

The Kalahari Meerkat Project - Publication List

Current as of 7th March 2008

For a searchable version, please go to www.kalahari-meerkats.com/mkdb

Animal Behaviour, 2008, 75, 951-962

Early body condition, time budgets and the acquisition of foraging skills in meerkats

Alex Thornton

Early body condition commonly has important downstream effects on fitness. One, as yet unexplored, mechanism behind these effects may be that condition in early life affects time budgets and hence opportunities to learn critical skills. Meerkat, *Suricata suricatta*, pups must choose between begging for food from helpers and foraging for themselves. I found that pups in good condition early in life invested more time in foraging than individuals in poor condition and subsequently developed greater foraging efficiency, which was maintained in later life. Young pups spent an average of 18% of their time foraging, even though all pups were initially incompetent foragers and gained few direct benefits from their attempts. Pups whose hunger was reduced through experimental provisioning increased their investment in foraging. This suggests that investment in foraging is mediated by available energy reserves and raises the possibility that, although foraging is energetically costly, pups may gain long-term benefits by practising. Surprisingly, manipulating body weight through long-term experimental provisioning did not result in increased investment in foraging or improved foraging efficiency. Possible explanations for this result are considered. The findings presented here provide some support for the hypothesis that high body condition allows individuals to invest time in costly foraging practice, leading to the development of skills. These effects, acting in tandem with other processes such as differential neural development, may help to explain common links between early condition and future fitness.

Keywords: downstream effects; early condition; foraging skills; learning; meerkat; *Suricata suricatta*

Animal Behaviour, 2008, 75, 943-949

The audience effect in a facultatively social mammal, the yellow mongoose, *Cynictis penicillata*

Aliza le Roux, Michael I. Cherry and Marta B. Manser

The audience effect has been shown in numerous group-living vertebrates but whether it is present in facultatively social species is unknown. We investigated the antipredator responses of the yellow mongoose, a mammal that dens in groups but primarily forages alone. To examine the effect that the social environment has on their communication, we performed a combination of field observations and experiments with live and model predators on a habituated population of mongooses. Social context affected both the communicative and the flight behaviour of yellow mongooses. Alarm vocalizations were used almost exclusively when individuals were in a group rather than solitary. The visual alarm signal, a raised tail, was predominantly used by solitary individuals when predators were outside attack range. This study apparently is the first to show an audience effect in a facultatively social mammal, suggesting that even rare social interactions lead to the ability to respond flexibly to predators depending on the presence or absence of conspecifics.

Keywords: alarm signals; audience; communication; *Cynictis penicillata*; sociality; yellow mongoose

Journal of Zoology, 2008, 274: 248-253

Radiocollars do not affect the survival or foraging behaviour of wild meerkats

K. A. Golabek, N. R. Jordan & T. H. Clutton-Brock

The practice of radiocollaring is increasingly being used in the study of wild animal populations. However, methods of tracking and monitoring are known to affect some species negatively. On a wild population of habituated meerkats *Suricata suricatta*, we investigated the potential costs and consequences of carrying a radiocollar for small carnivores, focusing on detailed aspects of foraging behaviour and survival. Radiocollared individuals were no more likely to be predated than non-collared individuals in the same social group. We also found that collaring did not affect foraging efficiency, with collared individuals being equally efficient foragers (four measures) while wearing a collar compared with the pre-collaring period. To control for group-specific events, changes in foraging efficiency after collaring were compared with the behaviour of control individuals from the same group and no significant differences were found. In conclusion, we found no evidence to suggest radiocollars impact negatively on the bearer's welfare, survival or foraging ability.

Keywords

adverse effects; energetic costs; monitoring; radiotelemetry; radiotracking; *Suricata suricatta*; survival.

Behav Ecol Sociobiol, 2008, 62: 821–829

Ontogenetic changes in alarm-call production and usage in meerkats (*Suricata suricatta*): adaptations or constraints?

Linda I. Hollén & Tim Clutton-Brock & Marta B. Manser

In many species, individuals suffer major mortality in their first year because of predation. Behaviours that facilitate successful escape are therefore under strong selection, but anti-predator skills often emerge gradually during an individual's early development. Using long-term data and acoustic recordings of alarm calls collected during natural predator encounters, we aimed to elucidate two largely unsolved issues in anti-predator ontogeny: (1) whether incorrect predator assignment is adaptively age-appropriate, given that vulnerability often changes during development, or whether age-related differences reflect true mistakes made by immature individuals; and (2) the extent to which the development of adult-like competence in alarm-call production and usage is simply a function of maturational processes or dependent upon experience. We found that young meerkats (*Suricata suricatta*) were less likely to give alarm calls than adults, but alarmed more in response to non-threatening species compared to adults. However, stimuli that pose a greater threat to young than adults did not elicit more calling from young; this argues against age-related changes in vulnerability as the sole explanation for developmental changes in calling. Young in small groups, who were more likely to watch out for predators, alarmed more than less vigilant young in larger groups. Moreover, despite similarities in acoustic structure between alarm call types, calls appeared in the repertoire at different rates, and those that were associated with frequently encountered predators were produced relatively early on. These results indicate that experience is a more plausible explanation for such developmental trajectories than maturation.

Keywords Meerkats . Alarm calls . Development . Experience . Maturation . *Suricata suricatta*

Proceedings of the Royal Society B, 2008, 275, 209–216

The number of subordinates moderates intrasexual competition among males in cooperatively breeding meerkats

Nobuyuki Kutsukake and Tim H. Clutton-Brock

For dominant individuals in cooperatively breeding species, the presence of subordinates is associated with both benefits (i.e. increased reproductive output and other group-living benefits) and costs (i.e. intrasexual competition on reproduction). The biological market theory predicts that dominant individuals are tolerant to same-sex group members when there are only a few subordinates, so as to maximize their own reproductive success. We investigated factors affecting aggression by dominant males and submission by subordinate males for a cooperatively breeding mammal, meerkats, *Suricata suricatta*. In this species, reproductive conflict occurs between the dominant male and the non-offspring males. As predicted, the number of subordinates in a group was positively associated with the aggression frequency by the dominant male and with the submission frequency by the subordinate males. Relative to the aggression frequency against male offspring, the frequency of aggression against non-offspring males was comparable in small groups, but was higher in large groups. These results indicate that reproductive conflict is present between the dominant male and the non-offspring males but is moderated in groups with small numbers of subordinates. This study provides an empirical data agreeing with the biological market theory in the context of intrasexual competition in cooperatively breeding species.

Keywords: aggression; intrasexual competition; meerkats *Suricata suricatta*; cooperative breeding; biological market

Science, 2007, 318, 1882-1185

Sexual Selection in Males and Females

Tim Clutton-Brock

Research on sexual selection shows that the evolution of secondary sexual characters in males and the distribution of sex differences are more complex than was initially suggested but does not undermine our understanding of the evolutionary mechanisms involved. However, the operation of sexual selection in females has still received relatively little attention. Recent studies show that both intrasexual competition between females and male choice of mating partners are common, leading to strong sexual selection in females and, in extreme cases, to reversals in the usual pattern of sex differences in behavior and morphology.

Animal Behaviour, 1st November 2007, 74, 1259-1268

The irrelevance of individual discrimination in meerkat alarm calls

Fabian Schibler and Marta B. Manser

Individual discrimination is an important element in the evolution of social behaviour and is particularly important in social living species which show intense intragroup interactions. Numerous previous studies, particularly with nonhuman primates, ground squirrels and marmots, demonstrate the widespread ability of various species to signal and perceive individual identity from vocalizations. The function of individually different alarm calls is thought to assist in the detection of unreliable individuals. This would allow individuals to optimize the benefits of antipredator behaviour by self-assessing the relative predation risk, and responding selectively to reliable callers. In this study we investigated whether meerkats, *Suricata suricatta*, a social mongoose, discriminated among alarm callers individually, and adjusted their response accordingly. Several parameters of the acoustic structure of meerkat alarm calls were measured and analysed with multivariate statistics. Within groups, the 10-fold cross-validation of a multinomial regression yielded, on average, 90% correct assignment. This strongly suggests that meerkats have individually distinct alarm calls. With a habituation-dishabituation playback experiment, we then tested whether meerkats use this information to discriminate between individual callers. Receivers did not distinguish between different individuals in the playback

experiments. In meerkats, unreliable callers appear to be uncommon, and the cost of being predated might exceed the costs of responding to an unreliable caller, thus rendering a reliability-based discrimination mechanism unnecessary. Although meerkat alarm calls contain information on individual identity, this information does not appear to be important to the receivers in this context.

Keywords: alarm call; acoustic structure; habituation-dishabituation playback; individual discrimination; meerkat; reliability; *Suricata suricatta*

The American Naturalist, October 2007, 170, 617-624.

Begging Signals in a Mobile Feeding System: The Evolution of Different Call Types

Hansjoerg P. Kunc, Joah R. Madden, and Marta B. Manser

In some species, dependent offspring join foraging providers and beg for food. Mobile offspring might benefit from evolving begging signals adapted to the different situations they are exposed to, but this possibility has been ignored. In cooperatively breeding meerkats (*Suricata suricatta*), dependent offspring use a repertoire of several begging calls when joining foraging adults. We found that these calls can be differentiated on the basis of their acoustic structure and that pups adjusted the use of specific call types according to the social context. Pups continuously gave “repeat” calls when they accompanied foraging adults, and playback of these calls increased provisioning by the adults. When pups saw adults with food, they switched from repeat calls to vigorous “high-pitched” calls; adults also preferred to “feed” loudspeakers broadcasting high-pitched calls rather than loudspeakers broadcasting repeat calls. The elaboration of different begging calls might reflect an adaptation to a situation where dependent young must solicit food from potential feeders while at the same time directing feeders to bring the prey item to themselves and not to another begging pup. Here we show that mobile but dependent offspring adapt to different contexts in a mobile feeding system by using a repertoire of begging calls.

