

Plenary Lectures

Structure and Function in Mammal Societies

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Traditional interpretations of the evolution of animal societies have suggested that their structure is a consequence of attempts by individuals to maximise their inclusive fitness within constraints imposed by their social and physical environments. In contrast, recent re-interpretations have argued that many aspects of social organisation should be interpreted as group-level adaptations maintained by selection operating between groups or populations. Here, I review our current understanding of the evolution of mammalian societies, focussing, in particular, on the evolution of reproductive strategies in societies where one dominant female monopolises reproduction in each group and her offspring are reared by other group members. Recent studies of the life-histories of females in these species show that dispersing females often have little chance of establishing new breeding groups and so are likely to maximise their inclusive fitness by helping related dominants to rear their offspring. As in eusocial insects, increasing group size can lead to a progressive divergence in the selection pressures operating on breeders and helpers and to increasing specialisation in their behaviour and life-histories. As yet, there is little need to invoke group-level adaptations in order to account for the behaviour of individuals or the structure of mammalian groups.

The use of a cichlid fish model to study social evolution

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The Lamprologine cichlids of Lake Tanganyika form an unique assemblage of closely related species, where about 20 out of 85 species show cooperative breeding. In this talk I will present an overview of experimental work carried out in these species, testing three key concepts in sociobiology: (1) the influence of ecological constraints and habitat saturation on cooperative breeding. (2) Determinants of reproductive skew and reproductive participation in social groups. (3) Group stability and within-group competition mediated by status-dependent growth.

Coordination and communication in meerkats

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Animals living in societies have to coordinate their activities with their group members. This is particularly true for species with high group cohesion and labour division. Meerkats (*Suricata suricatta*), cooperatively breeding mongoose, forage as cohesive unit and take turns in several behaviours, such as guarding and baby-sitting. On specific case studies, I will outline how we test hypotheses on mechanisms underlying coordination and group decision making involving vocal communication in this species. This will also illustrate why the work on meerkats, as a simple structured society, brings new insights into a field that has mainly been the attention of primate studies. Furthermore, I will briefly outline the potential of studying meerkats in comparison to other mongoose species with different social structure to answer ultimate questions on coordination and communication of animal societies.

The use of long-term pedigree data to understand the dynamics of adult traits in wild populations

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Evolutionary theory aims to explain how individuals are selected to translate resources efficiently into fitness, maximising their genetic contribution to future generations. Despite major research efforts, a full understanding of social evolution has only rarely been achieved. Unravelling the selective forces in a social setting is inherently difficult due to the complexities of measuring long-term fitness in wild systems. This prevents the adaptive basis of reproductive decisions from being assessed fully. In the case of social evolution, the 'environment' is set by social traits expressed by conspecifics, leading to an intricate feedback between selection and the environment. In this talk I am concerned primarily with how social interactions between individuals evolve as part of reproductive strategies. In the last decades, theoretical and empirical studies on cooperation and conflict over reproductive allocation have proliferated rapidly. This increased interest in the patterns of reproductive allocation has, at least partially, been stimulated by advances in molecular biology, and the unique features and availability of long-term data from some study species. I review how we have applied molecular techniques and long-term analyses to reveal some of the hidden life histories and trade-offs in avian societies, using the Seychelles warbler (*Acrocephalus sechellensis*) as a model system. These findings provide new insights into the evolution of cooperative breeding and mate choice, not only for the warbler, but for other animal societies more generally.

Altruism, infidelity and grandparents; cooperative breeding in the Seychelles

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The small and isolated nature of the Seychelles warbler population provides an excellent natural laboratory in which to study a complex social system. The manageable size of this population, combined with its confined nature, has allowed us to closely monitor individual behavior, life history decisions and interactions, across the whole population. Over the last decade or so we have used molecular techniques to reveal the hidden complexities of the Seychelles warblers' cooperative breeding system. We found that frequent subordinate maternity increases the direct benefits of being a subordinate, while surprisingly high levels of female infidelity drastically reduces the possibility for indirect benefits. Female subordinates are able to maximise the indirect benefits they gain by directing their helping effort to related individuals using associative learning cues (i.e. the continued presence of their putative parents within the territory). However, because of the high levels of infidelity, subordinates cannot trust their legitimacy through the male line; consequently they only use the continued presence of the putative mother, but not the putative father, as a reliable cue to determine when to feed related nestlings. The detailed long-term nature of our monitoring has also uncovered the presence, and adaptive significance, of 'grandparent' helpers in the Seychelles warbler, the first bird species in which this phenomenon has been observed. These findings show that a variety of different reproductive tactics can occur within, as well as across, taxonomic unit. They also highlight the fact that intensive, long-term and multidisciplinary studies, focusing on tractable systems, are needed to even approach a full understanding of social systems.

