contexts (animal ‘personality’), but that consistent differences also exist between individuals in their degree of responsiveness to environmental variation (plasticity). These two phenomena can be considered complementary aspects of the individual phenotype. How should this complex variation be studied? Here we outline how central ideas drawn from behavioural ecology and quantitative genetics can be combined within a single framework, based on the concept of ‘behavioural reaction norms’. We illustrate this conceptual approach using empirical examples from a variety of taxa, and demonstrate the importance of studying personality and plasticity (and their potential covariance) simultaneously, both for accurate quantification of behavioural differences and when inferring their fitness consequences. This integrative approach facilitates analysis of individual differences that have traditionally been studied separately as personality and plasticity, thereby enhancing understanding of their adaptive nature.

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## **Are personality differences in a small iteroparous mammal maintained by life-history trade-offs?**

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Despite increasing interest in behavioural ecology, animal personality is still a puzzling phenomenon. Several theoretical models have been proposed to explain the maintenance of intra-individual consistency and inter-individual variation in behaviour, which have been primarily supported by qualitative data and simulation models. Here, I took an empirical approach to test predictions derived from two main life-history hypotheses. These hypotheses posit that consistent individual differences in behaviour are favoured by either a trade-off between current and future reproduction or a link between life-history productivity and personality traits. Data on life-history were collected for individuals of a natural population of grey mouse lemurs (*Microcebus murinus*) in western Madagascar. Using open field and novel object tests, I quantified variation in activity, exploration and boldness for 121 individuals over three years. As predicted by the life-history trade-off hypothesis, I found systematic variation in boldness between individuals of different residual reproductive value. First, young males with low current but high expected future fitness were less bold than older males that have high current fecundity. Second, female mouse lemurs have low variation in assets and in boldness with age. In contrast to the life-history productivity hypothesis, body condition did only explain marginal variation in behaviours related to productivity (exploration) and did not explain variation in behaviours related to survival (boldness) for both males and females. Overall, these data indicate that a trade-off between current and future reproduction might ultimately maintain personality variation in mouse lemurs and thus provide first empirical support for the life-history trade-off hypothesis.

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## Geographic variation in gorilla behavior

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The question of whether any species except humans has ‘culture’ has generated much debate, partially due to the difficulty of showing that behavioral variation exhibited in the wild is a result of social transmission and to the exclusion of ecological and genetic explanations. Nonetheless, a starting point for demonstrating the existence of culture in a species is to show that there is geographic variation in particular behavioral traits that could be due to social transmission. Gorillas live in a wide variety of habitats across Africa and they exhibit flexibility in diet, behavior, and social structure that is likely related to ecological conditions. Here we apply the ‘method of exclusion’ to look for the presence/absence of behaviors in four populations of gorillas that could be candidates for cultural traits. We compiled observations for particular behaviors from well-habituated western gorillas (*Gorilla gorilla gorilla*) at the Bai Hokou and Mondika field sites in Central African Republic and from mountain gorillas (*Gorilla beringei beringei*) at Karisoke Research Center, Rwanda and Bwindi Impenetrable National Park, Uganda. Behaviors were classified for each study site as being customary/habitual, present, absent, or absence explained by ecological factors. We present results on behaviors for which we observed variability among species and populations and consider whether they are gestures, social interactions, or object related. Results indicate that there is geographic variation in gorilla behavior that may be due to social transmission, but future detailed studies are warranted to further test this hypothesis.

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## **Social and ecological effects on gene expression**

*Tung J*

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In socially complex species, including many primates, an individual's social milieu can have profound consequences for that individual's physiology, health, and, ultimately, reproductive success. Dominance rank, for example, has been linked to differences in stress physiology, testosterone levels, and access to mates in a number of species, and social integration is an important predictor of offspring survival and lifetime mortality risk in some wild primates. Such results indicate that the nature and quality of social interactions is of substantial evolutionary significance in socially complex animals. However, the interface between variation in the social environment and variation in genes and the genome is not yet well understood. Investigating this relationship will be key to understanding the conditions under which social behavior can either constrain or facilitate evolutionary genetic change. Here, I draw on my work on baboons and rhesus macaques to illustrate several ways in which such relationships emerge. First, I review recent work on the population genetic consequences of hybridization between wild yellow baboons and anubis baboons in East Africa, and link this process of change with admixture-related behavioral effects in hybrid males. Second, I present evidence from yellow baboons that maternal dominance rank can act as a mediating environmental factor in gene-environment interactions that influence gene expression phenotypes. Finally, I discuss an experimental study of captive rhesus macaque females that demonstrates the widespread impact of an individual's own dominance rank on whole genome gene expression and DNA methylation patterns. Together, these examples illustrate that social and behavioral factors can have a direct effect on multiple aspects of variation in genes and the genome: by influencing the rate and pattern of population genetic change, by altering the phenotypic consequences of functional genetic variation, and by serving as an important environmental determinant of genome regulation.

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## **Evolutionary transitions and constraints on adaptation**

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Attempts to account for the evolution of diversity in morphological, physiological and behavioural traits as adaptations to variation in ecology have encountered the problem that distributions of many traits appear to be more closely related to variation in phylogeny than to variation in ecology. For more than thirty years, quantitative studies have controlled for phylogenetic effects but have seldom attempted to explain them. We argue that phylogenetic effects are usually a consequence of past adaptations which constrain the form and direction of subsequent evolution. Recent methodological developments (including the development of gene-based supertrees and statistical methods for identifying the correlates of transitions between traits) now make it possible to reconstruct evolutionary sequences and to explore the ecological correlates of evolutionary transitions. We illustrate this approach with recent studies of the evolution of cooperative breeding in mammals which show that the evolution of reproductive suppression and cooperation is constrained both by the form of mating systems and by contrasts in litter size and breeding frequency. We suggest that this approach will become widely used and is likely to lead to important improvements in our understanding of the distribution and evolution of interspecific differences.

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## **Phylogenetic approaches to understanding primate behavioural diversity**

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Behaviour is often thought to be an evolutionarily flexible trait, especially when compared to morphology. There is some evidence to support this claim, yet there are additional studies that show an important connection between behavioural traits and the evolutionary history of species. Examining behavioural variation in an evolutionary context has been the subject of research for several decades, yet relatively recent advances in computer technology have enabled scientists to develop rigorous analytical approaches to ask new questions. One such analytical approach is to quantify the phylogenetic signal in biological traits. When phylogenetic signal is strong, closely related species exhibit similar traits, and this biological similarity decreases as the evolutionary distance between species increases. It is also possible that some traits exhibit low levels of phylogenetic signal, with closely related species displaying distinct biological differences. In addition to quantifying trait variation in an explicitly evolutionary context, some researchers believe that measuring phylogenetic signal can provide insights into the evolutionary mechanisms producing this variation. In this talk, I will quantify the degree of phylogenetic signal in several behavioural and ecological traits across a wide range of primates. I will discuss the possible mechanisms for this evolutionary diversity and why different behavioural traits have different relationships to phylogeny. Finally, I will place these findings into the context of modern socioecological theory to (hopefully) gain a better understanding of behavioural evolution and diversity.

