

Evolution of raised guarding behavior in meerkats, *Suricata suricatta*

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Abstract

In this article I will first briefly describe meerkats and their social behaviours and then examine the possible mechanisms by which the cooperative raised guarding behaviour of the meerkats may have evolved. I will look at the theoretical and empirical problems of applying these theoretical models to the evolution of cooperative guarding behaviour in meerkats and try to see if the evidence points conclusively to any one of the possible mechanisms examined. I will discuss kin selection, reciprocal altruism, Zahavi's handicap principle, group selection and Bednekoff's direct benefits model. Kinship selection is a gene level selection, reciprocal altruism, Zahavi's handicap principle and direct benefits model are all individual level selection models and group selection is selection at the group level so natural selection may have operated on three different levels on the trait of raised guarding. I will not make a distinction between the initial emergence and spread and the current maintenance of the behaviour. It may be sustained by the same mechanisms but this is not necessarily so and the mechanisms acting to maintain the behaviour may well be different from those that favoured its original emergence and spread.

INTRODUCTION

Meerkats or suricates, *Suricata suricatta* are cooperative diurnal mammals that live in arid parts of south Africa in groups of 2 to 30 individuals with two dominant animals: a male and a female that are parents to most (75% or more) of the offspring in the group, 2-15 adult helpers of both sexes and a variable numbers of juveniles under a year old (Clutton-Brocket al. 1999a; Clutton-Brock et al. 2002). Most group members are related to the dominant female and to each other but immigrant males, unrelated to other group members, may be present in some groups (Clutton-Brock et al. 1999a). All group members other than pups under the age of 3 months show cooperative behaviours such as baby-sitting, pup feeding, social digging and raised guarding (vigilance) (Clutton-Brock et al. 1999a), although there are individual and sex differences in time spent doing each of these apparently altruistic acts (Clutton-Brock et al. 2002). Although all four cooperative behaviours are intriguing, I will focus here only on raised guarding behaviour due to increased clarity of doing so and possibility that different mechanisms were responsible

for the evolution of different cooperative behaviours.

The animals forage for underground invertebrates (mainly insects and other arthropods) and small vertebrates (mice, frogs, snakes) by digging up to 20cm below ground and so they cannot see approaching predators – bird raptors, mammal carnivores (foxes, wild cats...) and snakes – when they are foraging and annual mortality rates are high (0.68 in Kalahari Gemsbok Park) (Clutton-Brock et al. 1999a). The animals do not share their prey, and sentinels that guard have to compensate for missing the opportunity to forage during guarding. They show three types of vigilance: guarding at the ground level while foraging, guarding at the burrow entrances and guarding from a raised position (mound or a dead tree). When a raised guard is on duty it announces its presence by vocalization (“watchman’s song”) and foraging animals become less vigilant as a result, i.e. other two types of vigilance decrease in frequency (Manser 1999). Raised guards also call out alarms specific to different types of approaching predators or intruders (avian predator, ground predator and snake or

a meerkat intruder) and their calls signal both the type of the predator and the urgency of the threat (Manser et al. 2002). The benefits of this behaviour to other group members may be that they spend less time scanning for predators themselves and thereby they interrupt their foraging less often, which may result in more prey being caught; i.e. their optimum level of vigilance decreases when others are on guard (See Figure 1).