Keywords: begging, meerkat, parent-offspring communication, sibling competition, vocal communication.

Current Biology, 2007, 17-12, R442

Quick guide: Meerkats

Adin Ross-Gillespie and Ashleigh S. Griffin

(no abstract)

Ethology, September 2007, 113, 1038–1047.

Persistence of Alarm-Call Behaviour in the Absence of Predators: A Comparison Between Wild and Captive-Born Meerkats (*Suricata Suricatta*)

Linda I. Hollén & Marta B. Manser

Performing correct anti-predator behaviour is crucial for prey to survive. But, are such abilities lost in species or populations living in predator-free environments? How individuals respond to the loss of predators has been shown to depend on factors such as the degree to which anti-predator behaviour relies on experience, the type of cues evoking the behaviour, the cost of expressing the behaviour and the number of generations under which relaxed selection has taken place. Here we investigated whether captive-born populations of meerkats (*Suricata suricatta*) used the same repertoire of alarm calls previously documented in wild populations and whether captive animals, as wild ones, could recognize potential predators through olfactory cues. We found that all alarm calls that have been documented in the wild also occurred in captivity and were given in broadly similar contexts. Furthermore, without prior experience of odours from predators, captive

meerkats seemed to distinguish between faeces of potential predators (carnivores) and non-predators (herbivores). Despite slight structural differences, the alarm calls given in response to the faeces largely resembled those recorded in similar contexts in the wild. These results from captive populations suggest that direct, physical interaction with predators is not necessary for meerkats to perform correct anti-predator behaviour in terms of alarm-call usage and olfactory predator recognition. Such behaviour may have been retained in captivity because relatively little experience seems necessary for correct performance in the wild and/or because of the recency of relaxed selection on these populations.

Animal Behaviour, September 2007, 74, 957-964.

Offspring competition and helper associations in cooperative meerkats

Sarah J. Hodge, T. P. Flower, T. H. Clutton-Brock

In cooperatively breeding vertebrates, helpers commonly vary in how much care they provide. We investigated whether meerkat, *Suricata suricatta*, pups responded to variation in helper feeding rates by associating with the most productive helpers preferentially throughout the period of pup care. Helpers varied widely in how much food they provided, and pup food intake increased with the time spent in exclusive association with productive helpers. Pups spent more time following productive helpers than poor helpers, and we confirmed the causality of this finding by conducting long-term feeding experiments which increased helper productivity and showed that pups spent significantly more time with helpers whose feeding rate had been experimentally raised. Pups aggressively defended helpers from approaches by litter-mates, but there was no evidence that pups defended productive helpers more strongly, or that larger pups were more likely to gain exclusive access to the most productive helpers. Our results provide evidence that, by associating with particular helpers, meerkat pups can influence how much care they receive during development. These findings highlight the importance of considering the behaviour of offspring, when investigating the way care is distributed in cooperative societies.

Keywords: aggression; brood division; fledgling; helper; meerkat; resource allocation; sibling competition; *Suricata suricatta*

Animal Behaviour, 23 August 2007, 74, 531-540

Scent-marking investment is determined by sex and breeding status in meerkats

Neil Jordan

Meerkats, *Suricata suricatta*, engage in cooperative territorial defence, including olfactory demarcation with latrines. Males from neighbouring groups frequently approach resident groups, but, due to high levels of reproductive skew, the potential fitness costs and benefits of deterring these males vary according to the sex and breeding status of residents. Although all individuals visited latrines for similar durations, latrine scent mark composition was highly male-biased. Male behaviour supported a mate-defence function as males scent marked at significantly higher rates than females and preferentially overmarked female scent marks. In contrast to males, female competition is most intense within the group, and females invested heavily in scent mark investigation, but did not selectively overmark existing scent marks of either sex. Monitoring of other females, particularly their reproductive status, may therefore be an important function of latrine visits for females. Rather than cooperatively contributing to territorial defence, individuals appear to participate selfishly at latrine sites, with ultimate explanations for scent marking potentially being related to both the sex and breeding status of group members.

Keywords: communication; conflict; latrine; mate defence; meerkat; odour; olfactory communication; scent marking; *Suricata suricatta*; territory defence

Animal Behaviour, 17 August 2007, 74, 507-517

The function of mobbing in cooperative meerkats

Beke Graw and Marta B. Manser

To show context appropriate antipredator behaviour, animals require information about a predator's 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.

Keywords: antipredator response; meerkat; mobbing; predator deterrence; risk assessment; *Suricata suricatta*

The American Naturalist, June 2007, 169, 758–767.

Motivation before Meaning: Motivational Information Encoded in Meerkat Alarm Calls Develops Earlier than Referential Information

Linda I. Hollén and Marta B. Manser

In contrast to historical assumptions about the affective nature of animal vocalizations, it is now clear that many vertebrates are capable of producing specific alarm calls in response to different predators, calls that provide information that goes beyond the motivational state of a caller. However, although these calls function referentially, it does not mean that they are devoid of motivational content. Studies on meerkats (*Suricata suricatta*) directly support this conclusion. The acoustic structure of their alarm calls simultaneously encodes information that is both motivational (level of urgency) and referential (predator specific). In this study, we investigated whether alarm calls of young meerkats undergo developmental modification and whether the motivational or the referential aspect of calls changes more over time. We found that, based on their acoustic structure, calls of young showed a high correct assignment to low- and high-urgency contexts but, in contrast to adults, low assignment to specific predator types. However, the discrimination among predator types was better in high-urgency than in low-urgency contexts. Our results suggest that acoustic features related to level of urgency are expressed earlier than those related to predator-specific information and may support the idea that referential calls evolve from motivational signals.

Keywords: meerkats, alarm calls, development, referentiality, motivational signals.

Proc. R. Soc. B, April 2007, 274, 1603–1609

Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal

Andrew J. Young, Goran Spong and Tim Clutton-Brock

In cooperatively breeding species, subordinates typically suffer strong constraints on within-group reproduction. While numerous studies have highlighted the additional fitness benefits that subordinates might accrue through helping, few have considered the possibility that subordinates may also seek extra-group matings to improve their chances of actually breeding. Here, we show

that subordinate males in cooperative meerkat, *Suricata suricatta*, societies conduct frequent extraterritorial forays, during periods of peak female fertility, which give rise to matings with females in other groups. Genetic analyses reveal that extra-group paternity (EGP) accrued while prospecting contributes substantially to the reproductive success of subordinates: yielding the majority of their offspring (approx. 70%); significantly reducing their age at first reproduction and allowing them to breed without dispersing. We estimate that prospecting subordinates sire 20–25% of all young in the population. While recent studies on cooperative birds indicate that dominant males accrue the majority of EGP, our findings reveal that EGP can also arise from alternative reproductive tactics employed exclusively by subordinates. It is important, therefore, that future attempts to estimate the fitness of subordinate males in animal societies quantify the distribution of extra-group as well as within-group paternity, because a substantial proportion of the reproductive success of subordinates may otherwise go undetected.

Keywords: extra-pair paternity; reproductive skew; multi-male groups; mating system

Proc. R. Soc. B, 2007, 274, p. 513–520

Helpers increase the reproductive potential of offspring in cooperative meerkats

A. F. Russell, A. J. Young, G. Spong, N. R. Jordan and T. H. Clutton-Brock

In both animal and human societies, individuals may forego personal reproduction and provide care to the offspring of others. Studies aimed at investigating the adaptive nature of such cooperative breeding systems in vertebrates typically calculate helper 'fitness' from relationships of helper numbers and offspring survival to independence. The aim of this study is to use observations and supplemental feeding experiments in cooperatively breeding meerkats, *Suricata suricatta*, to investigate whether helpers influence the long-term reproductive potential of offspring during adulthood. We show that helpers have a significant and positive influence on the probability that offspring gain direct reproductive success in their lifetimes. This effect arises because helpers both reduce the age at which offspring begin to reproduce as subordinates and increase the probability that they will compete successfully for alpha rank. Supplemental feeding experiments confirm the causality of these results. Our results suggest that one can neither discount the significance of helper effects when none is found nor necessarily estimate accurately the fitness benefit that helpers accrue, unless their effects on offspring are considered in the long term.

Keywords: early conditions; helper effects; fitness; kin selection; lifetime reproductive success

Animal Behaviour, 73, 13 March 2007, p. 613–622

Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence

Neil R. Jordan, Michael I. Cherry, Marta B. Manser

Many carnivores defend territories and deposit faeces and other scent marks at specific latrine sites. The role of latrines in territory defence is well established, but evidence suggests at least a subsidiary role in mate defence. We investigated latrine function in cooperative meerkats, *Suricata suricatta*. By analysing the spatial and temporal distribution of latrines we found patterns that might facilitate information transmission to a range of potential intruders. Each group of meerkats usually shared one latrine with each known neighbouring group, which probably allowed efficient intergroup monitoring of surrounding land tenure. The remaining latrines were primarily concentrated in territorial core regions. As transient groups and prospecting males enter territories unpredictably, this distribution may maximize the likelihood of latrine discovery. In large meerkat territories, the chance of intruders missing widely spaced boundary scent marks is high, and a core-marking strategy may therefore be more effective. Latrines were positioned close to refuge sites, which may further increase the likelihood of intercepting intruders, as prospectors are known to visit these sites regularly during intrusions. Although latrine use did not in-

during periods when resident females were sexually receptive, it was significantly more likely during the peak breeding period in general, and occurred at significantly greater rates during observation periods when prospecting males were encountered. As prospectors threaten resident male reproductive success, these results highlight the potential importance of latrines in mate defence.