How relatedness informs and influences behaviour of *Neolamprologus pulcher* in the wild

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Neolamprologus pulcher, a cooperatively breeding cichlid fish, is an ideal model species for the study of social evolution both in the field and in the laboratory. I will discuss primarily how examination of genetic relatedness within and among groups of *N. pulcher* reveals much about the evolution of the dispersal, parental, and alloparental behaviour of this cichlid. Relatedness of a potential disperser to others in the population appears to play a role in individual dispersal decisions, but not in breeding pair formation in the natural environment. Sex differences in dispersal and in how breeding vacancies are typically filled contribute to the overall patterns of relatedness between helpers and breeders: while mean relatedness within groups is rather low, helpers are more likely to be related to the breeding female in their group than they are to the breeding male. This differential relatedness within the group influences the work effort of helpers, and there is

evidence that benefits from both kin selection and pay-to-stay are involved in the evolution and maintenance of cooperation in this species. Additionally, I will review work on how social interactions influence physiological variation among *N. pulcher* individuals in the wild, such as how social environment relates to individual hormone levels and sperm characteristics.

Contributed Talks

***Neolamprologus pulcher* as a model system to study hormonal mechanisms of highly advanced social behaviours**

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The cichlid fish *Neolamprologus pulcher* is a widely-used model species for the study of highly advanced social behaviours, like parental and alloparental brood care, defence of territory, group interactions etc. However, the hormonal control mechanisms of these behaviours are still poorly understood. To study the hormonal regulation of social interactions, we investigated the effect of varying size differences between breeder and helper males on helpers' growth rates and steroid excretion levels from holding water of both male types. Contrary to our expectations, the results showed no effect of the size-difference between helper males and breeder males on hormone excretion levels. However, androgen and cortisol levels were significantly lower in helpers showing elevated levels of submissive behaviour towards the breeders, independently of the size of the breeder males. We further studied the hormonal control mechanisms of alloparental brood care in the same model species. Sex steroid and cortisol excretion levels in holding water of family fish with and without a brood were measured and compared to corresponding levels of non-breeding, size matched fish. We expected higher levels of sex steroid hormones in fishes showing brood care. Steroid hormone levels varied with social status, but not with brood care behaviour. Furthermore, pituitary prolactin mRNA expression levels of breeders and helpers were measured with quantitative PCR and compared to values obtained from similar sized individuals of non-breeding groups. Prolactin levels of test fish were manipulated by intraperitoneal injections and the behaviour of these fish towards experimentally presented test clutches was observed. Contrary to studies carried out in several bird and mammal species, the results suggest that prolactin is not involved in the regulation of brood care behaviour in *N. pulcher*. Finally we present some ongoing discussions on the measurement of steroid hormones in holding water, like the correction of hormone levels for body size and the significance of different excreted hormone fractions.

Evolutionary causes and consequences of individual variation in cooperative behaviour

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Behaviour is typically regarded as among the most flexible of animal phenotypic traits. In particular, cooperative behaviour is often assumed to be conditional upon the behaviours of others. However, recent research has demonstrated that behaviours are often less flexible than expected and that, in many species, individuals show consistent differences in the amount and the quality of behaviours displayed. This phenomenon has recently been termed “animal personality” or a “behavioural syndrome”. Such individual variation in behaviours often shows partial heritability and entails fitness consequences, so individual variation in behaviour can be subject to evolutionary change. This finding calls into question the generality of the assumption that the expression of cooperative behaviour is always highly conditional. Here, I illustrate with *Neolamprologus pulcher*, a cooperatively breeding cichlid, that cooperative behaviour can be conditional upon the behaviour of others (pay-to-stay) and that there is also variation among individuals in the propensity to cooperate (animal personality) which is correlated with other, presumably functionally independent behavioural traits (a behavioural syndrome). I shortly describe the evolutionary processes that have been invoked to explain the existence of individual variation in cooperative behaviour and discuss the consequences of consistent individual differences on the evolutionary stability of cooperation. I highlight how consistent individual differences in cooperativeness may emerge from social interactions, and depend on the presence and behaviour of social partners. Furthermore, I describe how consistent variation in cooperativeness can both, stabilize or disrupt cooperation in populations. I conclude that recognizing the existence of limits to flexibility and individual differences in cooperativeness is essential for an understanding of the evolution and prevalence of cooperation.