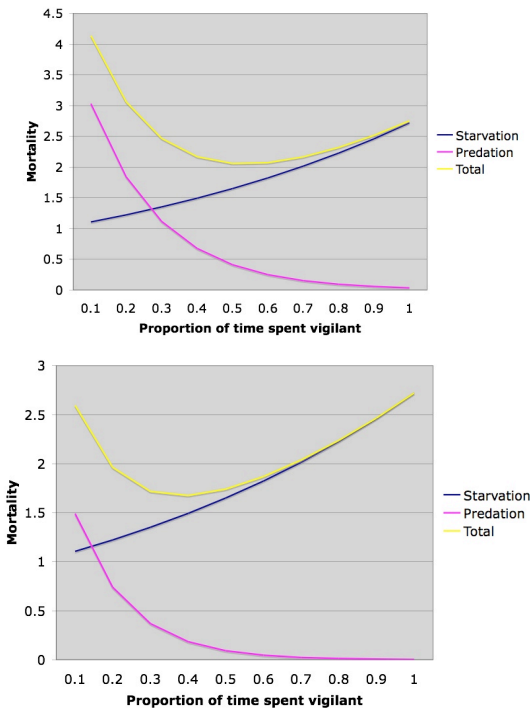


Figure 1: A simple model of expected mortality due to predation and expected mortality due to starvation as a function of proportion of foraging time spent vigilant (in raised guard). In a) where no other meerkat is on raised guard the optimum proportion of time spent in vigilance is around 0.5 or 50%. In b) when another guard is already on guard, the threat of predation is lower whilst the threat of starvation remains the same (assuming no competition for food) and so the total expected mortality can be reduced by being vigilant for a smaller proportion of time, around 0.4 or 40%. The same effect is seen when overall threat of predation is reduced due to the lower abundance of predators (1). So the presence of a raised guard reduces the time needed spent guarding by other meerkats to maintain lowest mortality threat. The equation used for model is for starvation: $y = \text{Exp}(a \cdot x)$; for predation: $y = b \cdot \text{Exp}(-c \cdot x)$ (Professor Alex Kacelnik, personal communication). In a) $a=1$, $b=5$, $c=5$; in b) $a=1$, $b=3$, $c=7$. Parameters were

made up for illustrative purpose only. Mortality on the y axis is in arbitrary units.

Henceforth, the raised vigilance by meerkats may count as altruistic behaviour-increasing the fitness of others at a cost to its own fitness-as long as it really is costly, in terms of loss in fitness, to perform the guarding. Five models have been put forth to explain the evolution of altruistic behaviour, behaviour that is seemingly paradoxical since Darwinian view of evolution is that traits that evolve are those that have helped individuals with those traits to survive and reproduce, natural selection favours those who are best adapted, and therefore altruistic behaviour would be removed by natural selection acting on the individuals to enhance their own survival and reproduction thereby preventing evolution of such altruistic behaviours.

GROUP SELECTION AND INCLUSIVE FITNESS THEORY

Natural selection operating at the group level was first mentioned as a possible mechanism for evolution of traits by Darwin himself (Sober and Wilson 1998). Group selection was often invoked to explain the actualities of the living world until the 1960s when criticisms seemed to have successfully refuted the possibility of natural selection operating at group level (Sober and Wilson 1998) the main criticism being that the selfishness at the lower levels of selection, namely individual organism level, would always be able to infiltrate an altruistic group and selfish individuals would get rewarded by exploiting the altruism of the other group members with no extra cost to themselves (Zahavi and Zahavi 1997). This would then not result in evolution of altruistic animals. In the case of meerkats, those individuals that would not guard would still benefit from the guarding of the others and therefore would have increased fitness with respect to other group members and the resulting group would never evolve altruistic guarding behaviour if

the group selection were the only process involved.

Once this was accepted two other explanations emerged, first one by Hamilton (1964), which became known as the theory of *kin selection*, and second one by Trivers (1971), the theory of *reciprocal altruism* (Zahavi and Zahavi 1997). Hamilton used the term 'inclusive fitness' to explain the evolution of social behaviour and altruism (Hamilton 1964a). According to this theory, each individual aims to evolve such behaviours that will maximize its inclusive fitness (Hamilton 1964a). Inclusive fitness is fitness gained by an individual in terms of genes 'identical by descent' passed on into the population (Hamilton 1964a). An altruistic gene may spread due to its help to its replicas in other related individuals, so altruism evolves at the individual level due to selfishness at the gene level (Hamilton 1964a). Hamilton's theory has become a textbook explanation of the evolution of eusocial behaviour in insects and that is what his original paper (Hamilton 1964b) discusses the most. However, the same theory can be used to attempt to explain evolution of other altruistic behaviours. The refined form of Hamilton's argument is that altruistic act will evolve if the costs of performing the act to the individual (c), in terms of number of offspring produced, are less than benefits to the receiver (b) multiplied by the relatedness coefficient between the two individuals (r)-the probability that the two individuals share a same gene over and above the average probability due to gene's average frequency in the population, or if $rb-c > 0$ (Krebs and Davies 1997).

Obviously, aggregation of animals in family groups would facilitate evolution of altruism in such groups since most altruistic acts towards conspecifics would be acts towards related individuals and the more related one is to another individual the higher the probability that the two share a same gene. Meerkats live in family groups of 2-30

individuals and so it may seem appropriate to postulate kinship selection as a mechanism of evolution of raised guarding behaviour. However, not all group members are always related since some groups accept immigrant males (Clutton-Brock et al. 1999a) and this may be a problem for kin selection model since these unrelated immigrants would benefit from selfish acts in a group of altruists. Yet, once the altruism has evolved, perhaps in the absence of immigration by unrelated individuals for whatever reason, the benefits to the altruists may be large enough to compensate for an occasional immigrant exploiter (Hamilton 1964b). On the other hand, immigrated individuals unrelated to the rest of the group still go on raised guards and this observation contradicts the predictions of the kin selection theory (Clutton-Brock et al. 1999a).