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**Till death do us part? – Intense sexual competition constrains tenure length in a serial monogamous, sexual monomorphic species**

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Traditionally, monogamous species have been described as showing low levels of sexual dimorphism and intra-sexual aggression. Although males and females of the genetically monogamous Azara's owl monkeys (*Aotus azarai*) are remarkably similar in body mass and physical measurements, males' canines are larger than females'. In other taxa, sex differences in canine size have been associated with intra-sexual competition leading to high variance in tenure lengths and reproductive success. We investigated factors leading to the termination of pair-bonds in owl monkeys of the Argentinean Chaco using long-term demographic and morphological data (N=14 groups, N=154 individuals). Median duration of pair-bonds was 7.7 years. There was no evidence that pair-intrinsic mechanisms terminated the bond, since broke-up pairs were as likely to have bred in the previous year as continuing pairs. Furthermore, individuals who changed partners had lower reproductive success than those that did not (7 vs. 8 offspring/10 yrs of tenure). Rather, behavioural evidence and health assessments of captured individuals indicated that serial monogamy is regulated by sporadic, but potentially very intense, bouts of intra-sexual aggression in both sexes. Ousted individuals showed significantly more scars and more ear wounds than same-aged animals still residing in their breeding group. Evictions almost invariably led to the subsequent death of the expelled individuals. We conclude that intra-sexual aggression can be intense in monogamous species with no sexual body size dimorphism. Lack of competition should therefore not be assumed automatically for monogamous and sexually monomorphic species.

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**Social flexibility in the slender mongoose – spatial groups, male associations and communal denning in a solitary carnivore**

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Some species exhibit a high degree of social plasticity, varying from solitary to group-living across their distribution range. By studying the same individuals in different social situations we can directly identify factors promoting solitary versus group-living without any confounding phylogenetic factors. Slender mongooses (*Galerella sanguinea*) are solitary foragers that show some degree of social flexibility. While single animals can be observed in about 80 % of the time, communal denning is common throughout winter months (33 % of nights), with sleeping associations of up to 5 animals. Thereby, adult females share burrows with males and independent offspring of their last litter, but not other adult females, whereas males share with adults of both sexes. Male slender mongooses occupy home ranges of several females often twice the size of females (2.2 km<sup>2</sup> vs. 0.92 km<sup>2</sup>). Some males show complete home range overlap with another male. These pairs associate regularly, sharing burrows throughout the year and form stable, amicable relationships. Both males in an association mate, though reproductive success is skewed towards the older male. Associated pairs can be related, e.g. half siblings but do not need to be. Slender mongooses, even though they live a mostly solitary lifestyle, are capable of complex social structures and interactions. Possible ecological pressures and benefits for this social flexibility, such as thermoregulation and increased reproductive success, and its behavioural consequences are discussed.

Notes:

## **Female reproductive competition in lemurs: what constrains and regulates group size?**

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In mammals with female philopatry, co-resident females inevitably compete with each other for resources or reproductive opportunities, thereby reducing the kin-selected benefits of altruism towards relatives. These counteracting forces of cooperation and competition among kin should be particularly pronounced in plurally-breeding species with limited alternative breeding opportunities outside the natal group. However, little is still known about the costs of reproductive competition on females fitness and the victims potential counter-strategies. Here we summarize long-term behavioral, demographic and genetic data collected on plurally-breeding primates from Madagascar to illuminate mechanisms and effects of female reproductive competition. In particular we focus on forcible eviction, potential reproductive restraint and female dispersal by comparing long-term data of three lemur species, Verreaux sifakas (*Propithecus verreauxi*), redfronted lemurs (*Eulemur rufifrons*) and ring-tailed lemurs (*Lemur catta*), differing in several socio-ecological traits to illuminate general constraints on (lemur) group size.

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## **Yellow-bellied marmots: insights from an emergent view of sociality**

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The yellow-bellied marmots (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory, near Crested Butte, Colorado, USA, have been under continuous study since 1962. The first four decades of the study, led by Ken Armitage, integrated demography and ecology to understand population dynamics and sociality. Over the past decade we had a natural experiment whereby the population tripled in size. Viewing sociality as an emergent process, whereby demography sets the stage for interactions between individuals that then may have consequences for group structure, we have employed social network statistics to study the causes and consequences of social interactions. We have determined that some social attributes are heritable, that social cohesion is established through age and kin structure, that well-embedded females (but not males) are less likely to disperse, and that there are a variety of fitness consequences of social attributes. Together, this integrative relationship-centered view expands on the traditional ecological model of sociality and offers a framework that can be applied to other systems.

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## **Rapid evolution of cooperation**

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Theory on the evolution of cooperation is largely based on mathematical models that assume weak selection, which means that cooperative behaviors are assumed to have vanishingly small effects on fitness. However, cooperative behaviors in nature can have very pronounced fitness effects. This is for instance demonstrated by the enormous impact of social bonds on infant and adult survival in baboons. We used an evolutionary agent-based model to investigate potential effects of rapid evolutionary dynamics that are created by strong selection pressures. The model assumes group-living individuals with female philopatry and male dispersal. We focus on cooperation in females, which is implemented as a costly behavior that benefits all other female group members. Our results show that compared to weak selection, strong selection decreases assortment of cooperators and defectors when cooperators are rare. In contrast, when cooperators are common strong selection increases assortment. Because assortment is a crucial determinant for the evolution of cooperation, strong selection creates a feedback between assortment and evolutionary dynamics. Because of this feedback, more costly cooperative behaviors can be sustained than expected for weak selection. However, this effect only emerges when cooperators are common. When cooperators are rare we found the opposite effect, which makes it more difficult to evolve costly cooperation in a population of defectors. This finding suggests that in many cases the evolution of cooperation could be more strongly constrained than previously anticipated. In addition, our findings emphasize the importance of exploring how evolutionary dynamics feed back on interaction patterns among individuals.

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## **A demographically explicit model of primate social evolution: what the socioecological model cannot explain**

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To explain the evolution of sociality in primates, primatologists generally rely on verbal arguments collectively known as the socioecological model. This model has recently been criticized for leaving much variation in primate social organization unexplained. We present a game-theoretical model for the evolution of group-formation among non-relatives, focusing specifically on multi-male associations in primates. We adopt a demographically explicit approach which allows for feedbacks between individual behaviour and population dynamics. We show that the rates of births and deaths as well as the dispersal decisions of individuals in the population determine the turnover rate of territories and, hence, the competition for breeding vacancies. Vital rates, such as fecundity and mortality, can thus have profound effects on the evolution of group-living. We show, however, that this effect also depends on whether and how individuals benefit from group-living. While some of our predictions are in accordance with the socioecological model, our model better than the former explains the great flexibility of primate social organization. Moreover, because vital rates are affected both by environmental factors as well as by life-history traits, we also hope to shed light on the debate of how adaptive or phylogenetically inert primate social behaviour can be.

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## **Flexibility and constraints: decision making in African elephant social networks**

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For large mammals, such as elephants, occupying extensive ranges with fine and coarse grained habitats as well as dynamic social encounters, associations represent strategic solutions to maximise reproduction and foraging, as well as protection from predation. African elephants live in multi-tiered social networks; the average female finds herself associating with between 2 and 500 other individuals on a daily or even hourly basis. Males, while less frequently in such large aggregations, have constant male associates (friends) and move between female groups to mate. These social networks can be examined over the very long-term (1973-2008) in an individually known population of ~1200 elephants in Amboseli, southern Kenya. We present data on the flexible nature of female groups in relation to opportunities for aggregation or constraints on grouping represented as decisions to remain in small parties. We explore the nature of male decisions to move among female groups, or to associate with other males in bull areas. While not examining the cognitive basis for decision making with regards associations, the patterns that are suggestive of clear choices and we explore those factors (friendship, leadership, age and knowledge) that structure these associations.