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

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Hamilton (1971) proposed the classic explanation of aggregation: group size is constrained by the carrying capacity of an environment, but sustained by predation risk. However, for species exhibiting high levels of fission-fusion (FF) social dynamics, predation risk appears to affect the size of the travel parties, but not the troop. FF alters the constraint on troop size by allowing an increased net dispersal during foraging (Lehmann et al., 2007). For some species e.g. hamadryas baboons, the lower limit of troop size might reflect an increased risk of predation at night. But for others such as

spider monkeys, chimpanzees, ravens, equids and humans, the full troop rarely assembles. These species are also characterised by unstable party configuration — on different days different animals associate. One possible selective force supporting troop size is information sharing. This could apply to temporary food resources such as ripe fruit, and may also be a preadaptation for culture. If so, we would expect two other constraints on troop size: the (Dunbar, 1992) time-budget limits on forming relationships, and inclusive fitness (Hamilton, 1964). We have already demonstrated through simulation theoretical conditions favouring selection for costly (altruistic) communication about food resources (Cacace and Bryson, 2007). We present here two new models. One where FF derives simply from oscillations in individually-assessed risk and hunger. This model also demonstrates emergent behaviour similar to border raids and border patrols. A further model shows FF without oscillating risk, but facilitating group exploitation of occasional resource bonanzas.

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The function of mobbing in meerkats (*Suricata suricatta*)

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To show context appropriate antipredator behaviour, animals require information about a predators' motivation to hunt, and consequently the level of danger to which they are exposed at any given moment. In addition to deterring a predator, mobbing behaviour, in which animals approach a potential predator, might also provide information useful in predation risk assessment. Here we present the results of an experimental study on meerkats (*Suricata suricatta*), which showed mobbing behaviour in a variety of predator contexts. Groups were presented with a number of predators of varying threat levels, and with non-threatening animals. Responses to these stimuli by the different individuals in the groups, and vigilance behaviour before and after each presentation, were compared. Meerkats seemed to use mobbing not only to deter predators, but also to gather information about potential threats and adjust their behaviour accordingly. In particular, mobbing of nondangerous animals indicates the role of this behaviour in contexts other than just directed towards predators. Differences between age categories suggest that mobbing changes with experience, and may allow young to learn about predators by observing adults. We conclude that mobbing has a broader function beyond predator deterrence, and facilitates situational risk assessment on which subsequent decisions may be based.

Birth synchrony and breeding success in the banded mongoose'

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Knowledge of the tactics that social animals use to maximise their reproductive success is essential if we are to understand how cooperative animal societies evolved. One little studied factor that could have a profound influence on breeding success is the timing of an individual's reproduction in relation to other group members. Despite its likely importance in low skew societies however, the selection pressures on reproductive timing have received remarkably little attention to date. Using a 14 year dataset from a wild population of banded mongooses, a low skew cooperative breeder, we investigate how the relative timing of female reproductive attempts affects their outcome. Our results indicate that females who give birth before other females in the group are more likely to lose offspring through infanticide. The offspring of those that give birth after other females however, are at a disadvantage when competing with older offspring for care. Together, these findings provide an explanation for the extraordinary degree of birth synchrony observed in banded mongoose societies, where 64% of reproductive attempts involve females giving birth on exactly the same day. These findings suggest that banded mongoose females gain substantial fitness advantages from synchronising reproduction and highlight the importance of considering reproductive timing when attempting to understand variation in reproductive success in animal societies.