RECIPROCAL ALTRUISM

Trivers (1971) presented a model that allows altruistic behaviour to evolve even between the two unrelated organisms (Trivers 1971). He argued that when costs of helping an unrelated individual are much smaller than the benefits to the helped individual natural selection would favour such behaviour if the helped individual reciprocates in the future the help to the helper at the similar cost/benefit ratio of doing so (Trivers 1971). Both individuals then receive large benefits at small costs regardless of whether they share the same genes or not, so it is the exchange of altruistic acts that favours the evolution of altruism not the indirect benefits via kin selection (Trivers 1971). The chances of altruistic behaviour being selected according to this model are greatest when:

- 1) many altruistic situations (when benefit to other > cost to itself) exist in a life time of altruists
- 2) the same set of individuals repeatedly interact

- 3) both individuals in a pair of altruists are able to gain equivalent benefits at equivalent costs of behaving altruistically.

Meerkats in the wild seem to fulfill all of these requirements for the evolution of raised guarding by reciprocal altruism. Firstly, they live with a constant threat from a variety of aerial and land predators (Clutton-Brock et al. 1999a) which means that altruistic situations where altruistic individuals may warn others by a quick, inexpensive call, and thereby often save life of another individual arise daily. High mortality rates (Clutton-Brock et al. 1999a) and evolution of specialized alarm calls for different classes of predators (4) support this conclusion. Second, meerkats live in long-lasting (with respect to individual's life span) groups of 2-30 individuals and so they encounter the same individuals over and over again (Clutton-Brock et al. 1999a). Although females disperse in parties to form new groups and males may join them or disperse in smaller parties to find a new group where they may breed (Clutton-Brock et al. 2002) members of both sexes spend on average at least a year in the group of birth and the rest of their lives mostly in newly formed groups (Clutton-Brock et al. 2002). So even though individuals may spend different parts of their lives with different groups, most of the time they will be interacting with the same individuals in the group they are with. Thirdly, benefits to any alarmed individual may well be life saving whereas costs of standing guard and giving out alarm call may be negligible to a well fed individual (Clutton-Brock et al. 1999a). Never the less, the ability of an animal to forage successfully may depend on other factors such as its age and general health and fitness and so it may cost some individuals significantly more to stand guard and give alarm calls than others which would suggest that the third requirement for the evolution of reciprocal altruism may not be realised for the

meerkats. However, further empirical evidence showing percentage of times different individuals in different health conditions spend guarding and quantification of costs to them of doing so may be illuminating.

Although meerkats seem to fit the requirements of Triver's model fairly well, his model is one of interactions of two individuals whereas meerkat guarding behaviour is interaction between several to many individuals. Furthermore, his argument about the evolution of warning calls in birds, a behaviour remotely similar to guarding and alarming behaviour in meerkats, states that such behaviour is selected for because it aids the caller by preventing the predator to specialize on caller's species or locality and so caller is primarily helping itself and benefits to others are a by-product, yet Trivers himself acknowledges that it would be "almost impossible" to collect the evidence that would allow one to discriminate between this mechanism and the kin selection (Trivers 1971). Zahavi (1997) believes that reciprocal altruism does not demonstrate how reinforcement of reciprocity can ever be implemented, i.e. it is not clear how an altruist could make sure the other individual repays the favour in the future and without the reinforcement reciprocal altruism is same as group selection in that it only shows that groups with altruists survive better than those without them (Zahavi 1997).

ZAHAVI'S HANDICAP PRINCIPLE

Having dismissed the above three models for the evolution of altruism, Zahavi (1997) argues for another model, based on the 'Handicap principle'. The main premise of this model is that the guarding individual gains direct benefit in terms of prestige within its group (Zahavi and Zahavi 1997). Prestige is defined as respect that an individual has in the eyes of the other group members, which in turn may allow them easier access to mating

opportunities and greater support by others in dominance or territorial fights (Zahavi and Zahavi 1997). Alarm call is said to be a signal to the predator informing it that it has been spotted and that surprise attack is prevented; therefore alarm calls have evolved to benefit directly both the predator and the signaller itself (Zahavi and Zahavi 1997). The fact that meerkats stand raised guards on the prominent spots such as dead trees or mounds (Clutton-Brock et al. 1999a) and also that they have specific calls for specific predator classes (Manser et al. 2002) supports this view in so much that it makes it clear to the predator that the alarm is indeed referred to itself and not to some other predator. Cheating by a meerkat that would call even when predator is not spotted would be prevented by the actual risk from unnoticed predators when exposed on guard (Zahavi and Zahavi 1997).