Keywords: carnivore; conflict; latrine distribution; mate defence; meerkat; odour; olfactory communication; scent marking; *Suricata suricatta*; territory defence

Nature, 444, 21/28 December 2006, p. 1065-1069

Intrasexual competition and sexual selection in cooperative mammals

T. H. Clutton-Brock, S. J. Hodge, G. Spong, A. F. Russell, N. R. Jordan, N. C. Bennett, L. L. Sharpe & M. B. Manser

In most animals, the sex that invests least in its offspring competes more intensely for access to the opposite sex and shows greater development of secondary sexual characters than the sex that invests most. However, in some mammals where females are the primary care-givers, females compete more frequently or intensely with each other than males. A possible explanation is that, in these species, the resources necessary for successful female reproduction are heavily concentrated and intrasexual competition for breeding opportunities is more intense among females than among males. Intrasexual competition between females is likely to be particularly intense in cooperative breeders where a single female monopolizes reproduction in each group. Here, we use data from a twelve-year study of wild meerkats (*Suricata suricatta*), where females show high levels of reproductive skew, to show that females gain greater benefits from acquiring dominant status than males and traits that increase competitive ability exert a stronger influence on their breeding success. Females that acquire dominant status also develop a suite of morphological, physiological and behavioural characteristics that help them to control other group members. Our results show that sex differences in parental investment are not the only mechanism capable of generating sex differences in reproductive competition and emphasize the extent to which competition for breeding opportunities between females can affect the evolution of sex differences and the operation of sexual selection.

Animal Behaviour 72, 6th October 2006, p. 1345-1353

Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics

Linda I. Hollén & Marta B. Manser

Given the strong selection on prey animals to escape predation, early development of correct avoidance strategies should be favoured. We studied the development of responses to conspecific alarm calls in a free-ranging population of meerkats in South Africa. Through behavioural observations of naturally occurring predator encounters and playback experiments, we monitored responses of young individuals from emergence (3 weeks) to 6 months of age and compared them with those of adults (>12 months). Although the total proportion of responses differing from those of adults was low during the observed period, the probability of responding like adults increased with age. Female young, who remained in closer contact to adults than did male young, were also more likely to show adultlike responses. The largest proportion of non-adultlike responses was shown before reaching independence at 3 months of age, and during this time young commonly ran immediately to a nearby individual when hearing an alarm call. After playbacks of alarm calls, young also reacted more slowly, resumed foraging sooner and spent less time vigilant than did adults. We conclude that young may need experience during early development to associate an alarm call correctly with the type of threat and appropriate response. Older group members may also serve as indirect models, perhaps helping young to form this association.

Animal Behaviour 72, 7th September 2006, p. 1059-1068

Social functions of allogrooming in cooperatively breeding meerkats

Nobuyuki Kutsukake & Tim H. Clutton-Brock

In social mammals, grooming may be used in care of offspring, to maintain pair bonds, or to placate dominant individuals. We examined grooming patterns in groups of the cooperatively breeding meerkat, *Suricata suricatta*. Dominant females produce over 80% of litters, but older subordinate females occasionally breed. Grooming between dominant individuals was the most common and symmetrical interaction. The dominant female received more and gave less in grooming interactions with subordinates. The dominant female groomed younger subordinates more frequently than older subordinates, suggesting that grooming by dominant females represents parental care, and also reflects the reproductive conflict between females. Older subordinates groomed the dominant female more frequently than did younger subordinates. Subordinates that were frequently attacked by the dominant female groomed her for longer durations than those that were not, and the duration of dominant female grooming by subordinates increased as birth of the dominant female's pups approached. These results support the idea that subordinates use grooming to placate the dominant female. Analysis of 'immediate reciprocity' (whether the groomee returned grooming of the groomer within the grooming bout) showed that subordinate females reciprocated more frequently than subordinate males when the dominant female initiated grooming. However, the dominant female reciprocated subordinate females less frequently than she did subordinate males. This suggests that the need to placate the dominant female may be higher for subordinate females than for subordinate males, possibly because of the risk of eviction caused by reproductive conflict between females.

PNAS, 103:32, 8 August 2006, p. 12005–12010

Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats

Andrew J. Young, Anne A. Carlson, Steven L. Monfort, Andrew F. Russell, Nigel C. Bennett, and Tim Clutton-Brock

In many animal societies, dominant individuals monopolize reproduction, but the tactics they employ to achieve this are poorly understood. One possibility is that aggressive dominants render their subordinates infertile by inducing chronic physiological "stress." However, this hypothesis has been discarded largely for cooperatively breeding species, where reproductive monopolies are often extreme. Here we provide strong support for the stress-related suppression hypothesis in a cooperative mammal, the meerkat (*Suricata suricatta*). When pregnant, dominant females subject some subordinate females to escalating aggression, culminating in temporary evictions from the group. While evicted, subordinate females suffer chronic elevation of their glucocorticoid adrenal hormone levels, reproductive down-regulation (reduced pituitary sensitivity to gonadotropin-releasing hormone), reduced conception rates, and increased abortion rates. Rather than constantly harassing all subordinate females, dominants only become aggressive when pregnant themselves (when subordinate reproduction would otherwise conflict with their own) and target those females with whom reproductive conflict is most likely (older, pregnant, and more distantly related females). Our findings suggest that dominant female meerkats employ stressful evictions to suppress reproduction among their probable competitors, when attempting to breed themselves. Given the lack of evidence for stress-related suppression in other cooperative breeders to date, it is clear that social stress alone cannot account for the reproductive failure of subordinates across such societies. However, our findings raise the possibility that, in some cooperative breeders at least, dominants may employ stress-related suppression as a backup mechanism to guard against lapses in reproductive restraint by their subordinates.

Keywords: cooperative breeding _ dominant control _ physiological _ reproductive restraint _ reproductive skew

Biology Letters, 2006, published online

Infanticide by subordinates influences reproductive sharing in cooperatively breeding meerkats

Andrew J. Young and Tim Clutton-Brock

In cooperative animal societies, dominant females typically show higher breeding success than subordinates, and are commonly believed to control the extent of reproductive sharing. However, studies of social insect societies reveal that subordinates too can interfere with the breeding attempts of others, with important implications for the distribution of fitness within colonies. Here, we show that subordinate females in a high-skew vertebrate (the meerkat, *Suricata suricatta*), also exert a substantial influence over the reproductive attempts of others. In meerkat societies, pregnant dominants are known to kill subordinate litters, but we show that pregnant subordinates also kill pups; not only those of other subordinates but the dominant's as well. Litters born to females of any rank were half as likely to survive their first 4 days if a subordinate was pregnant. However, dominant females were more likely than subordinates to give birth when no other females were pregnant, and so lost fewer litters to infanticide than subordinates. This is probably due in part to dominants employing counter-tactics to reduce the incidence of subordinate pregnancy. We discuss the broad implications of subordinates having a degree of control over reproductive sharing for future attempts to understand the distribution of reproduction in animal societies.

Keywords: reproductive skew _ cooperative breeding _ subordinate control

Science, 313, 14 July 2006, p. 227-229

Teaching in Wild Meerkats

Alex Thornton and Katherine McAuliffe

Despite the obvious benefits of directed mechanisms that facilitate the efficient transfer of skills, there is little critical evidence for teaching in nonhuman animals. Using observational and experimental data, we show that wild meerkats (*Suricata suricatta*) teach pups prey-handling skills by providing them with opportunities to interact with live prey. In response to changing pup begging calls, helpers alter their prey-provisioning methods as pups grow older, thus accelerating learning without the use of complex cognition. The lack of evidence for teaching in species other than humans may reflect problems in producing unequivocal support for the occurrence of teaching, rather than the absence of teaching.

Hormones and Behavior, 50, 9 March 2006, p. 94–100

Elevated prolactin levels immediately precede decisions to babysit by male meerkat helpers

Anne A. Carlson, Andrew F. Russell, Andrew J. Young, Neil R. Jordan, Alan S. McNeilly, Al F. Parlow, Tim Clutton-Brock

Recent studies suggest that decisions to care for the offspring of others in societies of cooperative vertebrates may have a hormonal basis. The crucial question of whether changes in hormone levels immediately precede or merely follow bouts of offspring care, however, remains largely unanswered. Here, we show that in wild groups of cooperatively breeding meerkats, male helpers that decided to babysit for the day had significantly higher levels of prolactin, coupled with lower levels of cortisol, before initiating a babysitting session compared with similarly aged individuals that decided to forage. In addition, these hormonal differences disappeared over the course of the day, suggesting that hormone levels changed in a fundamentally different way in meerkats that babysat versus those that foraged. In contrast, long-term contributions to babysitting were not significantly associated with plasma levels of prolactin, cortisol, or

testosterone in individual male helpers. Our results show, for the first time, that elevated levels of prolactin may immediately precede bouts of helping behavior but differ from recent findings on the same study population in which plasma levels of cortisol, but not prolactin, were significantly and positively associated with rates of pup feeding by male helpers. Together, these results lend significant weight to the idea that decisions to help in cooperative vertebrates have a hormonal basis, although different hormones appear to be associated with different types of care.

Keywords: Cooperative care _ Cooperative breeding _ Prolactin _ Cortisol _ Testosterone

Proc. R. Soc. B, 273, 2006, p. 571–577

Cortisol levels are positively associated with pup-feeding rates in male meerkats

Anne A. Carlson, Marta B. Manser, Andrew J. Young, Andrew F. Russell, Neil R. Jordan, Alan S. McNeilly and Tim Clutton-Brock

In societies of cooperative vertebrates, individual differences in contributions to offspring care are commonly substantial. Recent attempts to explain the causes of this variation have focused on correlations between contributions to care and the protein hormone prolactin, or the steroid hormone testosterone. However, such studies have seldom considered the importance of other hormones or controlled for nonhormonal factors that are correlative with both individual hormone levels and contributions to care. Using multivariate statistics, we show that hormone levels explain significant variation in contributions to pupfeeding by male meerkats, even after controlling for non-hormonal effects. However, long-term contributions to pup provisioning were significantly and positively correlated with plasma levels of cortisol rather than prolactin, while plasma levels of testosterone were not related to individual patterns of pup-feeding. Furthermore, a playback experiment that used pup begging calls to increase the feeding rates of male helpers gave rise to parallel increases in plasma cortisol levels, whilst prolactin and testosterone levels remained unchanged. Our findings confirm that hormones can explain significant amounts of variation in contributions to offspring feeding, and that cortisol, not prolactin, is the hormone most strongly associated with pup-feeding in cooperative male meerkats.

