NATIONAL CENTER FOR CASE STUDY TEACHING IN SCIENCE

Guarding Behavior in Meerkats: *Selfless Sentinels?*

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Introduction

Meerkats (*Suricata suricatta*) are diurnal mongooses that live in the Kalahari Desert in Africa in cooperative groups of 3–30 individuals. A dominant female does most breeding and young are cared for by helpers who bring food items and guard pups. Helpers are sexually mature but have not yet had their own pups. Meerkats spend 5–8 hours a day foraging for small invertebrates and vertebrates, often digging below ground to do so, and have a high risk of predation, especially by birds of prey. Foraging meerkats are unable to detect predators when they are digging, so they stop and look around occasionally to look for predators, and also take turns climbing to a higher position to look for predators (raised guarding); the individual that climbs to this position to guard is called the sentinel. When a group is foraging, an individual acts as sentinel about half the time. While guarding, meerkats make continuous calls that alert other group members to the fact that they are acting as sentinel, and they make alarm calls to signal the group to run to their burrows if a predator is spotted. Foraging meerkats spend less time looking for predators when another individual is acting as sentinel.

Figure 1. Meerkat family, South Africa Kalahari Desert. *Credit:* © Ecophoto | Dreamstime.com, ID 810602.

Figure 2. Meercat sentinel in Kalahari Desert. *Credit:* ©Jean-marc Strydom | Dreamstime.com, ID 1368803.

Question

1. Generate at least one hypothesis for why sentinel behavior has evolved in meerkats.

Part I – Paying the Price

One of the most commonly mentioned hypotheses for sentinel behavior in meerkats is that it evolved to protect the group. This hypothesis suggests that despite suffering an individual cost for being the sentinel, the behavior is favored by selection because the whole group benefits by avoiding predators. In animal behavior, this sort of selflessness is referred to as altruism, where the individual engaging in the behavior pays an individual cost in order to allow another to reap a benefit. In other words, altruism is the opposite of selfishness. To help us analyze how meerkat sentinel behavior might have evolved, and whether it could in fact be altruistic, we'll start by examining the individual costs the sentinel might experience by acting as sentinel.

Questions

1. What are some possible fitness costs of sentinel behavior for the sentinel?

2. Now, analyze the data in Figure 3 from Clutton-Brock *et al.* (1999). They tested hypotheses in a wild population of meerkats; half of helper meerkats were fed 25 g of hard-boiled egg for 30 successive days (fed), and half of them were not (control). Their contributions to guarding behavior were documented during that time period. GT refers to raised guarding, or sentinel behavior. Summarize the main experimental findings shown in this figure.

3. How might less time foraging translate to fitness costs for sentinels?

4. Do these results support, refute, or have no relationship to the researchers' hypothesis that there is a fitness cost to sentinel behavior?