Guarding behaviour may bring the guard gain is status (prestige) within the group by demonstrating its quality as a mating partner, pact member or a rival (Zahavi and Zahavi 1997). So altruistic acts, such as guarding and alarming the group are viewed as signals of altruist's ability, with the cost of altruistic acts, such as loss of foraging time or exposure to predator attacks, ensuring the reliability of the signals (Zahavi and Zahavi 1997). The cost equals the handicap, which equals the reliability or truth of the signal hence precluding cheaters (Zahavi and Zahavi 1997). So there is a direct benefit to an altruistic guard and no other special mechanism is needed to explain the evolution of such an act; furthermore, Zahavi (1997) believes this model applies to altruism in a wide variety of living organisms (Zahavi and Zahavi 1997). Nevertheless, the model arises from studies of Arabian babblers-territorial, group living birds that stand guard and give alarm calls, a system not unlike that seen in meerkats. On the other hand, babblers actually compete for performing altruistic acts such as guarding behaviour and avoid being pushed

away from their duty by others (Zahavi and Zahavi 1997). Also, they guard even when hungry and do not accept food from subordinates trying to feed them while guarding (Zahavi and Zahavi 1997). This and similar evidence makes babblers a perfect model system for explaining the prestige model of evolution of altruism. But meerkats differ in their behaviour from babblers.

First of all, the individuals that take guards are usually well fed individuals (Clutton-Brock et al. 1999a) and there are no reports to suggest that they refuse to be replaced by another guard. Furthermore, there is no evidence that they actually compete over taking guards either (Professor Clutton-Brock, personal communication). This may well be an artefact due to lack of aimed research to expose such behaviours, perhaps further research into exact order of replacements and time spent guarding with respect to dominance rank may demonstrate presence or absence of prestige behaviours within the groups of meerkats. This may be connected to the question of guard's reliability-whether certain individuals are trusted more than others when on guard, the prestige and reliability may be reflecting the same qualities of individual meerkats. In any case, as appealing as Zahavi's model is, there is no evidence to support it in meerkat guarding behaviour, regardless of the fact that it is well supported in babblers' guarding.

SOBER AND WILSON'S GROUP SELECTION AND BENDEKOFF'S DIRECT BENEFITS MODEL

Sober and Wilson (1997) attempted a resurrection of the group selection argument and argued that it is a necessary process for evolution of altruism (Sober and Wilson 1997) but others have dismissed their arguments on various grounds (Dawkins 1994, Dennett 1994). Sober and Wilson do not mention meerkat behaviour *per se* (Sober and Wilson (1997), although, larger meerkat groups

survive better, especially in the times of drought and smaller groups suffer higher mortality rates and lower breeding successes and often go extinct (Clutton-Brock et al. 1999b). However, current research supports the direct benefits models such as Bednekoff's model that states that guards reap direct benefits by early detection of danger (Clutton-Brock et al. 1999a) (see figures 2 and 3).

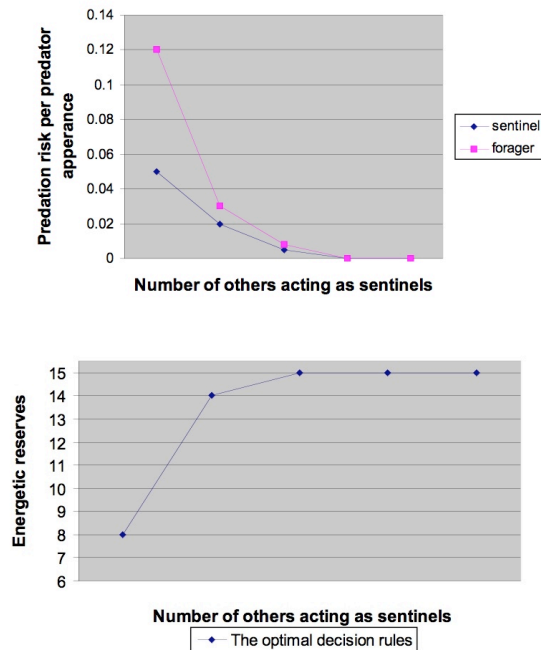


Figure 2: Bednekoff's model predicts that benefits to a guarding individual are selfish and that such an individual gains benefits even if no other individuals act as sentinels. The alarm given by the sentinel may have a direct benefit to it by deterring the predator or the risk involved in giving the alarm may be compensated for by kin selection or mutual dependencies. The safety of foragers due to sentinels' alarms is a by-product of sentinel protecting itself. Raised guarding is not costly but beneficial to sentinels, it is the optimal activity for a temporarily satiated individual in a constantly moving foraging group of interdependent animals.