Keywords: helper _ cooperative _ provisioning _ prolactin _ cortisol _ testosterone

Behav Ecol Sociobiol, 59, 2006, p. 541–548

Aggression and submission reflect reproductive conflict between females in cooperatively breeding meerkats *Suricata suricatta*

N. Kutsukake, T. H. Clutton-Brock

Abstract In many cooperatively breeding species, dominant females suppress reproduction in subordinates. Although it is commonly assumed that aggression from dominant females plays a role in reproductive suppression, little is known about the distribution of aggressive interactions. Here, we investigate the distribution of aggressive and submissive interactions among female meerkats (*Suricata suricatta*). In this species, dominant females produce more than 80% of the litters, but older subordinates occasionally breed. Dominant females commonly kill the pups of subordinates and usually evict older female subordinates from the group 1–3 weeks before the birth of the dominant female's litter. The aggression frequency of the dominant female toward subordinates and the submission frequency that each subordinate female showed to the dominant female increased as the age of the subordinate female increased and as the birth of the dominant female's pups approached. Moreover, as birth approached, both of these behaviors intensified more quickly between the dominant female and older subordinates than between the dominant female and younger subordinates. The aggression frequency of the dominant female toward each subordinate female predicted whether that subordinate female was evicted from the group; the submission frequency by each subordinate female predicted the timing of their eviction during the pregnancy period of the dominant female. These results support the idea that conflict between dominant and subordinate females increases with the age of subordinates and, since

older subordinate females are most likely to reproduce, suggest that dominant females may less easily control reproductive attempts by older subordinate females.

Keywords: Cooperative breeding _ Meerkats _ Aggression _ Reproductive suppression _ Reproductive conflict _ Eviction

Animal Behaviour, 70, 2005, p. 829-837

Trade-offs between extraterritorial prospecting and helping in a cooperative mammal

Andrew J. Young, Anne A. Carlson, Tim Clutton-Brock

Males commonly face a trade-off between investment in offspring care and time spent seeking additional breeding opportunities. Although this trade-off is central to our understanding of the evolution of male parental care, it has been largely ignored by studies of male alloparental care in cooperative societies, where male helpers could face a similar problem. We investigated whether male helpers in cooperative societies of meerkats *Suricata suricatta* trade off their cooperative contributions to pup feeding against extraterritorial prospecting for mating and dispersal opportunities. Not only did male helpers spend extended periods away from the group during pup care periods, but those that spent most time prospecting also contributed least to pup feeding when present in the group. Regular prospectors lost the most weight over the pup-feeding period and male testosterone levels increased in association with prospecting. As both reduced body condition and elevated testosterone have been shown to compromise the expression of offspring care, these findings provide likely explanations for the reduced pup-feeding rates of regular prospectors. Despite their lapses in contributions to cooperative activities, we found no evidence for punishment of prospectors by other group members, suggesting that helpers are able to adjust their contributions according to their own optima. These findings reveal that male helpers in cooperative species can face similar trade-offs to male parents in noncooperative species, between investment in offspring care and alternative fitness-maximizing tactics such as prospecting. We discuss the broader implications of this work for our understanding of both individual variation and sex differences in contributions to cooperative behaviour.

Animal Behaviour, 70, 2005, p. 559-569

Frequency of social play does not affect dispersal partnerships in wild meerkats

Lynda L. Sharpe

The adaptive significance of play is one of ethology's greatest enigmas, yet few of the many hypotheses advanced to explain play have ever been tested. I evaluated an aspect of the social-bonding hypothesis, which proposes that social play strengthens long-term bonds between individuals, enhancing future alliances. Using data from a wild population, I tested five predictions arising from the hypothesis that meerkats, *Suricata suricatta*, use play to strengthen ties with potential dispersal partners. Meerkats did not favour play with the most appropriate potential partners, that is, they did not prefer their own sex (although they disperse with animals of the same sex only) nor did they strive to play with younger animals (that they could dominate in a future group) or avoid playing with older animals (that they could not). Frequency of play was unrelated to the size of subsequent dispersal parties, or the likelihood of males undertaking prospecting forays with companions, and preferred playmates were not favoured as prospecting partners. Although meerkats preferred to disperse with littermates (and littermates were strongly favoured in play), they played no more frequently with their future dispersal partners than with matched controls with which they did not disperse. I conclude that the strengthening of long-term bonds between potential dispersal partners is not the function of social play in meerkats.

Animal Behaviour, 70, 2005, 551-558

Play does not enhance social cohesion in a cooperative mammal

Lynda L. Sharpe

The social cohesion hypothesis of play asserts that the adaptive function of social play is to strengthen affiliative ties between group members, thereby increasing cohesion within the social group. Although this hypothesis is frequently cited, it has never been quantitatively tested. I used data collected from a wild population of cooperative mongoose (the meerkat, *Suricata suricatta*) to test four predictions arising from the hypothesis: first, that an individual's frequency of play, and mean number of play partners, will be positively correlated with group size (because individuals in large groups must strengthen ties with a greater number of animals); second, an individual's frequency of play will be positively related to frequency of other affiliative interactions such as allogrooming; third, an individual's frequency of play will be positively correlated with level of contribution to cooperative group activities (based on the assumption that individuals that are closely bonded to their group will invest more heavily in the group than those with weak ties); and finally, an individual's frequency of play will be positively correlated with duration of tenancy in the natal group. The behaviour of young meerkats failed to fulfil any of these predictions, and I conclude that social play is unlikely to have the capacity to promote social cohesion in mammals.

Animal Behaviour, 69, 23th March 2005, p. 1273–1284

'False feeding' and aggression in meerkat societies

T. H. Clutton-Brock, A. F. Russell, L. L. Sharpe & N. R. Jordan

In cooperative societies, group members are expected to be punished for being lazy and so behaviours that exaggerate an individual's contribution to cooperation may be favoured by selection. In cooperative meerkats, *Suricata suricatta*, helpers vary in their level of care and, within breeding attempts, helpers can be categorized as 'generous' or 'lazy'. Lazy helpers were more likely to carry food to pups and then eat it themselves and lazy males received more aggression, supporting the idea that 'false feeding' could be an adaptive tactic used to exaggerate individual contributions to care. However, our results are also consistent with the more parsimonious idea that 'false feeding' occurs when individuals decide not to deliver food items after assessing the needs of pups relative to their own. Group members were not obviously deceived by 'false feeders' nor was 'false feeding' associated with any obvious benefit. In general, the frequency of 'false feeding' increased when the net benefits of feeding pups were likely to be low. The frequency of 'false feeding' increased with rising food item value and with decreasing pup dependency on food provided by helpers. Female helpers (which feed pups more than male helpers and preferentially feed female pups) 'false fed' less than male helpers and 'false fed' male pups more than female pups. We suggest that there is little unequivocal evidence of deception by helpers over contributions to care in cooperative vertebrates and that 'false feeding' may occur where helpers adjust their decisions immediately before feeding young or where they are subject to conflicting motivations.

Animal Behaviour 69, 2005, p. 1023-1029

Play fighting does not affect subsequent fighting success in wild meerkats

Lynda L. Sharpe

Despite more than three decades of research, the adaptive significance of play behaviour remains unknown. The practice hypothesis asserts that the primary function of play is to provide animals with the opportunity to practise and refine motor skills needed in adulthood. The apparent similarity between play fighting and serious fighting has led to the assertion that play is 'optimally designed' for the enhancement of combat skills. However, the practice hypothesis of play fighting has never been tested. I used data from a wild population of meerkats, *Suricata suricatta* (a cooperatively breeding mongoose that shows marked reproductive skew), to examine whether play experience improved an individual's subsequent fighting ability. First, meerkats showed no

sex difference in frequency of play fighting (consistent with the optimal design argument, since both males and females fight to obtain the dominant breeding position in a group). Second, frequency of play fighting was not positively correlated with the subsequent likelihood of winning play fights, or the degree of improvement in play-fighting success, as would be expected if play improved fighting manoeuvres (and such manoeuvres must be the same in both play fighting and serious fighting if motor skills are to be effectively practised). Finally, individuals that ultimately won fights for a vacant dominancy did not play fight any more frequently as youngsters, or show any greater success in winning play fights, than matched same-sexed littermates that they defeated in combat.

The American Naturalist, 165, no. 1, January 2005

Dispersal, Eviction, and Conflict in Meerkats (*Suricata suricatta*): An Evolutionarily Stable Strategy Model

P. A. Stephens, A. F. Russell, A. J. Young, W. J. Sutherland, and T. H. Clutton-Brock

Decisions regarding immigration and emigration are crucial to understanding group dynamics in social animals, but dispersal is rarely treated in models of optimal behavior. We developed a model of evolutionarily stable dispersal and eviction strategies for a cooperative mammal, the meerkat *Suricata suricatta*. Using rank and group size as state variables, we determined state-specific probabilities that subordinate females would disperse and contrasted these with probabilities of eviction by the dominant female, based on the long-term fitness consequences of these behaviors but incorporating the potential for error. We examined whether long-term fitness considerations explain group size regulation in meerkats; whether long-term fitness considerations can lead to conflict between dominant and subordinate female group members; and under what circumstances those conflicts were likely to lead to stability, dispersal, or eviction. Our results indicated that long-term fitness considerations can explain group size regulation in meerkats. Group size distributions expected from predicted dispersal and eviction strategies matched empirical distributions most closely when emigrant survival was approximately that determined from the field study. Long-term fitness considerations may lead to conflicts between dominant and subordinate female meerkats, and eviction is the most likely result of these conflicts. Our model is computationally intensive but provides a general framework for incorporating future changes in the size of multimember cooperative breeding groups.