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## **Simple rules of leadership emerging on the move *or*: Do humans swarm?**

*Boos M, Pritz J & Belz M*

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Are simple rules of swarming behavior applicable to humans? To what extent in human behavior, without any communication and with perception constrained to a local radius, (1) can directional group movement emerge and (2) can a minority influence this direction? Following Reynolds' (1987) flocking model and Couzin et al.'s (2005) simulation in which a minority with a preferred goal can lead an undecided majority, we apply a computer-based multi-client game that excludes any communication other than by movement. Human players are represented visually on a common virtual playfield. Modeled after economic games, we use monetary incentives to motivate game participants to move in directions and to reach goals. We show that a minority can lead a majority without any verbal or non-verbal signaling other than movement, even with limited perception of the players. We also identify a movement pattern predicting the success rate of the informed minority to influence the majority towards a goal by: (a) using similar movement paths, (b) taking the shortest possible path towards the goal, and (c) moving with fast and constant velocity. Our approach provides empirical evidence that humans need not use their advanced cognitive abilities and their complex interpersonal communication to coordinate their behavior. Simple characteristics of locomotor behavior suffice for a minority to gain the lead over a majority towards a goal.

Notes:

## **The neurogenetics of sociality: examining a functional role for V1a receptor genetic diversity**

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Social behavior is remarkably diverse both within and between species. While the expression of neuropeptide hormones that guide these behaviors tends to be phylogenetically conserved, remarkable differences exist in neuropeptide receptor patterns even in closely related species. Further, receptor expression often differs among individuals within a species, and both species differences and individual variation in expression patterns have been linked to natural variation in social behaviors. As such, we hypothesize that phylogenetic plasticity in the regulation of neuropeptide receptor expression is a major driving force in the evolution of behavior patterns. To illuminate genetic mechanisms contributing to both species differences and individual variation in neuropeptide receptor expression, we studied the roles of the proximal 5' flanking region and highly variable microsatellite element in the vasopressin receptor 1a gene (*Avpr1a*). We created three lines of knock-in mice in which 3.5 kb of the mouse *Avpr1a* 5' flanking region was replaced by prairie vole sequence, but each line differed only with regard to the microsatellite element – either from meadow vole or the prairie vole long or prairie vole short variants. We hypothesized that all of the mouse lines would express V1a receptors in a pattern more similar to prairie voles than mice. We further hypothesized that the meadow vole and prairie lines would show more robust differences in expression than the prairie vole long versus short lines. Contrary to our prediction, the expression pattern of V1a receptors was largely consistent with wildtype mice in all three lines, suggesting that the profound species differences are conferred by mechanisms distal to the proximal 5' flanking region. However, our data confirmed that both species differences and intra-species variation in microsatellite structure contribute to variation in gene expression. Mice with the prairie vole microsatellites had higher levels of V1aR in the thalamus, central amygdala, and dentate gyrus, compared to the mice with meadow vole microsatellite. These differences are consistent with those observed between prairie and meadow voles. Furthermore, comparison of mouse lines with long and short versions of the prairie microsatellite revealed differences in levels of V1a in the dentate gyrus. These observations suggest that while microsatellite variation is not likely to contribute to global species differences in expression patterns, it does produce quantitative changes in expression in selected brain regions, consistent with the hypothesis that highly mutable microsatellites may serve as evolutionary "tuning knobs" to produce variation in expression that may be functionally relevant. In parallel, phylogenetic studies also suggest that similar mechanisms may be relevant to in both human and non-human primates.

Notes:

## **The social modulation of behavioural development in rodents**

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Individual differences in behavioural profile develop during ontogeny. Using a comparative approach, this contribution focuses on the role of the social environment for the modulation of behavioural profile in rodents during early phases of life and adolescence. For gregarious species, the stability of the social environment in which the pregnant and lactating female lives is of major importance for foetal brain development and the behavioural profile of the offspring in later life. Social instability during these critical periods of development generally brings about a behavioural and neuroendocrine masculinisation in daughters and a less pronounced expression of male-typical traits in sons. Moreover, when mothers live in a socially threatening world during this time, anxiety-like behaviour of their offspring often is elevated in adulthood. These effects of the social environment are likely to be mediated by maternal hormones and/or maternal behaviour. In addition, they can be modulated significantly by offspring genotype. The behavioural effects of social stress during this phase of life are not necessarily pathological (nonadaptive) consequences or constraints of adverse social conditions. Rather, mothers could be adjusting the offspring to their environment in an adaptive way. Adolescence is another period in which behavioural development is particularly susceptible to social influences. There is some evidence that social experiences at this time alter and canalize behaviour and endocrine stress responses in an adaptive fashion, so that earlier influences on behavioural profile development can be complemented and readjusted, if necessary, to meet current environmental conditions. In terms of underlying neuroendocrine mechanism, a central role for the interaction of testosterone and stress hormones is suggested. In summary the social modulation of behavioural profiles from the prenatal phase through adolescence appears to represent an effective epigenetic mechanism for repeated and rapid adaptation.

Notes:

## **Brain size and the limits to behavioral flexibility in mammals**

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Developmental plasticity in behavior, generally called *flexibility*, is reflected in the capacity for individual learning ability, including innovativeness, and for socially acquiring cultural variants. This flexibility allows populations to adapt to ecological and social conditions that vary in space and time. I will illustrate flexibility in orangutans by showing that the extensive geographic variation in behavioral ecology, social organization and cultural variants seen in this taxon is achieved through behavioral flexibility of both the individual and cultural variety rather than developmentally canalized genetic adaptations. However, extensive comparative data suggest that the distribution across species in flexibility is limited by brain size. Here, I review recent comparative studies in birds and mammals that together show support for the expensive brain framework. Thus, we see larger brains can evolve in species where individuals receive energy subsidies as immatures that need to learn vital skills or share food as adults, where they can circumvent seasonal or irregular food shortages, or can reduce mortality through cognitive means, which allows them to reallocate energy away from production (i.e. growth and reproduction), and slow down their pace of life history. These broad patterns show that aspects of behavioral ecology, social organization and the external environment limit the opportunities for the evolution of behavioral flexibility. In conclusion, only taxa able to overcome limitations on brain size increases can afford to evolve behavioral flexibility. This flexibility, however, leads to reduced *demographic flexibility*, which may increase eventual risk of extinction and compromises the ability to adapt genetically to dramatic environmental change.

Notes:

## **Behavioural flexibility in a planning task: comparing chimpanzees and long-tailed macaques**

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Mental time travel, the capacity to disconnect from the present and remember past events or project expectations into the future, has long been considered uniquely human. Recent evidence, however, indicates that also some animal species are capable to pass tests of episodic-like memory and planning. We tested planning capacities in chimpanzees and in long-tailed macaques. Whereas chimpanzees were able to pass the task when presented, long-tailed macaques showed a much poorer performance, even on a simplified task. Only after training were the macaques able to pass the task. This difference in performance is probably related to species differences in their ability to combine information spontaneously.