Ecological factors that limit the extent of cooperative breeding in the El Oro Parakeet (*Pyrrhura orcesi*)

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It is a long-standing hypothesis that ecological factors play an important role in explaining why some individuals forego their own reproduction and help others to raise offspring instead. However, it is often difficult to experimental show which factors are limiting. In the endangered El Oro Parakeet (*Pyrrhura orcesi*), an endemic and threatened species of Ecuador, we show that one key limiting resource is the availability of nest cavities. This species lives in stable, social groups of up to 15 individuals. The availability of artificial nest boxes decreases group size but increases effective population size. We use polymorphic microsatellites to analyze the genetic structure of breeding flocks of *P. orcesi*. Behavioral observations at the nest boxes provide further insights into social interactions between group members. Combining genetic and behavioral analyses, we scrutinize mating opportunities or nest site occupation as potential benefit to group members. Taken together, our study shows that the manipulation of a key ecological resource, nest site availability, strongly influences the social system of an endangered

species. Available evidence suggests that other endangered *Pyrrhura* species have a similar breeding system. Our results are therefore likely to be useful for deriving effective conservation strategies for these parakeets that concomitantly affect their social system.

Kin recognition and its effects on cooperation and helping in *Neolamprologus pulcher*

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Cooperative breeding is often assumed to be driven by kin selection. However, few studies have established this experimentally by investigating whether firstly, individuals can recognise kin, and secondly, if this then affects their helping decisions. In this respect, laboratory studies are important as they allow us to explore social behaviours in a controlled environment. Here, we studied kin recognition and helping behaviour in a lab population of the cooperatively breeding cichlid *Neolamprologus pulcher*. Using a split clutch breeding design, each F1 had a group of familiar and unfamiliar siblings of the same age. We found that both juveniles and adult females could recognise and prefer to associate with unfamiliar kin over non-kin. Adult males did not appear to differentiate kin over non-kin. Moreover, familiarity did not significantly influence shoal choice decisions. Further, we showed that chemical cues played a more important role in kin recognition than visual cues for juvenile *N. pulcher*. However, in adult females, this difference in the importance of cues for recognition was not apparent. Next, we investigated the importance of kinship in determining helping, as well as group dynamics. Breeding pairs were set up in territories with two unfamiliar helpers: one was the offspring of the pair and the other was unrelated. All group members were observed during two standardized tasks (removing sand from the breeding shelter and defending the territory against a conspecific intruder), to assess their cooperativeness. Also, all individuals were scored for a range of behaviours including dominance, submission, activity levels and boldness during control periods. We found that relatedness did not affect the amount of helping behaviour shown by helpers in *N. pulcher*. Instead individual helpers that were more aggressive and showed more dominance behaviour, were found to do more helping. Therefore, although *N. pulcher* are able to recognise kin, kin selection alone does not seem to be determining an individual's level of cooperation. Instead other behavioural traits seem to be more important in determining how cooperative an individual is willing to be.

African grey parrots: an avian model for social intelligence studies.

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African grey parrots present great similarities with primates not only in their social life organization but also in their cognitive abilities. Indeed, they have a long life expectancy (long infancy period, Athan & Deter 2000) with a complex fusion-fission dynamics system (Bradbury 2003) where many individuals (hundred to thousand) of different age and sex interact. They are known to be smart (Emery & Clayton 2004; Pepperberg 2006; Raby *et al.* 2007) and even some times are called ‘feathered apes’ (Emery & Clayton 2004). In collaboration with several laboratories (University of Vienna with Drs Huber & Gajdon, University of Harvard with Dr Pepperberg and university of Pragua with Mgr Lindova) our team is working on the Social Brain Hypothesis (Dunbar, 1998) in psittacids. The birds are tested not only on cooperation task paradigm (Hirata & Fuwa 2007, Seed *et al* 2008) but also with token exchange paradigm (Brosnan & De Waal 2003) and deception experiment (Von Bayern & Emery, 2009). Using the same paradigm as it has been done in primates we tend to find convergent behavioral mechanisms in species phylogenetically distinct. Giving the diversity of breeding behaviors (polyandrogenous, mono or biparental care,) among parrots it could be interested to compare several species in their cooperative behaviors (collaboration with Edinburgh Zoo).