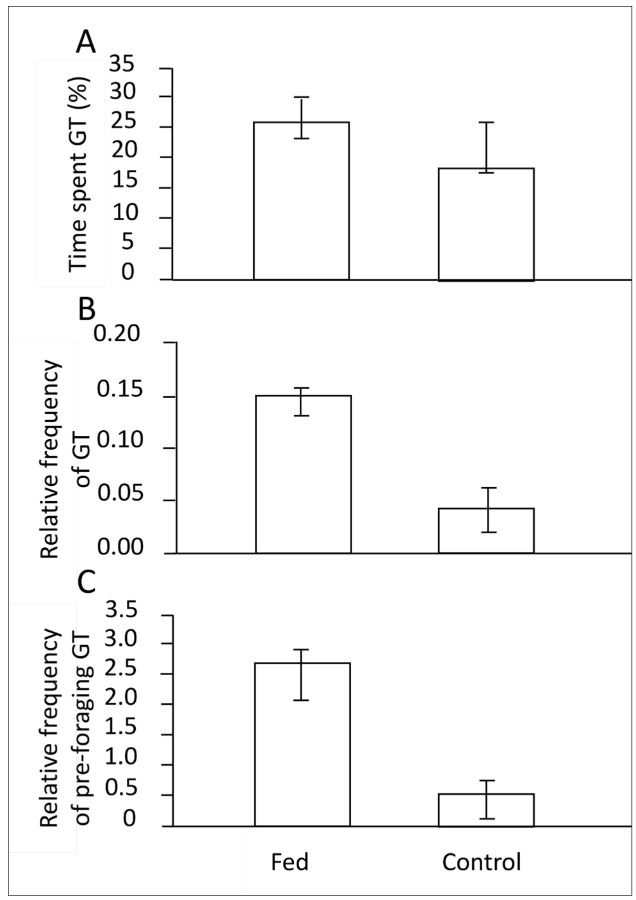

Figure 3. (A) Contributions to raised guarding (percent of foraging time on raised guard) by 10 individuals on days when they had been fed with 25 g of hard-boiled egg (fed) as compared with the mean contribution to raised guarding by the same individuals on five previous days when they had not been fed (control). Open bars show median values calculated across individuals; error bars show IQR (interquartile ranges). (B) Mean contributions to raised guarding by individuals in six groups fed each day over a 30-day period versus unfed controls in the same group. (C) Mean number of times fed and control individuals in six groups went on guard before starting to forage in the morning. *Credit:* Redrawn based on Figure 6 in Clutton-Brock *et al*. (1999).

Part II – For the Good of the Group?

The hypothesis mentioned in Part I, that sentinel behavior might have evolved even if the sentinel suffers an individual cost as long as the group benefits from the behavior, is a group selection hypothesis. Group selection suggests that the group can be the unit of selection, and thus traits can evolve if they increase group fitness (Wynne-Edwards, 1962). Altruistic (selfless) behaviors could theoretically evolve by group selection if the individual engaging in the behavior increases the fitness of the group by his/her selflessness. In the case of meerkats, group selection would suggest that altruistic sentinel behavior could evolve if it improves the fitness of the meerkat group (if groups with sentinels have higher fitness than groups without sentinels). To examine whether group selection can account for meerkat sentinel behavior, answer the following questions.

Questions

1. Imagine for a moment that sentinel behavior evolved by group selection, so meerkat groups that had sentinels tended to have higher fitness than meerkat groups without sentinels, with sentinel duty (and its associated costs) being shared among members of the group on an equal rotation "for the good of the group."
   a. In a meerkat group with sentinels taking equal turns on duty, who is paying fewer fitness costs: the foraging meerkats or the sentinel meerkat?
   b. Now imagine a meerkat with an allele for slightly more selfish behavior; this meerkat puts in less time on sentinel duty than do other meerkats. Does this meerkat's fitness increase or decrease?
   c. Does its allele for more selfish behavior increase or decrease in frequency in the population?
   d. Consider the definition of fitness you came to class with today. If there's an allele for altruism, or selfless behavior, what happens to it in an altruistic group?
2. If researchers have found that solitary meerkats spend as much time on raised guard as do meerkats in groups (Clutton-Brock *et al.*, 1999), does this information support, refute, or have no relationship to the group selection hypothesis for sentinel behavior?
3. Can group selection explain the evolution of meerkat sentinel behavior? Explain.

Part III – Benefits of Being Sentinel

If solitary meerkats spend time on raised guard as well, and if we know there's an individual fitness cost to the behavior because of lost foraging time, then there must be an individual fitness benefit that outweighs the individual cost of the behavior. If that were the case, then an individual acting as sentinel would have higher fitness than others, and the behavior (and corresponding allele(s)) would increase in frequency in the population. To explore the hypothesis that sentinel behavior evolved by individual selection, let's examine individual benefits experienced by the meerkats while on sentinel duty.

Questions

1. What are some possible individual fitness benefits of sentinel behavior for the sentinel?

2. Now, analyze some data from Clutton-Brock *et al.* (1999) as you did earlier. As before, these data result from a study of wild meerkats in the Kalahari. Summarize the main findings shown in Figure 4.