Notes:

## **A delay in synaptic maturation in the human cortex that might underlie increased learning abilities**

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The mammalian brain shows strong plasticity during postnatal development, with synaptogenesis and subsequent synaptic pruning guided by environmental cues. These processes underlie the rapid learning abilities observed in infants. Evolutionarily, extending this period of neural plasticity could provide an effective way for expanding the learning capacity for a species. Early neuroanatomical studies had noticed that the peak of synaptic density in the human prefrontal cortex (PFC), compared to that in the macaque PFC or in the human visual cortex, appears later in development. Here we studied this phenomenon across human, chimpanzee and macaque postnatal development using gene expression and metabolite profiling. We find that synaptic maturation in the human PFC is significantly delayed compared to not only macaques, but also chimpanzees. A delay of this magnitude is unmatched by developmental processes in the cerebellar cortex, or by other molecular pathways in the PFC. Using computational analysis, we predict that this extreme delay was driven by a number of key regulator genes, including a known regulator of synaptic development – MEF2A. Finally, analyzing human polymorphism data, we detect a signal of positive selection upstream of MEF2A, implying that a change in MEF2A expression profile had adaptive significance in humans. Furthermore, the data suggest this modification occurred after humans split from Neanderthals. We hypothesize that one or few modifications in key regulators of synaptic development arose recently and altered the timing of this process in humans, leading to superior learning capacities in human infants.

Notes:

**Diagnostic reasoning in long-tailed macaques (*Macaca fascicularis*)  
– limitations and constraints**

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Causal reasoning is a central cognitive competency and is required for diagnostic reasoning about unobserved information based on observable evidence. This ability increases flexibility, but presumably comes at a cost through an increase in required processing power, which may set limits to animals reasoning. Little is known about diagnostic reasoning in non-human primates and probing the limits of these skills may provide important information about the evolution of animal intelligence. Here, we investigated diagnostic reasoning in long-tailed macaques: subjects were confronted with choice tasks in which a reward was hidden underneath one of several hiding objects (e.g. cups, boards). Hiding the reward under a board that had been lying flat on the ground leads to an inclination of the board, and the presence or absence of an inclination could thus be used to infer the presence of the reward. However, we also included an inclined board resting visibly on a wooden block. In this case, the inclination was not indicative of the presence of the reward. The subjects received a series of tasks with varying degrees of complexity, i.e. we modified the number of objects and the number of actions the subjects had to track before making a choice. We found that the macaques performance was dependent on the level of complexity, as the subjects were not successful in all tasks, thereby outlining the limits of diagnostic reasoning in long-tailed macaques.

Notes:

## **Cognitive constraints in primates**

*Call J*

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Primates display considerable behavioral adaptability to changes both in the ecological and social environments. A considerable amount of work in the laboratory has been devoted to investigating the motivational and cognitive factors that either promote or prevent behavioral change, typically in the context of learning and problem solving situations. More recently, researchers have been attempting to relate that body of research with the socio-ecological factors that may have shaped the evolution of those tendencies. In this talk I will present several of the so-called constraints on flexibility and attempt to relate their existence to various socioecological factors.

Notes:

## **Social constraints on trial-and-error learning in raiding chacma baboons from the Cape Peninsula, South Africa**

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As a result of their exposure to natural, agricultural and urban environments, Chacma baboons in the Cape Peninsula exhibit considerable behavioural flexibility. Of particular interest is behaviour relating to urban environments, i.e. using roofs as sleeping sites, opening car doors and utilising a variety of human food sources (raiding). Raiding troops show large dispersion patterns and even raid nocturnally in the absence of natural predators. Waste containers (rubbish bins) are a major target of this raiding. Three versions of these containers occur in baboon home ranges: unmodified (easy to open), latched (requires manipulation) and locked (cannot be opened). We investigated the ability and speed with which baboons learnt to open latched containers. We predicted that dominant males would have priority of access to the containers, obtain the majority of food items therein and learn to open latches first. While dominant males did arrive first and monopolised the container food resources, they quickly lost interest in latched or locked containers. In contrast, sub-adult males showed willingness to test the latched containers for prolonged periods even in the absence of food rewards. It is these sub-adult males that first learnt to open latched containers. As expected females rarely enjoyed priority of access and did not show the willingness of sub-adult males to manipulate unprofitable containers. Thus, while free-ranging adult male and female baboons may be sufficiently dexterous and intelligent to open latched containers, social constraints deny them the free time that sub-adult males are afforded and they may therefore be slower in completing similar trial-and-error learning tasks.

Notes:

## Friendship in male macaques

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It is currently being debated whether animals have evolved social relationships equivalent to human friendships. Critics have questioned the existence of animal friendships arguing that cognitive constraints keep animals from prospectively managing enduring, long-term social bonds and suggested instead that animals flexibly choose social partners based on their current needs. With others we argue that partner choice may be based neither on current needs nor on expected future return but on a dyad shared history. Here we aim at investigating whether a) close social bonds of dispersing male macaques can be stable over several years, b) behaviors widely separated in time are linked by the individuals memories of past events, i.e. an implicit recognition of their social bond, and c) the symmetry of a dyad grooming exchanges is related to rank differences. We will present data from a longterm study on wild Assamese macaques from Phu Khieo Wildlife Sanctuary, Thailand and on semi-free ranging Barbary macaques from Affenberg Salem, Germany. Male Assamese macaques formed differentiated social bonds that were as stable as those of female baboons and persisted as long as four consecutive mating seasons. Partner choice for cooperation in agonistic coalitions against other males was predicted by affiliation patterns expressed several weeks earlier after controlling for current affiliation. Symmetry in grooming exchanges was not related to symmetry in dominance but increased with the strength of the social bond if the number of grooming interactions was held constant. We conclude that like female baboons and male chimpanzees male macaques form friendships.

Notes:

## **Evolutionary constraints on coalitionary behavior: insights from primate males**

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The benefits of coalitionary behavior seem ubiquitous, raising the question why this behavior is limited in its taxonomic distribution. In some primate species, males commonly form coalitions against other males to increase their reproductive success, however this behavior seems to be rare or absent in many other species. Coalitionary behavior has been hypothesized to be constrained by various factors such as brain size, degree of arboreality and group size, but the relative importance of these factors for primate males remains unknown. Here, we present the results of the first extensive survey on male coalitions in primates, based on a comprehensive review of published literature and a questionnaire sent to a large number of field researchers. Our results show that the ability to perform coalitionary behavior (defined as a joint aggression between two or more adult males against another adult male group member) is much more widespread across primates than previously anticipated. However, in most coalitionary forming taxa this behavior was reported as rare or extremely rare. Phylogenetic analyses revealed that average male group size but not brain size or degree of arboreality, act as an important constraint for the frequency of coalitionary behavior, with coalitions being more common in species with larger male group size. The finding that coalitionary behavior is observed under different ecological conditions and that it is independent of brain size suggests that this behavior is much less constraint than previously thought.

Notes:

## **Behavioural flexibility to climate change within the constraints of a multi-species community**

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Long term survival of animal species depends on their ability to adapt to a changing environment through a change in behaviour, diet or habitat use. Such adaptations are constrained by the presence of ecologically similar species that exploit alternative niches. Therefore, to understand how climate change will affect species biodiversity and distribution we need to understand the negative and positive impacts of sympatric species in multi-species communities on survival of individual species. We developed a model in which we use climate as an indicator for vegetation and time budgets as an indicator for inter-/intra-specific competition and ecological stress. The model shows us how flexible the species are in their behavioural responses to variations in climate. The model predicts maximum ecologically tolerable group sizes under varying climatic conditions and community structures. The genus used is *Cercopithecus*, which occurs in both multi-species and single-species communities throughout Africa. Rainfall, temperature, diet, group size and body mass were important predictors of *Cercopithecus* time budgets. The time spent moving was flexibly adapted to adjust for the presence of other *Cercopithecus* species, suggesting that there is significant inter-specific competition. Our analyses shows that *Cercopithecus* achieves much higher densities by forming multi-species communities than it would in single-species communities thanks to small inter-specific differences in niche occupation and behaviour. The modelling approach allows us to identify exactly which behaviour is affected by living in a community that fissions and fuses into single species-groups and how behavioural flexibility can help these species cope with climate change.