Keywords: cooperative breeding _ ESS model _ reproductive skew _ social queuing.

Interaction Studies, 5:3, 2004, p. 327–344.

Vocalize to localize: A test on functionally referential alarm calls

Marta B. Manser and Lindsay B. Fletcher

In this study of the functionally referential alarm calls in the meerkats (*Suricata suricatta*), we tested the hypothesis that the ability to refer to a specific location was an important factor in the evolution of discrete vocalizations. We investigated what information receivers gained about the location of the predator from alarm calls with high stimulus specificity compared to alarm calls with low stimulus specificity. Furthermore, we studied whether visual cues about the localization of the predator may be available from the posture of the caller. We described the general behaviour of the caller, the caller's posture, and in particular its gaze direction. We then observed receivers responding to the different call types, to determine whether the acoustic structure of the calls was enough for them to respond in the appropriate way, or whether they used additional visual cues from the caller. We tested this with specific manipulation experiments, using three setups of playback experiments: (1) no caller visible; (2) model guard with specific gaze direction; and (3) live sentinel. Natural observations and experiments confirmed that in high urgency situations the meerkats have enough information from the acoustic structure of the call to respond appropriately. When hearing low urgency calls that are less stimuli specific, meerkats used visual cues as an additional source of information in a few cases. This may indicate that functionally

referential calls evolved to denote the location of the predator, rather than the predator type or its velocity of approach. However, when discussing this result in comparison to other functionally referential calls, such as the food associated calls and recruitment calls, this localization hypothesis does not appear to apply to the functionally referential calls in general.

Keywords: evolution _ vocalization _ *Suricata suricatta* (meerkat) _ localization

Animal Behaviour, 68, 2004, p. 151-157

Spatial representation of shelter locations in meerkats, *Suricata suricatta*

Marta B. Manser & Matthew B. Bell

We used observations and manipulation experiments to investigate how meerkats, social mongooses living under high predation pressure, find shelter from predators quickly within their territory. We played back alarm calls to foraging meerkats and dug new boltholes and covered existing ones to see whether location or other cues were used. Meerkats almost always ran to the bolthole closest to them. This was not done by a simple rule of running back to a bolthole they had just passed, nor by escaping in any direction and finding a bolthole by chance. Meerkats nearly always ignored the boltholes that we dug but ran to those we had covered up. Our results support the hypothesis that meerkats know in which direction to run when an alarm call is given, without scanning the area for visual or olfactory cues of shelters. As meerkats have more than 1000 boltholes in their territory, our results suggest that they have detailed knowledge of the direction and the distance of specific locations. However, this does not necessarily mean that they have a spatial map of their territory; our results may be explained by place recognition or reorientation of specific landmark features.

Animal Behaviour, 68, 2004, p. 1029-1040

Behavioural tactics of breeders in cooperative meerkats

T. H. Clutton-Brock, A. F. Russell, L. L. Sharpe

In eusocial invertebrates, queens commonly show morphological and behavioural modifications to their role as the principal breeders in their colonies. With the exception of naked mole-rats, *Heterocephalus glaber*, morphological modification of breeders has yet to be shown in cooperative vertebrates, but the behaviour of dominant individuals may be modified so as to maximize reproductive success. We studied the cooperative behaviour of dominant and subordinate adults in meerkats, *Suricata suricatta*, and found that the decision rules governing the contributions of dominant breeders differed from those of subordinate helpers. Dominant breeders contributed less than adult helpers to babysitting and pup feeding, but raised their individual contributions to pup care to a greater extent when helper:pup ratios were low. In contrast to subordinates, dominant breeders did not increase their contributions when they foraged successfully. Finally, while subordinates of both sexes assisted in rearing the young when dominants bred, dominant females contributed little when subordinates attempted to breed, and male helpers (but not females) reduced their contributions to the care of pups. Our results suggest that the division of labour between breeders and helpers in meerkats is intermediate between that of facultatively cooperative species, where parents are principally responsible for rearing young, and that of specialized eusocial species, which show a well-defined division of labour between breeders and workers.

Hormones and Behavior, 46, 2004, p. 141– 150

Hormonal correlates of dominance in meerkats (*Suricata suricatta*)

Anne A. Carlson, Andrew J. Young, Andrew F. Russell, Nigel C. Bennett, Alan S. McNeilly, and Tim Clutton-Brock

In cooperatively breeding meerkats (*Suricata suricatta*), individuals typically live in extended family groups in which the dominant male and female are the primary reproductives, while their offspring delay dispersal, seldom breed, and contribute to the care of subsequent litters. Here we investigate hormonal differences between dominants and subordinates by comparing plasma levels of luteinizing hormone (LH), estradiol and cortisol in females, and testosterone and cortisol in males, while controlling for potential confounding factors. In both sexes, hormone levels are correlated with age. In females, levels of sex hormone also vary with body weight and access to unrelated breeding partners in the same group: subordinates in groups containing unrelated males have higher levels of LH and estradiol than those in groups containing related males only. When these effects are controlled, there are no rank-related differences in circulating levels of LH among females or testosterone among males. However, dominant females show higher levels of circulating estradiol than subordinates. Dominant males and females also have significantly higher cortisol levels than subordinates. Hence, we found no evidence that the lower levels of plasma estradiol in subordinate females were associated with high levels of glucocorticoids. These results indicate that future studies need to control for the potentially confounding effects of age, body weight, and access to unrelated breeding partners before concluding that there are fundamental physiological differences between dominant and subordinate group members.

Animal Behaviour, 66, 2003, p. 989–997

Social play does not reduce aggression in wild meerkats

L. L. Sharpe, M. I. Cherry

Of the numerous hypotheses advanced to explain the adaptive significance of play, several assert that social play increases social harmony, cementing alliances and reducing aggression between group members or littermates. These hypotheses are frequently cited, but their validity remains unknown. We examined the relation between social play and aggression in juvenile meerkats, *Suricata suricatta*, living in a wild population in the southern Kalahari Desert. We tested the hypothesis that social play reduces aggression, by examining rates of play, play partner choices, the structure of social play and rates of aggressive interactions during foraging. We found no relation between frequency of play and level of aggression, either between individuals or during the course of development. Pups that played together frequently were just as aggressive towards one another as pairs of pups that played infrequently, and play interactions had no subsequent effect on the likelihood of aggression. In contrast, aggressive interactions during foraging inhibited the subsequent likelihood of play, and high levels of aggression during foraging changed the structure of social play, with victimized pups avoiding play wrestling. We conclude that social play does not reduce aggression in young meerkats.

PNAS, 100, 18 March 2003, p. 3333–3338

Cost minimization by helpers in cooperative vertebrates

A. F. Russell, L. L. Sharpe, P. N. M. Brotherton, and T. H. Clutton-Brock

When parents invest heavily in reproduction they commonly suffer significant energetic costs. Parents reduce the long-term fitness implications of these costs through increased foraging and reduced reproductive investment in the future. Similar behavioral modifications might be expected among helpers in societies of cooperative vertebrates, in which helping is associated with energetic costs. By using multivariate analyses and experiments, we show that in cooperative meerkats, *Suricata suricatta*, helping is associated with substantial short-term growth costs but limited long-term fitness costs. This association forms because individual contributions to cooperation are initially condition dependent, and, because when helpers invest heavily in cooperation, they increase their foraging rate during the subsequent nonbreeding period and reduce their level of cooperative investment in the subsequent reproductive period. These results provide a unique demonstration that despite significant short-term costs, helpers, like breeders, are able to reduce the fitness consequences of these costs through behavioral modifications.

Behavioral Ecology, 14.4, 2003, p. 486–492

Breeding success in cooperative meerkats: effects of helper number and maternal state

A. F. Russell, P. N. M. Brotherton, G. M. McIlrath, L. L. Sharpe, and T. H. Clutton-Brock

Studies of cooperatively breeding birds and mammals generally concentrate on the effects that helpers have on the number of reproductive attempts females have per year or on the number and size of offspring that survive from hatching/weaning to independence. However, helpers may also influence breeding success before hatching or weaning. In the present study, we used an ultrasound imager to determine litter sizes close to birth, and multivariate statistics to investigate whether helpers influence female fecundity, offspring survival to weaning, and offspring size at weaning in cooperative meerkats, *Suricata suricatta*. We found that the number of helpers in a group was correlated with the number of litters that females delivered each year, probably because females in large groups gave birth earlier and had shorter interbirth intervals. In addition, although pup survival between birth and weaning was primarily influenced by maternal dominance status, helper number may also have a significant positive effect. By contrast, we found no evidence to suggest that helpers have a direct effect on either litter sizes at birth or pup weights at weaning, which were both significantly influenced by maternal weight at conception. However, because differences in maternal weight were associated with differences in helper number, helpers have the potential to influence maternal fecundity and offspring size within reproductive attempts indirectly. These results suggest that future studies may need to consider direct and indirect helper effects on female fecundity and investment before assessing helper effects on reproductive success in societies of cooperatively breeding vertebrates.

Key words: differential allocation _ fecundity _ helper _ maternal effects _ ultrasound _ weight

Animal Behaviour, 66, 2003, p. 531–540

Meerkat helpers do not specialize in particular activities

T. H. Clutton-Brock, A. F. Russell, L. L. Sharpe

Differences in the relative contributions of individual helpers to cooperative activities in vertebrate societies are sometimes interpreted as evidence of functional specialization and have been compared with the incipient subcaste systems found in some social insects. However, it is not yet clear whether some helpers specialize in particular tasks throughout their life span or whether variation in cooperative behaviour represents a temporary, age-related polyethism. We describe the development of cooperative behaviour in female helpers in meerkats, *Suricata suricatta*, an obligately cooperative mammal where young produced by the dominant female are reared by up to 30 helpers. Using a combination of field experiments and long-term records of the development of individuals, we investigated whether particular helpers specialize in particular activities. In the first year of life, variation in body weight affected overall levels of involvement in cooperative behaviour as well as relative contributions to different activities, generating contrasting activity profiles between light and heavy helpers. However, the effects of body weight disappeared by the second year of life, and individual differences in foraging success became the principal factor affecting contributions to cooperative behaviour. Contributions to different cooperative activities were positively correlated across individuals, with some helpers consistently contributing more than others to all cooperative activities. Our study provides no evidence that meerkat helpers specialize in particular cooperative activities.