A, The model predicts that sentinels always have lower predation risk than foragers, but the risk decreases substantially for all group members once a single sentinel that will alarm the group is up; here, the approximate risk of predation for foraging and guarding individuals is plotted against the number of raised guards already present in a group of five. *B*, Animals make decisions based on their satiation/energy reserve state and the actions of the others. This graph shows

optimal decision rules for an individual in a group of five; if its energy reserves are below the line it forages, if they are above the line it acts as a sentinel. Whilst benefits of going on guard when no other guard is up are large, they decrease and the benefits of foraging increase when there is already a guard up. (Graphs adapted from Bednekoff 1997)

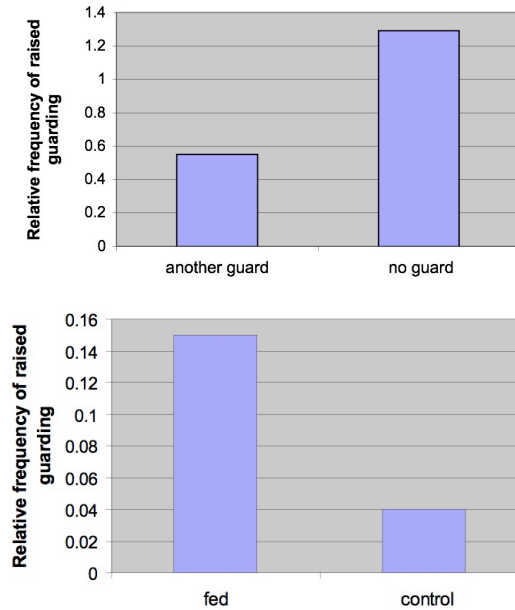


Figure 3: Clutton-Brock et al. (1999a) presented empirical support for the Bednekoff's model's predictions. There is no evidence that sentinels suffer higher predation; they actually position themselves closer to safety of bolt-holes than do the foragers (Clutton-Brock et al. 1999a). Solitary sentinels spend similar amount of time on raised guard as group members and unrelated individuals in groups also act as sentinels (Clutton-Brock et al. 1999a). Here, empirical support for two predictions of the Bednekoff's model are presented: 1) individuals should respond to reduced guarding by other group members by going on guard themselves and 2) individuals should spend more time guarding if their energy reserve levels are higher. *A*, The frequency of going on raised guard is almost twice as large when there is no guard present than when there is already a guard present. *B*, Fed animals acted as sentinels three times as often as control animals. (Graphs are simplified from Clutton-Brock et al. 1999a)

Although evidence points out that meerkats may benefit directly from going on raised guards, it does not tell us much about evolution of alarm calls or "watchman's song"

both of which are unlikely to have evolved by direct benefits to guards (Clutton-Brock et al. 1999a). Furthermore, there is evidence of different times spent guarding in habitats with different predation threats, which suggests that learning may play an important role in patterns of guarding behaviour we observe and that this should be taken into account when we evaluate existing models of evolution of such behaviours (Clutton-Brock et al. 1999a).

Discussion and Conclusion

Four general models for the evolution of altruism have been examined and none of them seem to *a priori* fit the evidence for the evolution of meerkat raised guarding behaviour. Group selection is still not generally accepted as a coherent mechanism widely occurring in nature (Sober and Wilson 1997). Kin selection may have played a role in evolution of some aspects of the behaviour such as “watchman’s song” but the non-related group members pose complication for the kin selection explanation. The reciprocal altruism also may have a role in the evolution of the behaviour, but there are general criticisms for this mechanism as well as lack of evidence that the reciprocity is enforced in meerkat groups. Zahavi’s prestige mechanism is still unsupported by the evidence for meerkat groups. Sober and Wilson’s group selection mechanism does not discuss guarding behaviour as such and it has been criticized as not much different from the original group selection arguments (Dawkins 1994, Dennett 1994). The mechanism of the evolution of raised guarding behaviour in meerkats is still an open question although recent evidence (Clutton-Brock et al. 1999a) supports the new direct benefits model (Bednekoff 1997). However, it seems that several mechanisms may have played a role in the evolution of different aspects of raised guarding behaviour in meerkat groups

(Clutton-Brock et al. 1999a) and perhaps the same is true for other social systems and other examples of altruistic behaviour across the animal taxa. Understanding the evolution of social behaviours in model species and societies, such as meerkats and their society, may help us eventually better understand evolution of the human social behaviours.

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