Notes:

## **Dealing with a changing world: can behavioural flexibility save apes from the effects of climate change?**

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Primates are known for their behavioural flexibility and their ability to adapt to new environments. This allows some species to survive in habitats that are undergoing significant changes, often based on human activities. In this study we use a modelling approach in order to assess if primate behavioural flexibility can buffer them against the effects of climate change. We use a time budgets model, to predict African ape distribution under a uniform worst-case climate change scenario and assess how behavioural flexibility in terms for grouping patterns and diet composition affects ape group sizes. We found that chimpanzees appear to have already exploited most of their capacity for flexibility, and so fissioning into even smaller parties and/or changing dietary patterns would hardly have any effect on their group sizes. Gorillas, on the other hand, could benefit from splitting into parties and/or adopting a more frugivorous diet, as this would allow them to increase their group size. As expected we found that the worst-case global warming scenario is likely to significantly alter the delicate balance between different time budget components, thereby changing ape distribution patterns, especially for gorillas. Our simulations further indicate that gorillas are to some extent buffered against these effects if they can respond flexibly in terms of diet composition and grouping patterns. Thus, behavioural flexibility may offer apes new survival prospects in a fast changing environment.

Notes:

# **Abstracts of Posters**

## **Physiological plasticity, energy saving, and resilience to environmental hazards**

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\*presenting author

Vertebrates seem to largely compensate global changes by phenotypic plasticity. However, the mechanisms that allow such plastic phenotypic adjustments are rarely identified. We present a summary of our work on the role of torpor flexibility (a plastic energy saving mechanism) in the adaptive response to environmental hazards. For secondary consumers, global changes may largely result in unpredictable fluctuations in food availability. A large number of organisms that evolved in energetically limiting, highly seasonal, and poorly predictable environments, developed efficient energy saving mechanisms to overcome food unpredictability. We used calorie restriction experiments on a small Malagasy primate, the grey mouse lemur, to address two questions: (i) to which extent is the use of daily torpor flexible, and can it be adjusted to compensate a food shortage? (ii) Is this flexibility adaptive? If not, what could be the constraints? We show that (i) the passive part of torpor (body temperature drop) is highly flexible, being adjusted after only a few days of food shortage. This flexibility is reinforced by former exposure to moderate food shortage (acclimation effect). (ii) Stable performances suggest that this flexibility is adaptive for moderate food shortage. However, in the case of parasitic aggression, the pyrogenic, innate immune response is maintained despite food shortage. It indicates that energy allocation between competing traits may limit the efficiency of torpor-based energy saving.

Notes:

**Flexibility in the mating strategies of male olive baboons (*Papio hamadryas anubis*): routes used by males of differing dominance rank**

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Recent studies suggest the evolutionary significance of alternative mating strategies in explaining male reproductive success. We focused on a proposed alternative male mating strategy in olive baboons (*Papio hamadryas anubis*), called “following”, in which 1-8 males maintain proximity to and coordinate their activities with a consorting pair. Two groups of habituated olive baboons were observed in Kenya from September 2009 to July 2010. We describe the behavior of males of differing dominance ranks surrounding 100 observed consort takeovers (72 by followers, remaining 28 by non-followers). Takeovers by high- and mid-ranking males involved following as a strategy more often (87 and 80 % of takeovers, respectively) than takeovers by low-ranking males (56 %). High-ranking males had a higher proportion of following episodes resulting in a takeover than did low-ranking males; mid-ranking males were intermediate (Kruskal-Wallis  $H=8.043$ ,  $a=3$ ,  $p=0.0179$ ; Dunn’s Multiple Comparison Test  $p<0.05$ ). Both follower and nonfollower males used four tactics to affect a consort takeover: solo challenge, coalitionary challenge with another male, and exploitation of both an abandoned consort female and another male’s challenge. Only low- and mid-ranking males used the coalitionary challenge route ( $\chi^2$ ,  $df=2$ ,  $0.01>p>0.05$ ), and a majority of solo challenges were by high-ranking males ( $\chi^2$ ,  $df=2$ ,  $0.05>p>0.001$ ). Notably, a majority of both these takeover types were by followers (89 and 94 %, respectively). As primates are known for displaying a higher degree of behavioral flexibility than the taxa underlying the foundation of alternative strategy theory, our understanding of such strategies improves existing models.

Notes:

**Context-dependant dispersal and fine-scale relatedness structure in a solitary rodent, the eastern chipmunks (*Tamias striatus*)**

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Solitary species do not form distinct kin groups, however, an increasing number of studies shows that relatedness is important for shaping the spatial distribution of individuals in a population. However, few studies have assessed the flexibility of the social and relatedness structure of solitary species under variable environments. We studied the impact of environmental conditions on the spatial distribution of related individuals in a wild eastern chipmunk population (*Tamias striatus*), a solitary rodent of North America. Eastern chipmunks depend on the seeds of masting trees for their reproduction and survival and synchronize their reproductive events with seed production. We combined the analysis of the spatial genetic structure of adults with direct estimates of juvenile dispersal distance during six contrasted years with different dispersal seasons, population sizes and seed production. We found that seed production, dispersal season and sex affected juvenile dispersal distances. These effects were detectable through the fine-scale spatial genetic structure of adult females. We also found a constant difference in spatial genetic structure between males and females that was representative of male biased dispersal behaviour. This study suggests that environmental conditions can shape the fine-scale relatedness and social structure of females even in the absence of strong natal philopatry and cooperation among individuals.

Notes:

**A comparative study of vocal complexity in wild chacma baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*)**

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Comparative research suggests that mammalian species living in complex social groups benefit from having complex vocal repertoires. Yet, while the function of vocal complexity in ecological contexts is clear, less is known about the function of vocal complexity in social contexts. If social interactions drive the evolution of vocal complexity, calls used in affiliative social contexts may be particularly varied in socially complex species as they may help maintain social cohesion in a variety of social contexts. To test this hypothesis, we take advantage of the contrasting social systems of two closely related terrestrial primate species chacma baboons (*Papio ursinus*) and geladas (*Theropithecus gelada*) to investigate the social elements that may influence complex primate vocal behaviour. We predict that geladas, which live in a unique multi-level fission-fusion society, (a) will produce more distinct affiliative call types relative to other calls in their repertoires and (b) will utilize affiliative calls more frequently than chacma baboons, which live in relatively static multi-male multi-female social groups. To test these hypotheses, we analysed vocalisations (chacma = 259 calls; gelada = 443 calls) and focal observations (chacma = 560 h; gelada = 582 h) from geladas living in the Simien Mountains National Park and chacma baboons from the Okavango Delta of Botswana. Preliminary results suggest that geladas call at a lesser rate than chacmas but have a larger repertoire of calls used in affiliative contexts. Our results support a causal connection between the nature of social interactions and vocal complexity in primates.

