

Hawks, Doves, and mongooses

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In 1795, philosopher Immanuel Kant proposed rules to promote perpetual peace among nations (1). He first required that all nations be republics, because when “the consent of the subjects is required to determine whether there shall be war or not, nothing is more natural than that they should weigh the matter well, before undertaking such a bad business” ref. 1, p. 122. In contrast, a despotic ruler “does not lose a whit by the war, while he goes on enjoying the delights of his table or sport, or of his pleasure palaces and gala days. He can therefore decide on war for the most trifling reasons, as if it were a kind of pleasure party” ref. 1, p. 123. In a PNAS paper that marries evolutionary game theory with tests of data from a long-term study of banded mongooses (Fig. 1), Johnstone et al. (2) confirm Kant’s insight that destructive intergroup fighting becomes more likely when leaders have more to gain, or less to lose, from fighting than do their followers.

For this study, Johnstone et al. (2) adapt the classic Hawk–Dove model for intergroup contests, examining the range of conditions favoring aggressive (“Hawk”) and peaceful (“Dove”) strategies. The Hawk–Dove model has yielded numerous insights into the evolution of animal conflict since Maynard Smith and Price’s 1973 paper (3), which sought to

explain why animal contests are frequently less destructive than we might expect: snakes wrestle with rivals, rather than using their fangs, and stags lock antlers rather than stabbing with their prongs. They found that a peaceful mutant can invade a world of Hawks, because Doves less frequently pay the costs of fighting (3). Updating this model to examine contests among groups, Johnstone et al. (2) find that when leaders gain more—or lose less—from fighting than their followers, costly fighting among groups can prevail, even if this reduces to the fitness of followers.

This model seems plausible for humans, especially in large-scale societies where rulers can order conscripted soldiers into battle. But does it apply to other animals? Among mammals, destructive intergroup fighting occurs most prominently among some primates—particularly humans and chimpanzees—and social carnivores, including lions, spotted hyenas, and wolves (4). Johnstone et al. (2) test their theoretical model using 19 y of field data from another social carnivore, the banded mongoose, which has many advantages as a study species. Banded mongooses inhabit open landscapes with good visibility. They live at high densities in small territories, enabling researchers to follow the lives of many different social groups—28 groups in this study (2). Being small bodied, they are much more easily followed on foot and handled than, say, lions or wolves. Researchers regularly trap the study subjects, measuring body mass, obtaining samples for genetic analysis, and marking individuals to distinguish them clearly during observation (5). Continuous, detailed, long-term study of these mongooses has resulted in a dataset of intergroup encounters large enough to permit detailed statistical analysis.

While banded mongooses might look harmless, they engage in fierce intergroup fights, with rates of death from intergroup fighting rivaling those of chimpanzees and human hunter-gatherers (2). Moreover, while females instigate most intergroup fights, it is more often males who pay the price. Of 19 adults killed in intergroup fights, 17 were males (2).

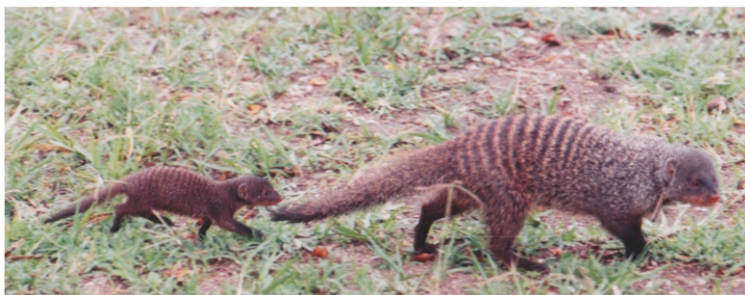


Fig. 1. Banded mongooses from the study population at Queen Elizabeth Park, Uganda. The adult is wearing a radio collar. Image credit: Becky Sun (photographer).