Social facilitation and reciprocity in the cooperatively breeding cichlid *Neolamprologus pulcher*

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Individuals of social groups often temporally coordinate their behaviours, for instance in defence or foraging. Temporal coordination is assumed to act as a mechanism for the evolution of cooperation in social groups, which might either be simultaneous (social facilitation) or sequential (reciprocal altruism). In the present study, we investigated whether and under which circumstances social partners would apply simultaneous and sequential cooperation in the cooperatively breeding cichlid *Neolamprologus pulcher*. We tested this with randomly selected experimental partners in situations where they could either cooperate or defect in digging sand away from their shelter or in defence against a predator. We found that the social partners temporally coordinated their territory maintenance behaviour with the partner. Further, the data indicated that if the social partner had defected in a previous phase, the latency to begin digging and time intervals between subsequent digging bouts increased compared to when the partner had cooperated. These results support the hypothesis that temporal coordination of behaviour can facilitate cooperation.

***Allobates femoralis* (Aromobatidae): a handy fellow for anuran sociobiology**

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Dendrobatoid frogs of the families Aromobatidae and Dendrobatidae are renowned among herpetologists for their complex behaviour that renders them unique among anurans in several aspects. Inter-individual communication and communication networks, territoriality and site fidelity by one or both sexes, complex mating behaviour and mating systems, extended brood care by one or both parents and brood parasitism, aposematism and mimicry are traits that turn these poison frogs into exciting and promising model organisms for sociobiology as well. With 267 members (94 Aromobatidae, 173 Dendrobatidae) the superfamily comprises species with a broad variety of distributions and histories, ranging from old, pan-Amazonian to evolutionary young and locally endemic forms. Several species are thought to be in the actual process of allopatric speciation by separation and differentiation. In recent years, highly variable molecular markers (microsatellites) have become available for an increasing number of species, allowing for analyses of small scale phylogenies, relatedness and parentage. Molecular methods also unravelled dendrobatoid phylogeny in great detail, enabling to track the evolution of behaviour through resolved genetic lineages.

In the pan-Amazonian species(complex) *Allobates femoralis*, males defend long-term territories by prolonged calling and physical aggression, while females show fidelity to small resting sites. Male communication is best described as a communication network, as calls range much further than typical inter-individual distances. Females eavesdrop on male acoustic interactions and commute to neighbouring males from their resting sites for courtship and mating. The terrestrial clutch is deposited inside the male's territory and after initial development the father has to transport the tadpoles to small bodies of water. However, observations of female tadpole transport indicate a more complex brood care and plasticity thereof.

Our recent work is focusing on the mating system, population genetics, reproductive success, spatial behaviour and communication of *Allobates femoralis*. With this talk we want to introduce our study species to an audience beyond herpetology and hope for input for new research questions.

Long-term studies on social complexity in an avian model system, the greylag goose (*Anser anser*)

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Ever since the late K. Lorenz established a semi-tame flock of greylag geese in Upper Austria, their social system has been the main focus of investigations spanning from purely behavioural observations in the past to modern approaches, including experimentally induced challenges, heart rate measurement, non-invasive faecal hormone metabolite analyses and presently genetic relatedness under natural conditions in an intact social environment. All individuals' life histories and reproductive success have been monitored closely over the past three decades. Our recent work focused on comparing concepts of primate social organization with data collected from this flock, and this revealed a more elaborate social structure than previously recognized, including female-centred social organization, complex and long-lasting family bonds, alliance formation, and cooperation. Observational and experimental data suggest social support to be the main mechanism for explaining the structure of the flock, with females being the main beneficiaries both behaviourally and physiologically. In sum, we consider our long-term greylag goose data set as one of the most detailed studies of any avian social system, revealing fascinating details about their social complexity, which widely resembles mammalian systems.

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Social flexibility makes the striped mouse a good model to study proximate and ultimate reasons of solitary versus group living

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Behavioral flexibility to optimize individual fitness occurs in many species and is regulated by evolved physiological mechanisms. If flexibility in social behavior exists in both sexes, this can lead to changes in the social organization of a species or population, a phenomenon called social flexibility. However, social flexibility can be costly, as indicated by the fact that many species have a relatively stable social organization. Social flexibility can be of advantage in unpredictably changing environments. For example the African striped mouse (*Rhabdomys pumilio*) can either live solitarily or form extended family groups with communal breeding, paternal care and helpers at the nest. As a diurnal species which is easily habituated to the presence of observers and that inhabits an open habitat, it can be observed directly in the field, which is unusual for a mouse like rodent. As individuals breed only during one breeding season and die / disappear afterwards, we get data of a new generation every year. We are able to permanently monitor 12 social groups, getting individual life history data, genetic samples and blood samples for