Science, 291, 19 January 2001, p. 478-

Cooperation, Control, and Concession in Meerkat Groups

T. H. Clutton-Brock, P. N. M. Brotherton, A. F. Russell, M. J. O'Riain, D. Gaynor, R. Kansky, A. Griffin, M. Manser, L. Sharpe, G. M. McIlrath, T. Small, A. Moss, S. Monfort

“Limited control” models of reproductive skew in cooperative societies suggest that the frequency of breeding by subordinates is determined by the outcome of power struggles with dominants. In contrast, “optimal skew” models suggest that dominants have full control of subordinate reproduction and allow subordinates to breed only when this serves to retain subordinates’ assistance with rearing dominants’ own litters. The results of our 7-year field study of cooperative meerkats, *Suricata suricatta*, support the predictions of limited control models and provide no indication that dominant females grant reproductive concessions to subordinates to retain their assistance with future breeding attempts.

General and Comparative Endocrinology, 130, 2003, p. 148–156

Radioimmunoassay of prolactin for the meerkat (*Suricata suricatta*), a cooperatively breeding carnivore

Anne A. Carlson, Linda Nicol, Andrew J. Young, Al F. Parlow, and Alan S. McNeilly

We report the development and validation of a highly specific heterologous radioimmunoassay (RIA) to measure meerkat prolactin (PRL) by using rabbit antiserum to human prolactin and canine [125I]iodo-PRL. Dilutions of meerkat pituitary standard and plasma gave parallel inhibition curves in the assay. Gel filtration of meerkat pituitary extracts and canine [125I]iodo-PRL run separately on a Sephadex G-100 generated identical peaks of activity, and Western blot analysis of meerkat pituitary extract with the human prolactin antiserum used in the RIA gave a molecular weight similar to canine prolactin (21 kDa). We carried out a biological validation of the prolactin assay by administering three different doses each of sulpiride and cabergoline to adult male meerkats. Increasing doses of sulpiride and cabergoline caused substantial increases and decreases, respectively, in the plasma prolactin of the study animals as expected. Activation of the stress response in meerkats by capture and ketamine hydrochloride anesthesia caused short-term but significant increases in prolactin levels in individuals bled repeatedly. The RIA developed and described here was able to determine plasma concentrations of prolactin in all animals sampled. We conclude, however, that it will be important in all future studies to confine blood sampling times to 4–7 min after capture/administration of anesthesia to avoid the confounding effects of the stress response on prolactin levels.

Keywords: Prolactin _ RIA _ Meerkat _ Validation _ Co-operative breeder

Animal Behaviour, 64, 2002, p. 113–121

Experimental provisioning increases play in free-ranging meerkats

L. L. Sharpe, T. H. Clutton-Brock, P. N. M. Brotherton, E. Z. Cameron, M. I. Cherry

The sensitivity of play to variations in food availability has been cited as evidence of the costliness of play, since energetically stressed animals dispense with costly behaviours. However, the causality of the relationship between nutrition and play has not been adequately tested. Using weight gain as a measure of food intake, we documented the food consumption of free-ranging meerkat, *Suricata suricatta*, pups and found that long-term nutritional status (weight gain over a 6-week period) was positively correlated with rates of play. We confirmed the causality of this relationship by conducting long-term (4–8 weeks) provisioning experiments that raised the nutritional status of experimental pups, subadults and adults. Experimental animals more than doubled their rate of play compared with their nonprovisioned controls. Short-term variations in food consumption (daily weight gain) were not correlated with subsequent rates of play, and we used a short-term feeding experiment to document the transitory effects of hunger satiation. We established that an increase in available energy contributed to the increase in rates of play, rather than the animals simply having more time available to play as a result of being released from the constraints of foraging. We conclude that play in meerkats was energetically costly, and must be adaptive given that the cost of play to juveniles (in terms of future reproductive success) was potentially high.

Journal of Animal Ecology, 71, 2002, p. 700–709

Factors affecting pup growth and survival in co operatively breeding meerkats *Suricata suricatta*

A. F. Russell, T. H. Clutton-Brock, P. N. M. Brotherton, L. L. Sharpe, G. M. McIlrath, F. D. Dalerum, E. Z. Cameron, J. A. Barnard

1. We examined the relative importance of maternal, environmental and social factors for post-weaning pup growth and survival in a co-operatively breeding mammal, the meerkat *Suricata suricatta*.
2. Pup daily weight gain was primarily influenced by the number of carers per pup and the daily weight gain of those carers. Rainfall and daily temperatures had additional positive and negative effects, respectively, on weight gain of pups born to subordinates.
3. Pup overnight weight loss was primarily influenced by the amount of weight pups gained during the day, and their age. However, pups also lost considerably more weight overnight when temperatures were cold, although such effects were less in large groups.
4. Pup growth rates were positively influenced by the number of carers per pup and carer condition, and negatively influenced by high daytime temperatures.
5. Pup weight at independence was positively associated with weight at emergence and pup weight gain during provisioning, but negatively associated with the extent of overnight weight loss.
6. Pup survival between emergence and independence was related to maternal status, pup sex and overnight weight loss, as well as to group size, daytime temperature and monthly rainfall.
7. Thus, in meerkats, social factors largely, but not wholly, replace the importance of maternal factors that are commonly found to govern reproductive success in nonco-operatively breeding social vertebrates.

Key-words: condition, helpers, kin selection, maternal, social, weight.

Science, 297, 12 July 2002, p.253-256

Evolution and Development of Sex Differences in Cooperative Behavior in Meerkats

T. H. Clutton-Brock, A. F. Russell, L. L. Sharpe, A. J. Young, Z. Balmforth, G. M. McIlrath

In cooperatively breeding birds, where helpers of both sexes assist with the provisioning and upbringing of offspring who are not their own, males tend to contribute more than females to rearing young. This sex difference has been attributed to paternity uncertainty, but could also occur because males contribute more where they are likely to remain and breed in their group of origin. In contrast to most birds, female meerkats (*Suricata suricatta*) are more likely to breed in their natal group than males. We show that female meerkat helpers contribute more to rearing young than males and that female helpers feed female pups more frequently than males. Our results suggest that sex differences in cooperative behavior are generated by sex differences in philopatry and occur because females derive greater direct benefits than males from raising recruits to their natal group. These findings support the view that direct, mutualistic benefits are important in the evolution of specialized cooperative behavior.

Science, 296, 5 April 2002, p. 69-72

Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates

Tim Clutton-Brock

In cooperatively breeding vertebrates, nonbreeding helpers raise young produced by dominant breeders. Although the evolution of cooperative breeding has often been attributed primarily to kin

selection (whereby individuals gain “indirect” benefits to their fitness by assisting collateral relatives), there is increasing evidence that helpers can be unrelated to the young they are raising. Recent studies also suggest that the indirect benefits of cooperative behavior may often have been overestimated while the direct benefits of helping to the helper’s own fitness have probably been underestimated. It now seems likely that the evolutionary mechanisms maintaining cooperative breeding are diverse and that, in some species, the direct benefits of helping may be sufficient to maintain cooperative societies. The benefits of cooperation in vertebrate societies may consequently show parallels with those in human societies, where cooperation between unrelated individuals is frequent and social institutions are often maintained by generalized reciprocity.

TRENDS in Cognitive Sciences, 6.2, February 2002, p. 55-57

Suricate alarm calls signal predator class and urgency

Marta B. Manser, Robert M. Seyfarth and Dorothy L. Cheney

Human speech encodes both referential and affective information, but evidence for a similar phenomenon in animal vocalizations has been lacking. Recent work on suricates, an African mongoose, shows that animal alarm calls simultaneously encode information about both predator type and the signaler’s perception of urgency.

General and Comparative Endocrinology, 122, 2001, p. 158–171

Longitudinal Gonadal Steroid Excretion in Free-Living Male and Female Meerkats (*Suricata suricatta*)

Allison M. Moss, T. H. Clutton-Brock, and S. L. Monfort

Slender-tailed meerkats (*Suricata suricatta*) are small, diurnal, cooperatively breeding mongooses of the family Herpestidae. A prerequisite to fully understanding the mating system of meerkats is the development of a normative reproductive–endocrine database. This study examined longitudinal gonadal steroid excretion in all adult and juvenile individuals of both sexes within a social group of free-living meerkats sampled across an entire breeding season. The specific objectives of this study were to (1) validate noninvasive (fecal and urinary) gonadal steroid hormone monitoring techniques in male (testosterone) and female (estrogens, progestagens) meerkats; (2) test the feasibility of using these noninvasive methods under field conditions; (3) characterize the endocrine correlates associated with the female reproductive cycle, including estrus, gestation, and postpartum estrus; (4) examine longitudinal androgen excretion in males; and (5) determine whether social status (i.e., dominant versus subordinate) affected gonadal steroid excretion. In females, the results demonstrated the physiological validity of noninvasive monitoring in meerkats by corresponding excretory hormone concentrations to major reproductive events (i.e., estrous, pregnancy, parturition). Hormone excretory patterns during estrous intervals suggested possible mechanisms whereby reproductive suppression may operate in female meerkats. In males, androgen excretion did not correspond to changes in reproductive and aggressive behaviors, suggesting that dominance, and hence breeding access to females, was not regulated strictly by gonadal steroid production. The consistency in androgen excretion among male meerkats indicated that reproductive suppression may be mediated by behavioral (i.e., intermale aggression) rather than physiological (i.e., depressed spermatogenesis) mechanisms.