3. Does sentinel behavior benefit the group or the sentinel? Who benefits most?

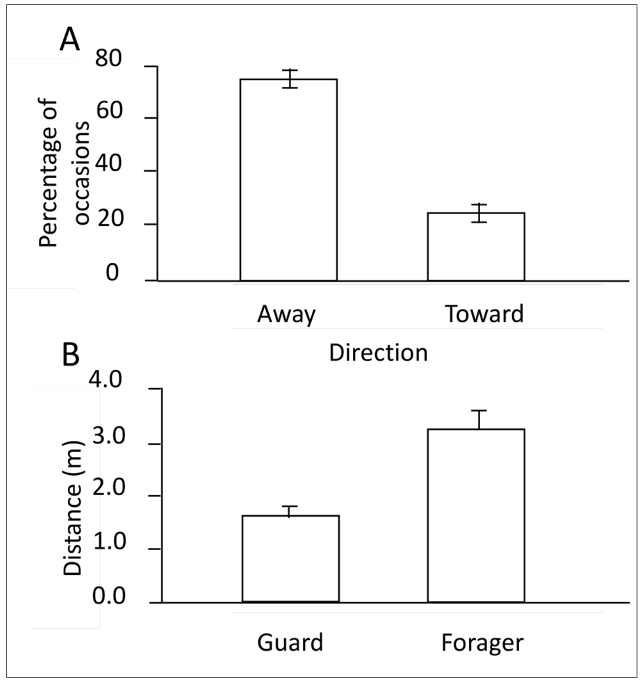

Figure 4. (A) Median proportion of the time that 20 individuals spent looking toward versus away from foraging group members when on raised guard. Median values (open bars) and IQRs (error bars) calculated across values for 20 individuals are shown. (B) Mean distance to the nearest bolt-hole for guards and foraging animals. Mean distances (open bars) and SDs (error bars) calculated across individual values are shown. *Credit:* Redrawn from Clutton-Brock *et al.* (1999).

4. Clutton-Brock *et al.* (1999) also report that "during over 2000 hours of observation, no raised guards were attacked or killed by predators, probably because raised guards were usually the first to detect them." Summarize the benefits and costs of sentinel behavior to the sentinel.

Part IV – Summary

Group selection, while giving rise to tempting hypotheses for animal behavior, has been found in scientific studies to be an important selection process only in certain very specific cases (such as when the fates of all organisms in the group are linked). In most other cases researchers have found that even where group selection hypotheses made some sense initially, there was often an individual selection hypothesis that was supported through scientific testing. In other words, group selection rarely explains the evolution of traits better than individual selection can, and in evaluating hypotheses about behavior, we should be wary of hypotheses that point to pure altruism or pure group selection without also considering individual selection hypotheses.

Questions

1. Given the data you just analyzed, provide an explanation for the evolution of sentinel behavior in meerkats, being careful to avoid explanations that require altruism or group selection.

2. Reciprocal altruism is a type of altruism where individuals take turns helping each other, even if one individual has to wait for the payoff (e.g., I'll scratch your back today if you'll scratch mine tomorrow). It tends to occur mostly in groups of social animals that continue to interact with each other over time.
   a. Considering what you have learned today, why do you think that repeated future interactions are key to the evolution of reciprocal altruism?

   b. Do you consider reciprocal altruism to be a selfless behavior? Why or why not?

3. What new questions do you have now about apparently altruistic behavior in animals?

Assessment

1. Imagine that you're talking with a friend who has just watched a nature documentary about meerkats. Your friend says, "Meerkats are so cute! They even protect each other by taking turns looking out for predators so that the whole group stays safe!" Respond to your friend by explaining the problem with this summary, based on what you've learned in the meerkat lesson.

2. Use a key piece of evidence from the figures in the meerkat case to justify the role of natural selection in the evolution of meerkat sentinel behavior.

3. In meerkats, another behavior that they exhibit is helping care for young. Adult helpers remain in the colony for a few years, feeding and caring for the young of the dominant female before having any of their own offspring. Circle the letter below (i.e., *a, b, c, d*) of any hypotheses about helping behavior that are based on group selection.
   a. Helping allows the non-breeding adults to learn how to care for young before having their own.
   b. Caring for the young of the dominant female ensures that more young survive, improving the genetic quality and size of the colony.
   c. Non-breeding adults spend more time foraging if they are collecting food for young, and occasionally when the young are full the helpers get to eat the excess food themselves.
   d. Adult helpers are treated less aggressively than non-helpers by the dominant breeders in the colony.

4. In another study, Santema and Clutton-Brock (2013) studied how adult helper behavior differed depending on whether pups of the dominant female were present in the foraging group or stayed behind at the burrow. Bipedal vigilance refers to helpers standing on their hind legs to look for predators.
   a. Summarize the findings presented in Figure 5.
   b. Based on what you see here, and what you know about meerkat fitness and selection, describe what must be true about the fitness costs and benefits of guarding behavior for female helper meerkats.

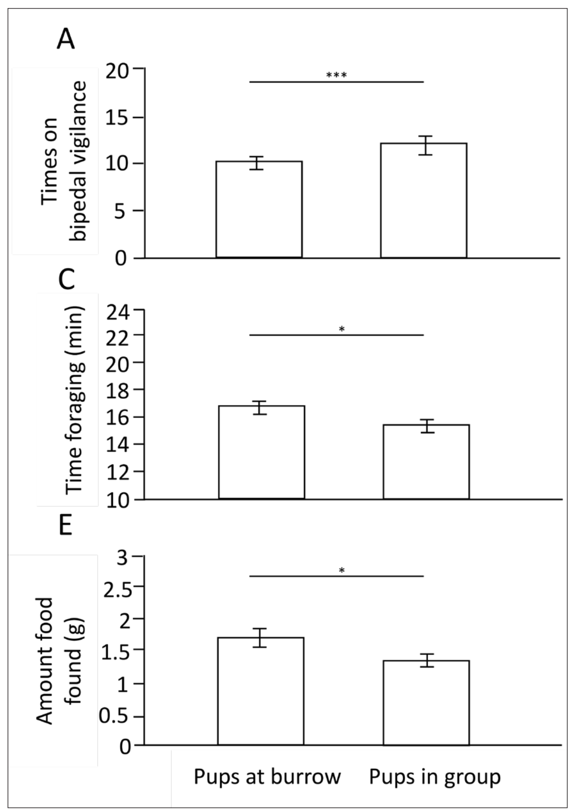

Figure 5. (Redrawn from Santema and Clutton-Brock, 2013, for female helpers only.) Relation between whether or not pups are present in the foraging group and (a) number of times performing bipedal vigilance, (c) time spent foraging and (e) amount of food found for female helpers. Bars represent mean per 30 min observation ± SE. *P = 0.05; ***P = 0.001.

References

Clutton-Brock, T.H., M.J. O'Riain, P.N. Brotherton, D. Gaynor, R. Kansky, A.R. Griffin, and M. Manser. (1999). Selfish sentinels in cooperative mammals. *Science* 284(5420): 1640–4. <https://doi.org/10.1126/science.284.5420.1640>

Santema, P. and T.H. Clutton-Brock. (2013). Meerkat helpers increase sentinel behavior and bipedal vigilance in the presence of pups. *Animal Behaviour* 85(3): 655–61. <https://doi.org/10.1016/j.anbehav.2012.12.029>

Wynne-Edwards, V.C. (1962). *Animal Dispersion in Relation to Social Behavior*. Edinburgh: Oliver and Boyd.

Figure 6. Four Meerkats running in dryland in Kgalagadi transfrontier park, South Africa. *Credit:* © Patrice Correia | Dreamstime.com, ID 228975433.