Notes:

## **Hormonal correlates of socio-sexual behaviors in female mountain gorillas**

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Reproductive strategies of female mountain gorillas remain poorly understood. Given that female gorillas disperse between social units, it has been assumed that mate choice by females occurs primarily in the form of choice of the group, yet there is evidence that mate choice is not so simple in gorillas, especially in multimale groups. Indeed, females mate with more than one male, even on the same day. As is the case with many other primate species, females do not mate only at the likely time of conception, but also while pregnant, possibly as a means to confuse paternity. Finally, males may use coercive behavior (aggression) as a method of mating courtship, even in one-male groups where there is no competition among males. To understand female reproductive strategies, it is necessary to consider patterns of copulations not only in relation to mating solicitations and aggression from males, but also with the knowledge of the reproductive status of the females. However, only one preliminary study with a very limited data set has used hormone analysis and found that the time of ovulation coincides with the 1-2 day period of behavioral estrus. To better understand reproductive strategies of female mountain gorillas, we conducted a broad study in eight gorillas groups monitored by Karisoke Research Center in Rwanda. On a daily basis, we collected behaviors, urine and fecal samples from the focal individuals. In total, we collected 3667 urine samples and 3918 fecal samples of 22 females over the course of approximately 82 cycles. Behavioral observations included copulations, solicitations and aggressions. Here we present the first results on immunoassay validations as well as on behavioral patterns in relation to the timing of ovulation.

Notes:

**Personality traits influence levels of parasite infection in grey mouse lemurs (*Microcebus murinus*)**

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Animal personality, i.e. consistent inter-individual differences in behaviour, influence the ways in which individuals interact with their environment. Recently, it has been suggested that the evolution of animal personality may in part be driven by the differential risk of parasite infection between personality types. For instance, traits such as activity, exploration and boldness towards novel objects may affect the rate at which an individual comes into contact with infectious stages of parasites. However, empirical evidence for the relationship between host personality and level of parasitism experienced is still scarce. The aim of this preliminary study was to test whether more proactive individuals of a natural population of grey mouse lemurs (*Microcebus murinus*) have a higher parasite infection risk. Using repeated open-field and novel object tests, we quantified variation in activity, exploration and boldness for 47 individuals. Intestinal parasite loads of the same individuals were evaluated via repeated faecal egg counts that allowed us to quantify parasite prevalence, intensity and helminth genus richness. After controlling for animal age and ecological season, helminth prevalence and the total intensity of infection were found to be greater for individuals that showed higher levels of activity and exploration and rated higher in boldness. Helminth genus richness was positively correlated with the individual activity and exploration score and a nearly significant association with boldness was found. Overall, these preliminary results imply that personality traits can indeed have an influence on the level of parasitism an individual experiences and may therefore have fitness consequences in natural populations.

Notes:

## **Rank effects on feeding behaviour and energy intake in wild female Assamese macaques**

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The effects of female dominance rank on energy intake are discussed as part of a larger study on food resource characteristics, feeding behaviour, competition, fitness, and social structure in wild Assamese macaques (*Macaca assamensis*). Because competitive regimes are alleged to differ in the way they affect individual foraging efficiency the relationship between rank and energy intake can be used as an indication of the mode and strength of the competition individuals experience which ultimately affects female social structure. Over 3000 hours of focal animal data were collected during two one year periods (October 2007 - September 2008 and Mai 2010 - April 2011), including all adult female members (N=12, and N=15, respectively) of a group of wild Assamese macaques at Phu Khieo Wildlife Sanctuary in north-eastern Thailand. Item specific feeding times were combined with information on bite rates, bite weights and nutritional content of important food items to calculate the gross energy intake per female. In addition monthly information on forest phenology (including up to 650 trees) was used to assess seasonal patterns in food availability and the manner in which this affects the intensity of feeding competition. First analyses suggest that energy intake is largely independent of food availability and positively related to dominance rank. This indication of strong within group contest competition for food suggests that the adaptive benefit of acquiring and maintaining a high dominance rank accrues from priority of access to high quality food resources.

Notes:

## **Cortisol in mother milk shapes the coordinated development of behavior and physiology**

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Glucocorticoids in mother's milk have been associated with infant behavioral phenotype in rodents, macaques, and humans presumably by shaping the HPA axis. However infant behavioral activity budgets are necessarily constrained by available energy. Cortisol, usually thought of only in the context of stress physiology, is actually a metabolic hormone that ties together both of these perspectives. Energy utilization and the metabolic function of cortisol become particularly critical during challenging conditions, e.g. nutritional stress, predator encounters, and social conflicts – the same environmental conditions that have been implicated in the development of behavioral phenotype. We hypothesize that behavioral phenotype is organized in concert with the metabolism by energetic conditions during early development. We will expand upon our previous findings that milk energy is correlated with milk cortisol and predicts infant behavioral phenotype, using a larger sample of rhesus macaque mother-infant dyads (N=113) from the California National Primate Research Center. Here we show that changes in milk cortisol across lactation precipitate changes in infant growth velocity after controlling for maternal and infant covariates (model  $\text{adj}R^2=0.3$ ,  $p<0.0001$ ). In adulthood the HPA axis, metabolism, and behavior do not exist apart from one another. Here we present a synthesis of emerging evidence that suggests that the organization of these interconnected systems is likely shaped, in part, by mother's milk during ontogeny.

Notes:

**Ecological and anthropogenic influences on the distribution and conservation of cross river gorillas (*Gorilla gorilla diehli*) in Nigeria**

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The distribution of endangered species is influenced by both ecological conditions and levels of anthropogenic disturbance. Cross River gorillas (*Gorilla gorilla diehli*) occur in the most northwestern region of the four subspecies of gorillas and their habitat differs in many respects from that of other gorilla populations. The population is small (~ 300 gorillas) and their habitat is highly fragmented. In many cases large areas of forest unoccupied by gorillas are interspersed between the locations where gorillas do occur. These areas could potentially support a much larger gorilla population, but the suitability of the habitat is unknown. In particular, the influence of ecological factors (such as food availability) in relation to anthropogenic factors on the distribution of the gorillas and their habitat utilization is poorly understood and limits our knowledge about how currently unoccupied areas could be utilized as the population potentially expands. Surveys of three protected areas in Nigeria were conducted to assess gorilla food distribution and levels of anthropogenic disturbance in areas occupied by gorillas and areas currently not used by gorillas. A total of 380 vegetation plots spaced 1.5 km apart were surveyed and over 400 km of guided reconnaissance transects covered over a total area of c. 1000 km<sup>2</sup>. A socio-economic survey of 12 communities neighbouring gorilla habitat was also conducted to examine how local culture and economics influence occurrence of illegal activities. Data from these surveys will be combined with remotely-sensed data to model Cross River gorilla habitat suitability. Data analysis is currently underway.

Notes:

## **Benefits of male sociality and cooperation in Madagascar's largest carnivore**

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Male sociality and cooperation is found in only a few carnivore species and have been attributed to benefits such as territory defense or enhanced access to females through advantages in contest with other males. In fosas (*Cryptoprocta ferox*, Eupleridae), both solitary males and associations of two or three individuals co-exist within a single population. We studied wild fosas in Kirindy Forest, Madagascar to quantify benefits of male sociality in this species. We found that associated males gained higher body mass and size than solitary males, and that sexual dimorphism was developed by associated males only. Associated males inhabited ranges which were twice as large but did not travel more in a day compared to solitary males, indicating higher foraging efficiency. Dietary comparison based on stable carbon and nitrogen analyses revealed that associated males manage to take down larger and more agile prey than solitary males. Anecdotal observation and dynamic body accelerometry of simultaneously tracked individuals revealed that this was most likely due to cooperative hunting by associated males. In the context of mating, associated males achieved higher mating success, which was determined by their higher body mass and related advantage in male contest competition. Our results indicate that enhanced access to food resources by cooperative hunting is a key to physical competitiveness in fosas. We argue that male sociality must not be limited to joint defense of territory and females, but that cooperation in food acquisition can be highly beneficial in sexually dimorphic species.