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The destructiveness of banded mongoose battles appears to result from some unusual features of their social system. Like their close relatives, meerkats, banded mongooses live in tightly knit societies that defend group territories and breed cooperatively. Unlike meerkats, which typically have a single breeding pair (6), banded mongooses have multiple breeding females and males in each group (2). Females in a group go into estrus at the same time. Males compete intensely to guard estrous females, following them nose to tail. Nonetheless, when the pups are born, group members work together to raise them. Because both males and females usually stay in the group where they were born, groups consist mainly of close kin, and all group members have a genetic interest in the pups' welfare (2, 5). Such close-knit family groups have a downside, however: mating with close kin results in inbred pups. Females therefore have a genetic interest in finding mates from other groups. When estrous females go looking for mates in enemy territory, their mate guards follow them. Fights erupt as rival males try to chase off the mate guards and mate with the visiting females. If they succeed, the resulting pups will be genetically more diverse, bigger, and more likely to survive (2).

Males in many species defend their reproductive interests by chasing off rival groups. Insofar as this intergroup effort benefits females, such as by improving access to food resources, males can be considered "hired guns" (7, 8). Johnstone et al. (2) imply that male banded mongooses are not only hired guns, but are also underpaid. They are strongly motivated to engage in intergroup fights, because their reproductive success is at stake, but it appears that estrous females lead males into battle not to win the fight but to shake them off (2). Females don't necessarily benefit from the fighting itself—they might prefer to just sneak off and mate with unrelated males if they could, but the diligent mate guarding of their resident group males prevents this. Whether females gain other benefits from intergroup fighting, such as increased territory size and access to more food resources, remains a question for future research.

Johnstone et al.'s (2) model focuses on costs and benefits to individual fitness. However, because groups consist mainly of kin, and outbred pups are more likely to survive, males may gain indirect benefits from females' efforts to mate outside the group. The willingness of males to care for all pups born to the group, even though 18% are sired by extragroup males (2), supports this view.

Banded mongooses have an unusual social system, but Johnstone et al.'s (2) adaptation of the Hawk–Dove model is general and should thus apply broadly to other species. For example, it helps explain why meerkats avoid intergroup fights rather than seek them out. Because breeding pairs of meerkats are not close kin, the interests of breeding males and females are more closely aligned; females don't need to run off to the neighbors to get good genes (2).

The number of mammalian species in which leaders can effectively exploit followers, however, might be small. Instead, what Johnstone et al. (2) term "heroic leadership" might more often apply. Leaders invest more in intergroup effort because they have more to gain (9). Among chimpanzees, for example, groups of males defend a feeding territory for themselves, their mates, and offspring (10). Participation in territorial behavior appears to depend on willing volunteerism rather than coercion. High-ranking males sire more offspring, and so have more to gain from defending and feeding the community's young. Males with greater mating success participate more often in patrols (11), and high-ranking males travel farther into enemy territory (12). Similarly, among lions, there is no evidence of punishment for individuals that fail to approach simulated intruders (13, 14). Instead, group territory defense appears to depend on mutualism, in which all individuals have a strong stake in repelling intruders (13).

Human warfare traditionally involves fights among groups of men (15). Leaders potentially can exploit followers, insofar as they can gain more of the spoils of war, while being less exposed to the costs. In small-scale societies, however, the interests of leaders and followers may largely coincide. A review of the ethnographic literature suggests that individuals in small-scale societies are motivated to participate in warfare by the possibility of rewards (16). When leaders join war parties, they expose themselves to much the same risks as followers, and benefits such as territory defense and keeping dangerous rivals at bay can be shared by all. The interests of leaders and followers likely diverge more sharply in larger-scale societies, where rulers can order soldiers to face death on the battlefield (15). The robust finding that democracies rarely wage war against other democracies (17) supports predictions from both Kant (1) and Johnstone et al. (2) that closer alignment of the interests of leaders and followers provides a path toward peace.

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