Key Words: fecal steroids _ urinary steroids _ progestagens _ estrogens _ testosterone _ suricates _ meerkats

Molecular Ecology Notes 1, 2001, p. 83-85

A panel of microsatellites developed for meerkats (*Suricata suricatta*) by cross-species amplification and species-specific cloning

A. S. Griffin, B. Nürnberger, J. M. Pemberton

We describe the compilation of a panel of 12 polymorphic microsatellite loci suitable for inference of parentage and relatedness in the cooperatively breeding meerkat (*Suricata suricatta*). First, three of 70 microsatellite primer pairs characterized from other carnivores, specifically cat (*Felis catta*), dog (*Canis familiaris*) and grey seal (*Halichoerus grypus*) revealed polymorphic microsatellites in meerkats. Second, a further nine loci were isolated from meerkats by screening a plasmid library with a 32P-labelled (CA)₁₅ probe.

Keywords: cross-species amplification _ meerkat _ microsatellite _ species-specific cloning _ *Suricatasuricatta*

Animal Behaviour, 61, 2001, p. 705–710

Contributions to cooperative rearing in meerkats

T. H. Clutton-Brock, P. N. M. Brotherton, M. J. O’Riain, A. S. Griffin, D. Gaynor, R. Kansky, L. Sharpe, G. M. McIlrath

In vertebrate societies where young are reared communally, nonbreeding helpers are usually closely related to young but often vary widely in their contributions to feeding them. Evolutionary explanations of helping behaviour have focused on whether differences in the level of contributions between helpers are related to variation in kinship. We investigated the contribution of helpers in meerkats, *Suricata suricatta*. The helpers varied widely in the number of food items they gave to pups and individual differences were related to variation in foraging success as well as to sex and age. When we controlled the influence of these variables, the level of contributions that helpers made to rearing pups was not significantly correlated with variation in kinship to the litters they were rearing.

Science, 293, 28 September 2001, p. 2446-2449

Effects of Helpers on Juvenile Development and Survival in Meerkats

T. H. Clutton-Brock, A. F. Russell, L. L. Sharpe, P. N. M. Brotherton, G. M. McIlrath, S. White, E. Z. Cameron

Although breeding success is known to increase with group size in several cooperative mammals, the mechanisms underlying these relationships are uncertain. We show that in wild groups of cooperative meerkats, *Suricata suricatta*, reductions in the ratio of helpers to pups depress the daily weight gain and growth of pups and the daily weight gain of helpers. Increases in the daily weight gain of pups are associated with heavier weights at independence and at 1 year of age, as well as with improved foraging success as juveniles and higher survival rates through the first year of life. These results suggest that the effects of helpers on the fitness of pups extend beyond weaning and that helpers may gain direct as well as indirect benefits by feeding pups.

Behavioral Ecology, 12.5, 2001, p. 590–599

Offspring food allocation by parents and helpers in a cooperative mammal

P. N. M. Brotherton, T. H. Clutton-Brock, M. J. O’Riain, D. Gaynor, L. Sharpe, R. Kansky, and G. M. McIlrath

In cooperatively breeding species, helpers and parents commonly face two decisions when they find a food item: first, whether to feed the item to a young group member or to eat it themselves; and second, which offspring to feed. Little is known about the factors that influence these decisions in cooperative mammals, though optimal foraging theory provides a basis for a range of predictions. In this article we describe pup feeding behavior by helpers and parents in a cooperative mongoose, the meerkat (*Suricata suricatta*). When meerkat pups begin accompanying the group, they beg food from older group members, who dig up dispersed prey

items. As predicted, the probability of a prey item being fed to a pup shows a positive relationship with prey size and a negative relationship with pup distance. Meerkats apparently follow a “feed the nearest pup rule” and are more likely to feed the nearest pup if it is hungry. Hungrier pups beg more and follow older group members more closely. Across all age categories, females feed pups more frequently than males, both in terms of the relative frequency of feeds, and the proportion of prey biomass found by each individual that is fed to pups. Females also feed female pups significantly more than male pups, while males feed pups of both sexes equally. These sex biases in feeding contributions may result from female group members benefiting more than males from higher pup survival, and in particular higher female pup survival, because females are the philopatric sex.

Proceedings of the Royal Society London B, 268, 2001, p. 2315-2324

The acoustic structure of suricate’s alarm calls varies with predator type and the level of urgency

Marta B. Manser

The variation in the acoustic structure of alarm calls appears to convey information about the level of response urgency in some species, while in others it seems to denote the type of predator. While theoretical models and studies on species with functionally referential calls have emphasized that any animal signal considered to have an external referent also includes motivational content, to our knowledge, no empirical study has been able to show this. In this paper, I present an example of a graded alarm calls system that combines referential information and also information on the level of urgency. Acoustically different alarm calls in the social mongoose *Suricata suricatta* are given in response to different predator types, but their call structure also varies depending on the level of urgency. Low urgency calls tend to be harmonic across all predator types, while high urgency calls are noisier. There was less evidence for consistency in the acoustic parameters assigned to particular predator types across different levels of urgency. This suggests that, while suricates convey information about the level of urgency along a general rule, the referential information about each category of predator type is not encoded in an obvious way.

Keywords: alarm calls _ functionally referential _ level of response urgency _ suricates _ social mammals

Proceedings of the Royal Society London B, 268, 2001, p. 2485-2491

The information that receivers extract from alarm calls in suricates

Marta B. Manser, Matthew B. Bell and Lindsay B. Fletcher

Field observations and acoustic analyses have shown that suricate (*Suricata suricatta*) alarm calls vary in their acoustic structure depending on predator type. In this study, we tested whether receivers responded appropriately when hearing a call in the absence of a predator. Although the only way for suricates to escape from predators is to retreat to boltholes, responses to playbacks could be divided into distinct categories. The subjects responded differently to alarm calls given in response to aerial or terrestrial predators and to recruitment calls emitted in response to snakes and deposits on the ground. Suricates also showed rather distinct responses to low, medium and high urgency aerial calls. Differences in the response were less obvious for different levels of urgency in the terrestrial and recruitment calls. Suricate receivers thus gain information about both the predator type and level of urgency from the acoustic structure of their calls.

Keywords: alarm calls _ functionally referential _ level of response urgency _ receivers _ suricates

Behav Ecol Sociobiol, 48, 2000, 471–477

Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats (*Suricata suricatta*)

M.J. O’Riain, N.C. Bennett, P.N.M. Brotherton, G. McIlrath, T.H. Clutton-Brock

Meerkats live in co-operatively breeding familial groups in which reproduction is monopolised by a dominant pair of breeders. Offspring of the breeders are behaviourally subordinate, and typically remain in their natal group as sexually mature, non-breeding helpers. In this study, we investigated the proximate factors limiting subordinate reproduction. Evidence for reproductive suppression by dominants was investigated by comparing life history, behaviour and hormonal profiles of dominants and subordinates. Baseline levels of plasma luteinising hormone (LH) were significantly higher in dominant than in subordinate females. However, following an exogenous injection of gonadotrophin-releasing hormone (GnRH), both categories had comparable concentrations of circulating LH. There were no significant differences in pre- or post-GnRH challenge LH levels in dominant or subordinate males. Reproduction in both dominant and subordinate females rarely occurred in the absence of unrelated males. Given that groups typically comprise parents and offspring, lack of suitable mates emerged as the primary constraint on subordinate reproduction. When this constraint was removed, subordinates typically bred but at a lower rate than dominants. This difference in reproduction may be attributed to intrasexual competition manifested through direct interference by dominant females through subordinate evictions, infanticide and the abandoning of subordinate litters. We argue that differences in reproductive regulation within mammalian co-operative breeding systems may be explained by differences in the mating strategy (inbreeding versus outbreeding) and the probability that subordinates in obligate outbreeding species will encounter unrelated opposite-sex partners.

Keywords: Suppression · Co-operative breeding · Inbreeding avoidance · Social

Proc. R. Soc. Lond. B, 267, 2000, p. 301-305

Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*

T. H. Clutton-Brock, P. N. M. Brotherton, M. J. O’Riain, A. S. Griffin, D. Gaynor, L. Sharpe, R. Kinsky, M. B. Manser and G. M. McIlrath

Evolutionary explanations of cooperative breeding based on kin selection have predicted that the individual contributions made by different helpers to rearing young should be correlated with their degree of kinship to the litter or brood they are raising. In the cooperative mongoose or meerkat, *Suricata suricatta*, helpers babysit pups at the natal burrow for the first month of pup life and frequent babysitters suffer substantial weight losses over the period of babysitting. Large differences in contributions exist between helpers, which are correlated with their age, sex and weight but not with their kinship to the young they are raising. Provision of food to some group members raises the contributions of individuals to babysitting. We discuss the implications of these results for evolutionary explanations of cooperative behaviour.

Keywords: mammals _ cooperation _ helping behaviour

Behav Ecol Sociobiol, 48, 2000, p. 429–437

The effect of pup vocalisations on food allocation in a cooperative mammal, the meerkat (*Suricata suricatta*)

Marta B. Manser, Greg Avey

In the meerkat (*Suricata suricatta*), a cooperative mongoose, pups follow potential feeders while the group is foraging and emit incessant calls when soliciting food from them. In contrast to a ‘stationary’ brood of chicks, in which nestlings are fed at a fixed location, meerkat pups are ‘mobile’ and become spread out. The question arises whether meerkat pups that experience different constraints to those facing chicks have evolved similar begging strategies. This paper describes the vocalisations that meerkat pups emit in the context of begging and investigates the

influence of these calls on food allocation by older group members and on the behaviour of littermates. Meerkat pups use two types of calls when soliciting food from a potential feeder. The most common is a 'repeat' call, which pups emit continuously when following an older forager over several hours a day. In addition, when a potential feeder finds a prey item, the pups next to it emit a bout of calls with increased calling rate, amplitude and fundamental frequency, termed 'high-pitched' calls. Observations, together with playback experiments, showed that more prey was allocated to pups that called longer and more intensely. The pup closest to a feeder was almost always fed. The probability of emitting high-pitched calls did not depend on the time since a pup had received food, and the change from repeat to high-pitched calls occurred suddenly. The main function of the high-pitched call, therefore, does not appear to be to signal a pup's hunger state. More likely, the two calls, in the context of begging, may be an adaptation to energetic constraints in a mobile feeding system. Pups, which are dispersed during foraging, may emit repeat calls over long periods to prevent potential feeders from eating all the prey themselves. At the moment a potential feeder finds prey, pups may give the more intense high-pitched calls to direct feeders to bring the food item to them and not to a littermate. Therefore, unlike the stationary feeding system where chicks emit one type of begging call when the feeder approaches the nest, meerkats, with a mobile feeding system, have evolved two discrete types of vocalisations in the context of begging.