Notes:

**The effect of rank on the structure of social relationships among female Assamese macaques (*Macaca assamensis*)**

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Analysis of wild female baboons has shown that the strength of a female social relationships is strongly related to indicators of her long-term fitness, i.e. infant survival and life expectancy, independent of her rank. This has led to the suggestion that social relationships may provide females with a means of compensating for the constraints their lifelong rank position has on their overall fitness. We investigated the role of rank and sociality in wild female Assamese macaques at Phu Khieo Wildlife Sanctuary, Thailand. Over 2000 hours of data were collected over one year from all the adult females (N=15) of one social group. Data collection included focal, continuous and ad libitum sampling as well as daily group scans. A combination of traditional and more recently available social network analysis measures were used to provide a detailed overview of the structure of female social relationships and to understand what effect, if any, rank has on these structures. Initial analysis indicates that while rank had a significant effect on who an individual interacted with it had no effect on the number of strong social relationships a female formed. Also rank had no influence on measures of an individual structural importance and cohesiveness within the female social network. These results indicate that female social relationships in Assamese macaques function independently of their dominance system and therefore provide further support for the theory that females may use their social relationships as a means to compensate for constraints placed upon them by their fixed rank positions.

Notes:

## **Social knowledge in a fluid, multi-level society: a case study of male Guinea baboons (*Papio papio*)**

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Many group-living animals, such as primates, are known to produce individually distinctive calls and distinguish between familiar and unfamiliar individuals. Primates who live in large, fluid societies are faced with various social partners, which requires the recognition of a high number of individual call variations, compared to animals living in smaller, stable groups. In the present study we used playback experiments to test for recognition of group membership in male Guinea baboons (*Papio papio*). These baboons live in large fission-fusion societies and exhibit a multi-level social organization. The basic level of the Guinea baboon society is the party, composed of two to three males, several females and their offspring. Two to three parties (= gang) may travel and forage together and may eventually aggregate into larger groups (= community). Males exhibit a notable amount of socio-positive interactions, primarily with males of their own gang, and are highly tolerant towards each other. By presenting male approach grunts from males of the same, neighbouring and strange gangs, respectively, we examined the males responses in relation to different social levels of the Guinea baboons society. Males showed a significantly stronger response to calls of males of their own gang compared to males of strange gangs and neighbouring gangs. However, the response to males of neighbouring gangs varied among individuals. Our results indicate that recognition abilities of male Guinea baboons may be based on social familiarity and that males are able to keep track of individuals they are regularly interacting with.

Notes:

**Cognitive performances are improved in response to a chronic nutritional constraint in middle-aged primates (*Microcebus murinus*)**

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Impairments in both physiological and behavioural states are increasing with aging in most mammals, which probably constrain their ability to adjust their behaviour to environmental variations. The chronic caloric restriction (CR) retards aging processes by increasing longevity, reducing pathology and maintaining physiological functions. Among the aged-related decrements, the cognitive decline appears to be a strong predictive marker to evaluate aging but little is known about possible slowing effect of such a restrictive diet on age-related cognitive impairments. We present the only results available on cognitive performances in response to a nutritional constraint through age in a primate. Mouse lemurs were assigned at adult age (3 years) to two different groups: a control (CTL) one fed *ad libitum* (N=16) and a CR one fed 70 % of the CTL caloric intake (N=16). Cognitive performances: emotional memory, spatial memory, exploratory behaviour and anxiety, and motor performances were evaluated at 4, 5 and 6 years. Signs of aging in CTL and CR animals were detected at the motor test: the performances decreased with age, independent of treatment. Emotional memory was drastically affected by age in CTL animals, while CR animals maintained high performances even at 6 years of age. CR treatment induced a transient deficit in spatial memory but this negative effect was reversed after 1 year of treatment. Anxiety significantly decreased with time in both groups. These first outcomes provided evidences of the beneficial effects of a chronic nutritional constraint on specific mnesic functions independent of motor decline in a primate through age.

Notes:

## **The pro-social behaviour of intolerant primate species**

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Pro-sociality was considered uniquely human, yet has recently been shown in several animal species too. Its evolution is attributed to cooperative breeding and tolerance. However, in an experiment, we demonstrated that also non-cooperative breeding, despotic long-tailed macaques can be pro-social, especially towards kin. Moreover, dominance rank determined pro-social behaviour in an unexpected way; high-ranking individuals grant, while low-ranking individuals withhold their partner access to food. Thus, pro-social behaviour is not used by subordinates to obtain benefits from dominants, but by dominants to emphasize their dominance position. In a second experiment subjects could choose to give to either a friend or a non-friend, since we expected that individuals are more pro-social towards their friends. There was, however, only a minor indication that long-tailed macaques prefer to give to their friends. In contrast, subordinates avoid giving to the individual closest in rank. We conclude that pro-sociality to kin is consistent with tolerance, yet pro-sociality of dominant individuals and to distantly ranked individuals suggest that it may also mediate in competitive strategies. Currently, we are conducting similar tests in the Arnhem chimpanzee colony. Also chimpanzees are considered rather intolerant, and therefore, pro-social behavior of this species is unexpected. However, thus far, studies on pro-social behavior of chimpanzees are inconclusive. We hope to also present some preliminary results of our study on chimpanzees at the conference.

Notes:

**Coping style is related to reproductive success in female wild eastern chipmunks (*Tamias striatus*)**

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The behavioral and physiological reaction of an animal to stressful or challenging situations is called coping style. While accumulating evidence shows that wild animals from the same population often differ in their coping style, the relationship between coping styles and reproductive success has not received a lot of attention. Here we take advantage of a long-term individual survey in a wild population of eastern chipmunks (*Tamias striatus*) to document individual coping styles and to establish the relationship between coping style and litter size at weaning. Each summer, individuals were trapped on a grid in southern Quebec. We estimated their pattern of space use from the trapping data, measured their docility when handled and their propensity to enter into a traps (an index of boldness). We ran novel environment tests to quantify each female's level of exploration, vigilance and thigmotaxy (the tendency to stay close to the walls, an index of anxiety in rodents). Our results support the coping style model with fast exploring females being also less docile and more likely to enter traps. More vigilant females in the novel-environment test were captured farther from the center of their home range. More thigmotactic females produced bigger litters. In this population, thigmotaxy and vigilance affected different components of the female's reproductive effort (i.e. space use during the mating season and litter size). Our results suggest that coping style may play an important role in the reproductive tactics expressed by female chipmunks.

Notes:

**Can evolutionary history explain the mixed troop associations of Hanuman langurs (*Semnopithecus entellus*) and Nilgiri langurs (*Semnopithecus johnii*) of South Western Ghats of South India?**

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Mixed species associations of primates are known to occur due to variety of reasons such as common food or habitat preferences, to minimize predation risks, role in defense against parasites, fluctuations in subgroup size etc invoking mutualism or commensalism as the causal factor for stable mixed-species associations. Most of these inferences have been derived out of studies from African colobines. A review of natural history data did not indicate any support to the known explanations available so far for such association in Asian primates. Thus the present study aimed at understanding why mixed species groups in Asian colobines occur taking association between Hanuman langur and Nilgiri langur (family: Cercopithecidae, sub family: Colobinae) in Western Ghats of South Western India as a case study. Apart from foraging as probable explanation (without much data), available evidences did not substantiate aforesaid reasons to explain the occurrence of mixed species group formations among these langurs. Since Hanuman Langurs and Nilgiri Langurs are closely related species as shown in available phylogenetic data, it is possible that the mixed species group formations in the present case might be due to shared evolutionary history than ecological or behavioral attributes. This hypothesis once empirically tested has the potential to reexamine mixed species associations in colobines as it has a larger bearing on the socioecological understanding of primates.