hormone measurements of hundreds of individuals each year. Field experiments are possible, and the striped mouse can be kept and bred easily under standardized laboratory conditions, in which we can mimic natural variation in social systems. My long term field studies (2001 until today) indicate that the social organization of a population depends on environmental conditions, especially population density and intensity of reproductive competition, which itself is a product of differences in climate and associated changes in food availability. Depending on ecological conditions, the solitary living tactic can either be doing the best of a bad job with low reproductive success, or it can be equal in success to the group-living tactic, or it can even be superior with the highest reproductive success. Solitary living striped mice differ from group living striped mice in the age they enter puberty and in both steroid and protein hormone levels. Evolved endocrine mechanisms underlie social flexibility in the striped mouse, which enable individuals to maximize their reproductive success under changing environmental conditions.

Early social environment determines social competence in a cooperatively breeding fish

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Social competence describes the ability to respond appropriately to a social challenge. It is favoured by natural selection if it helps to obtain or maintain resources successfully and is hence especially important in species with complex social organization such as cooperative breeders. The role of other family members for the acquisition of social competence during ontogeny is purely understood. In humans, children growing up in more complex social structures acquire better adult social competence. We hypothesize that this may reflect a general pattern in animals, and that the presence and behaviour of mothers and fathers during early ontogeny is important for the social performance later in life. We tested this hypothesis with a split brood design in the highly social, cooperatively breeding cichlid *Neolamprologus pulcher*. Half of the experimental broods were raised with parents with or without helpers and the other half without older family members. During early rearing young kept with older family members performed more aggressive and submissive behaviours than their siblings raised alone. After being transferred to a neutral environment lacking adult conspecifics the test fish were socially challenged at three different life stages by a resource competition and a social integration trial. Fish that had been raised with older family members used aggression more economically when dominant, they behaved more readily submissively when subdominant allowing them to stay closer to a contested shelter, and they showed a greater propensity to act as helpers. Most remarkably, they differentiated between opponents with different raising history, which was not the case for young raised in the absence of parents. Our results confirm that the social raising conditions in a family persistently affect the economy and adequacy of individual reactions to social challenges, which is reminiscent of social competence effects known from humans.

Generalized reciprocity on social interaction networks

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Cooperation between non-related individuals can evolve by generalized reciprocity. Unlike direct or indirect reciprocity, this mechanism of cooperation does not require individual recognition: under generalized reciprocity, individuals who received help reciprocate to an arbitrary social partner. Due to its simplicity, generalized reciprocity is of particular interest to explain cooperation in animals without highly developed cognitive skills, but it is also more vulnerable to cheaters. In fact, generalized reciprocity has been shown to be evolutionarily stable only in small groups. It is not fully clear to what extent this problem prevents the evolution of cooperation through generalized reciprocity under realistic conditions, since groups in animal societies are typically highly structured. To quantify the effect of this social substructure, we explicitly consider the network of interactions within the social group, and relate the potential for the evolution of generalized reciprocity to structural properties of the social interaction network. We show that generalized reciprocity can be stable in large groups if the social network shows signs of modularity, a feature that many real-world examples of social networks exhibit.

Benefits of secondary predator cue inspection and recruitment calling in meerkats

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In socially foraging species the exchange of information on perceived predation risk among group members enables each individual to adjust anti-predator behaviour to the immediate level of danger. One way to adjust anti-predator behaviour to the current risk is by attending to secondary predator cues (SPC). In cooperative breeding meerkats (*Suricata suricatta*), which forage as social unit and display coordinated anti-predator behaviour, individuals encountering a SPC react strongly, and recruit the whole group. We investigated experimentally the benefits and costs of this behaviour for the actor (recruiter) and the recipients (recruited group members) in wild meerkats. Presentations of SPC caused the group to interrupt foraging and to inspect the cue. In subsequent foraging sessions, meerkats increased their anti-predator behaviour and decreased foraging investment. However, the actor did not change in its anti-predator behaviour whether recruitment was experimentally disabled or not. Crucially, the exposure to the

SPC decreased the latency of the group to detect and to alarm at a dummy predator. We therefore argue that the major selective force behind recruitment and information transfer is early predator detection by any group member, rather than reduction of anti-predator behaviour by the actor.