Keywords Begging vocalisations · Parent-offspring conflict · Sibling competition · Mobile feeding system · Meerkat · Suricate

Journal of Animal Ecology, 57, 2000, p.561-572

Predation group size and mortality in a cooperative mongoose *Suricata suricatta*

T. H. Clutton-Brock, D. Gaynor, G. M. McIlrath, A. D. C. Maccoll, R. Kansky, P. Chadwick, M. Manser, J. D. Skinner, P. N. M. Brotherton

In social mammals where group members cooperate to detect predators and raise young, members of small groups commonly show higher mortality or lower breeding success than members of large ones. It is generally assumed that this is because large group size allows individuals to detect or repel predators more effectively but other benefits of group size may also be involved, including reduced costs of raising young and more effective competition for resources with neighbouring groups.

1. To investigate the extent to which predation rate affects survival, we compared mortality rates in two populations of suricates (*Suricata suricatta*), one living in an area of high predator density (Kalahari Gemsbok Park) and one living in an area of relatively low predator density (neighbouring ranchland). Most aspects of feeding ecology and growth (including time spent feeding, daily weight gain, growth, adult body weight, breeding frequency and neonatal mortality) were similar in the two populations. In contrast, mortality of animals over 3 months old was 1.7 times higher in the Park than on ranchland.

2. Mortality of juveniles between emergence from the natal burrow and 6 months of age was higher in small groups than large ones in the Park but significantly lower in small groups than large ones on ranchland. Adult mortality declined in larger groups in both areas.

3. The tendency for survival to be low in small groups had far-reaching consequences for the risk of group extinction. During a year of low rainfall in the Park, all groups of less than nine animals became extinct and population density declined to around a third of its initial level. We argue that high group extinction rates are to be expected in species where survival declines in small groups and mortality rates are high.

Key-words: cooperative breeding _ demography _ mammals _ mortality

Proceedings of the Royal Society London B, 266, 1999, p. 1013-1019

Response of foraging group members to sentinel calls in suricates, *Suricata suricatta*

Marta B. Manser

In the suricate (*Suricata suricatta*), a cooperatively breeding mongoose, one individual typically watches out for predators while the rest of the group is foraging. Most of the time these sentinels announce their guarding duty with special vocalizations. The response of foraging group members to these calls was investigated by analysing observational data, and by performing playback experiments. The use of special calls by sentinels, and the responses of the foraging group members to them, suggest that the coordination of vigilance is strongly influenced by vocal communication. Sentinel calls decreased the time spent alert by the foraging group members. Other group members were less likely to go on guard when a sentinel was vocalizing. Both the proportion of time during which guards overlapped, and the proportion of time the group was unprotected without a guard, decreased when sentinels announced their duty, due to better coordination of the rotation of sentinels. Suricates, however, do not appear to use sentinel calls to mediate a strict rotation of guarding duty.

Keywords: sentinel calls _ sentinels _ vigilance _ cooperative breeding _ suricates

Science, 284, 4 June 1999, p. 1640-1644

Selfish Sentinels in Cooperative Mammals

T. H. Clutton-Brock, M. J. O'Riain, P. N. M. Brotherton, D. Gaynor, R. Kansky, A. S. Griffin, M. Manser

Like humans engaged in risky activities, group members of some animal societies take turns acting as sentinels. Explanations of the evolution of sentinel behavior have frequently relied on kin selection or reciprocal altruism, but recent models suggest that guarding may be an individual's optimal activity once its stomach is full if no other animal is on guard. This paper provides support for this last explanation by showing that, in groups of meerkats (*Suricata suricatta*), animals guard from safe sites, and solitary individuals as well as group members spend part of their time on guard. Though individuals seldom take successive guarding bouts, there is no regular rota, and the provision of food increases contributions to guarding and reduces the latency between bouts by the same individual.

Ethology, 105, 1999, p. 851-866

Co-operative Rearing by Slender-tailed Meerkats "*Suricata suricatta*" in the Southern Kalahari

S. P. Doolan, D. W. Macdonald

Slender-tailed meerkats or suricates (*Suricata suricatta*) are small, gregarious and largely insectivorous mongooses which inhabit the arid and semi-arid areas of southern Africa. We describe four elements of co-operative rearing of the young: 1. babysitting at the den, 2. creching on foraging trips, 3. provisioning with prey items away from the den, and 4. allonursing, including spontaneous lactation. Individual band members differed markedly in contributions to co-operative rearing. All adults and yearlings guarded the den and helpers actively defended young against predators. Breeders babysat significantly less than did non-breeding adults. Differences in age-sex class contributions were also evident in creching behaviour. The feeding of kittens by provisioners extended from soon after their first emergence from the den at 2-3 wk of age to effective foraging independence at 10-12 wk. Breeding females initially contributed little care other than nursing. Allonursing occurred in six of 25 closely observed litters, including three incidents of spontaneous lactation when subordinates nursed the young of higher-ranking females. Such co-operation is likely to be critical to the survival of these highly sociable mongooses in a semi-arid environment such as the Kalahari where food availability can fluctuate enormously.

Proc. R. Soc. Lond. B, 265, 1998, p. 185-190

Costs of cooperative behaviour in suricates (*Suricata suricatta*)

T. H. Clutton-Brock, D. Gaynor, R. Kansky, A. D. C. MacColl, G. McIlrath, P. Chadwick, P. N. M. Brotherton, J. M. O'Riain, M. Manser and J. D. Skinner

Functional interpretations of helping behaviour suggest that it has evolved because helpers increase their direct or indirect fitness by helping. However, recent critiques have suggested that helping may be an unselected extension of normal parental behaviour, pointing to evidence that all mature individuals commonly respond to begging young (whether they are parents, relatives or non-relatives) as well as to the lack of evidence that cooperative activities have appreciable costs to helpers. Here we provide an example of one form of cooperative behaviour that is seldom performed by parents and has substantial energetic costs to helpers. In the cooperative mongoose, *Suricata suricatta*, non-breeding adults commonly babysit young pups at the natal burrow for a day at a time, foregoing feeding for 24 hours. Parents rarely contribute to babysitting, and babysitting has substantial energetic costs to helpers. Members of small groups compensate for the reduced number of participants by babysitting more frequently, and neither the proportion of time that babysitters are present nor the survival of litters vary with group size.

Keywords: cooperation _ carnivores _ breeding costs _ guarding

Proc. R. Soc. Lond. B, 265, 1998, p. 2291-2295

Infanticide and expulsion of females in a cooperative mammal

T. H. Clutton-Brock, P. N. M. Brotherton, R. Smith, G. M. McIlrath, R. Kansky, D. Gaynor, M. J. O'Riain and J. D. Skinner

In cooperative groups of suricates (*Suricata suricatta*), helpers of both sexes assist breeding adults in defending and feeding pups, and survival rises in larger groups. Despite this, dominant breeding females expel subordinate females from the group in the latter half of their (own) pregnancy, apparently because adult females sometimes kill their pups. Some of the females that have been expelled are allowed to rejoin the group soon after the dominant female's pups are born and subsequently assist in rearing the pups. Female helpers initially resist expulsion and repeatedly attempt to return to their natal group, indicating that it is unlikely that dominant females need to grant them reproductive concessions to retain them in the group.

Keywords: dispersal _ cooperative breeding _ reproductive skew

African Journal of Ecology, 37, March 1999, p. 69

Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari

T. H. Clutton-Brock, A. Maccoll, P. Chadwick, D. Gaynor, R. Kansky and J. D. Skinner

In most respects, the demography of Kalahari suricates (*Suricata suricatta*) resembles that of other social mongooses. Average group size varies from four to nine, and groups typically include several mature females, of which one is responsible for the majority of breeding attempts. Breeding females show a postpartum oestrus; gestation is around 60 days; litter size is three to five pups at emergence and females rarely breed before the age of 24 months. In contrast, annual survival rates (0.20 for pups and 0.43 for animals over one year old) are lower than those recorded in other species. Breeding frequency is related to rainfall and breeding can cease altogether when rainfall is unusually low. In a year when this occurred, group size eroded rapidly and over 60% of groups became extinct. Total numbers were slow to recover during the following year because emigration by females was infrequent and new groups did not form in vacant ranges created by the extinction of groups. High rates of group extinction have been found in other cooperative breeders and may occur because breeding success and survival show inverse density dependence.

TREE, 13. 7, July 1998, p. 288-296

Reproductive skew, concessions and limited control

T. H. Clutton-Brock

Models of reproductive skew in cooperative and eusocial societies suggest that dominants allow subordinates to breed to induce them to remain peaceably in the group. However, it is not yet clear how widely the assumptions of these models apply to animal societies, and many of the trends that they predict are consistent with the simpler suggestion that there is a struggle for reproduction between dominants and subordinates, whose outcome depends on the potential costs and benefits of the contest to both parties. Models of reproductive skew that incorporate contests of this kind and empirical studies that can discriminate clearly between reproductive concessions and failures of control are now needed.