Notes:

## Male-male relationships in Guinea baboons (*Papio papio*) suggest a tolerant social style

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While the social system of savannah (*Papio anubis*, *P. cynocephalus* and *P. ursinus*) and hamadryas baboons (*P. hamadryas*) is well understood, less is known about Guinea baboons (*P. papio*). Here we present the first results from a study of male-male relationships in wild Guinea baboons. This species exhibits a multi-level social organization, where parties join into gangs, and gangs into the larger community. 470 hours of continuous focal data of 14 males belonging to five different parties were recorded during the dry seasons of 2010 and 2011 near our field site Simenti in the Niokolo Koba National Park in south-eastern Senegal. The dataset includes social interactions, proximity measures and greeting behavior. Overall, male Guinea baboons spent about 10 % of their time engaging in socio-positive interactions such as grooming and contact sitting. 21 % of these positive interactions were spent with another male. Moreover, males exhibit a complex and potentially costly greeting behavior. Of all male-male interactions, 20 % were positive; 12 % were agonistic and about 68 % were greetings. Male-male socio-positive interactions, coalitions and greetings occurred most likely within the male's party (89 %; 100 %; 71 %) whereas severe aggression predominantly took place between males of different parties (71 %). The social interaction patterns between males differed from those of savannah and hamadryas baboon males, which rarely engage in socio-positive interactions with other males. Future studies need to clarify whether male-male tolerance in Guinea baboons is related to kinship, as unpublished genetic data tentatively suggest, and elucidate the function of their peculiar greeting behavior.

Notes:



## **Grooming in female Barbary macaques: role of dominance, kinship and relationship quality**

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The aim of this study was to evaluate the influence of dominance, kinship and relationship quality on grooming distribution among Barbary macaque females. This study focused on 17 Barbary macaque females living in the Upper Rock Natural Reserve, Gibraltar. These females were over three years old. Behavioural observations were conducted between November 2007 and February 2008 and between October 2008 and February 2009. Animals were observed using focal continuous sampling simultaneously with focal instantaneous sampling. There was a mean of 29.5 hours of behavioural data per individual for a total of 497 hours for all observed females. The number of individual focal sessions (one session lasted 30 min) for each female ranged from 30 to 32 in the first season and from 23 to 29 in the second season. Linear mixed effect models (LMM) were used to test the effect of proposed factors on grooming distribution. Grooming was represented by two measurements: frequency of grooming and time of grooming separately for each season. The results suggest that choice of grooming partner is definitely not random. Dominance, kinship, and relationship quality are important for grooming distribution among social partners in female Barbary macaques. However, the most important factor for the grooming distribution is relationship quality, which is explained by rather tolerant dominance style of Barbary macaques, when dominance and kinship are not so important (although not negligible) factors. These results have also important implications for further research of factors effecting grooming distribution in groups of non-human primates.

Notes:

## **Numerical competence is determined by the representational format of the stimuli**

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A range of animal species possess an evolutionarily ancient system for representing number, which provides the foundation for simple arithmetical operations such as addition and numerical comparisons. Surprisingly, non-human primates tested in ecologically, highly valid quantity discrimination tasks using edible items often show a relatively low performance, suggesting that stimulus salience interferes with rational decision making. To investigate whether food or non-food items are more appropriate to investigate numerical abilities, we systematically varied the discriminatory stimulus (food/non-food) and reward scheme. We tested six olive baboons and ten long-tailed macaques housed at the German Primate Center in different two-choice tasks using 1 to 8 raisins or little black pebbles as choice stimuli. We show that quantity discrimination was indeed significantly enhanced when monkeys were tested with inedible items compared with food items (84 versus 69 % correct). More importantly, when monkeys were tested with food, but rewarded with other food items, the accuracy was equally high (86 %). The results indicate that the internal representation of the stimuli, not their physical quality, determined performance. Reward replacement apparently facilitated representation of the food items as signifiers for other foods, which in turn supported a higher acuity in decision making.

Notes:

## **A preliminary study: testing personality in wild ravens**

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Ravens (*Corvus corax*) live in groups with high fission-fusion dynamics and engage in complex social interactions, e.g. when competing over food. In such challenging situations, different individuals show different coping strategies, which amongst others is expected to depend on their personality traits, defined as consistent differences in behaviour across time and contexts. Ravens generally adjust their behaviour flexibly to the needs and requirements of stressful situations, however, personality traits put constraints on the degree of flexibility. We investigated the foraging behaviour of individually marked wild ravens in the Cumberland Game Park, Austria, under different feeding conditions, focusing on a possible link between risk taking (when to land/approach food), social factors (dominance, affiliation) and personality. For the latter, 42 trapped ravens were individually tested for tonic immobility (TI), an innate fear response characterized by a temporary and reversible motor inhibition. Additionally, we assessed their immune status (haematocrit levels, differential blood count) and took several size related measurements (e.g. weight, length of tarsus, head, beak). Preliminary results indicate that TI responses vary considerably between individuals (0.46-10.0 sec) but are constant over repeated tests within adult individuals. Moreover, we expect that birds with short TI responses tend to be more dominant and willing to take more risks.

Notes:

## **Torpor use is constrained by body condition and ambient temperature in a small Malagasy primate**

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Seasonality of resources represents a major constraint for sedentary animals to complete their annual life cycle. In Madagascar, during the dry season, animals have to adjust their behavior and physiology to cope with food and water shortage combined with low ambient temperature. Hibernation and daily torpor are efficient, adaptive responses based on energy saving mechanisms. The gray mouse lemur (*Microcebus murinus*), a small Malagasy primate, reduces its energy expenditure by exhibiting spontaneous daily torpor when conditions become unfavorable. Although the determinants of torpor use have been largely studied, its dependence on body condition has not been quantified so far. During the onset of the dry season (April - May 2011), we monitored skin temperature of free-ranging gray mouse lemurs in the dry deciduous forest of Kirindy (western Madagascar). We show that torpor depth (minimal skin temperature) depends on both an environmental constraint the ambient temperature and an internal constraint the body condition (i.e. size-scaled body mass). Hence, the heaviest a mouse lemur, the deeper its torpor. This positive relationship between torpor depth and body condition is only weakly reinforced by ambient temperature (non-significant interaction). The statistical model for this relationship enables to predict whether an individual should use torpor or not according to its body condition and the local climate. Fattening before the dry season would constrain individual ability to rely on torpor to make it throughout the dry season. Lean individuals would be left with the alternative strategy: maintaining a sustained foraging activity despite the scarcity of food and water.

Notes:

## **The flexibility of coalition formation in Barbary macaques**

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Male coalitions against other males can vary both within and between species in terms of the dominance rank constellation of allies and targets as well as the size and function of the coalition. The Pandit/van Schaik model for coalition formation is a mathematical model relating observed variation in coalition formation to variation in male contest competition potential. The model implicitly assumes full flexibility both within and between species, implying that under different contest potential a primate species can show enough behavioral flexibility to alter the type of coalitions they form. We examine this flexibility of one non-human primate species, the Barbary macaque (*Macaca sylvanus*). Data from two wild groups were collected in the Middle Atlas Mountains, Morocco, during two mating seasons between October 2009 and January 2011, and were compared to published data from two mating seasons from a free-ranging group at Affenberg, Salem. Our comparisons suggest that patterns of coalition formation are highly flexible within species and even in one group across time and that the variation is not entirely explained by variation in male contest competition.

Notes: