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Cooperation in Social Carnivores

Jennifer E. Smith
Biology Department, Mills College, Oakland, CA, USA

Synonyms

Altruism; By-product mutualism; Carnivorans

Definition

Cooperation is a helpful act performed by one individual that benefits a second individual of the same species; here we focus on cooperative interactions between two or more individuals belonging to the same species in the mammalian Order Carnivora.

Introduction

Humans show an unprecedented capacity for empathy and prosocial behavior, but understanding the origins and maintenance of cooperation is an evolutionary puzzle. Why do individuals help others at a personal cost to themselves? Anthropologists have made excellent progress in tackling this long-standing question. To reveal the human origins of cooperation, traditional approaches include the study of the fossil record to reconstruct material cultures and tools used by our ancestors. Other workers study the behavioral patterns of living nonhuman primates to uncover the conditions shaping cooperation. In 1969, Schaller and Lowther proposed the novel idea that studying the lives of extant social carnivores might offer new clues about the origins of cooperation in early hominins beyond those available from these traditional approaches. Here, I synthesize the substantial information currently available about the ways social carnivores cooperate and then discuss how these insights inform our understanding of cooperation in mammals, including early hominins.

Extent of Cooperation in Mammalian Carnivores

The mammalian Order Carnivora contains ~300 extant species that together are global in distribution, occupying a range of habitats and dietary niches (e.g., herbivores, omnivores, carnivores; Wilson and Reeder 2005). The vast majority of carnivores (~85–90%) are solitary, with conspecifics interacting only to mate or raise young. In contrast, the social carnivores interact regularly with each other, forming social groups or societies. Although the social carnivores evolved from noncooperative ancestors, individuals within these extant species cooperate with group-mates to hunt large game, defend resources, guard against predators, attack others, and/or rear

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young (Smith et al. 2012, In press). Moreover, older and socially dominant individuals often emerge as leaders in the domains of group movement, food acquisition, within-group conflict mediation, and between-group interactions (Smith et al. 2016).

Because social carnivores are relatively elusive and long-lived, studies spanning one or more decades capture some of the best information about cooperation in social carnivores (Smith et al. in revision). Thus, for brevity, I focus on key examples from long-term studies to elucidate the ways this cooperation has coevolved with other traits across Carnivora (Smith et al. 2012). In doing so, I explain the clues that these species of Carnivora offer into understanding cooperation more generally.

Hunting of Large Game

Group life permits individuals in many of the social carnivores to improve their ability to acquire energy-rich prey that vary both spatially and temporarily in the predictability. Spotted hyenas (*Crocuta crocuta*), African lions (*Panthera leo*), African wild dogs (*Lycaon pictus*), and wolves (*Canis* spp.) are among the best-studied of the cooperative hunters. For these species, multiple hunters are often required to secure a single prey animal, each of which represents energy-rich food item that may weigh hundreds of kilograms. Across the Carnivora, additional meat gained from cooperative hunting appears to permit mothers to increase their investment in current reproductive effort by increasing offspring number and also to increase their own body size relative to that of males; cooperatively hunting species often produce more offspring and are less sexually dimorphic than species lacking cooperative hunting (Smith et al. 2012).

Natural selection favors individuals to hunt in optimal group sizes. Whereas spotted hyenas most often hunt alone or in pairs and lions hunt in intermediate groups, wild dogs gain the greatest per capita energy gain when hunting in the large groups (reviewed by Smith et al. 2012). Foragers must balance the benefits of group hunting with the ensuing costs of competition for access to food once prey is obtained. Intense feeding competition often favors groups structured by fission-fusion dynamics in most social carnivores. Individuals regularly break up (fission) from group-mates to hunt on their own or in small subgroups during times of food scarcity but then gather (fusion) into large subgroups to feed when food is abundant.

Coalition Formation and Defense of Resources

Despite their highly cooperative nature, within-group competition regularly occurs among social carnivores over limited resources. Intragroup coalitions form when two or more individuals join forces to direct aggression towards two or more members of their group. Among the carnivores, the patterns of evolutionary forces favoring coalition formation are perhaps best-studied for spotted hyenas living in female-dominated societies. Maternal rank is passed on from mother to offspring. As in many Old World monkeys, individual spotted hyenas learn their social ranks based upon a process of associated learning and repeated maternal interventions during fights (Holekamp et al. 2012). Spotted hyenas also bias their social support towards kin during intragroup disputes but gain direct benefits from reinforcing the status quo by attacking subordinates. Thus, kin selection and direct benefits appear to favor intragroup coalitions via the inclusive (direct + indirect) fitness benefits.

Intergroup coalitions involve multiple group-mates joining forces to direct attacks towards conspecifics belonging to a different social group. This behavior occurs in spotted hyenas, meerkats, and other species of the Carnivora. Interestingly, although meerkat groups are comprised of closely related group-mates that cooperate in intergroup conflicts, group warfare in spotted hyenas involves kin and nonkin joining forces to attack members of other social groups. As such, spotted hyenas cooperate in group attacks against neighboring group despite their low levels of genetic relatedness with group-mates, presumably

gaining direct benefits from their cooperative actions.

Predator Protection

Cooperative defense against predators includes mobbing of predators (e.g., group members collectively fend off potential predators by attacking them) or cooperative vigilance, defined here as any behavioral adjustments that reduces the risk of predation for members of the group. In general, mothers of species that cooperatively defend themselves from predators invest more in current reproduction, weaning offspring at later ages than do mothers of noncooperative species of the Carnivora (Smith et al. 2012). Species living in dense populations are most likely to cooperatively defend themselves from predators, presumably because cooperative defense is mainly a numbers game, requiring a large number of individuals to detect and cooperatively mob predators. Because their small body sizes make them vulnerable to predation, meerkats offer important insights into the evolution of cooperative defense against predators. Sentinels take turns looking out for predators and make alarm call to warn others of threats. Interestingly, meerkats gain both direct and indirect benefits from this behavior, with sentinels typically only assuming this role when they have feed and the costs to the caller are low (reviewed by Smith et al. in revision).

Alloparenting

Alloparental care is defined here as all aspects of care in which individuals guard, groom, carry, play with, feed, or nurse the offspring of others (Creel and Creel 1991). As in many nonhuman primates, alloparenting is correlated with an increased brain size relative to body size in carnivores, suggesting that alloparenting enhances energy required to sustain neural tissue across the Carnivora (Smith et al. 2012).

Carnivores may engage in communal care of offspring that are not their own as members of plural or singularly breeding societies. Plural breeders with communal care include Artic foxes (*Alopex lagopus semenovi*), European badgers (*Meles meles*), banded mongooses (*Mungos mungo*), lions, and white-nosed coati (*Nasua narica*; Lukas and Clutton-Brock 2012). Shared communal dens allows for protection against infanticidal male lions (Packer et al. 1990). Similarly, spotted hyenas benefit from group defense of young from predation by lions (Smith et al. 2012). Singularly breeding carnivores in which only one member of a sex typically breeds is seen in many species belonging to the dog and mongoose families. In these groups, reproduction is typically restricted to one breeding pair and alloparenting is provided by nonbreeders, often including allonursing. One of the best-studied mongooses, the meerkat, has one breeding pair that actively evicts subordinate helpers if they attempt to breed (Lukas and Clutton-Brock 2012).

Conclusion

Although the extent to which early hominins ate meat is unclear, this article elucidates the numerous ways beyond group hunting that the social carnivores cooperate, all of which are also relevant to the ways that early hominins likely cooperated. Social carnivores therefore offer new interesting opportunities to study of convergent evolution in cooperation and will likely continue to shed new light on the origins of cooperation in early hominins. Species from both groups cooperatively hunt large game, defend resources, guard against predators, and rear young. For example, early hominins were themselves likely hunted or otherwise killed by carnivores (reviewed by Smith et al. 2012). The evolution of cooperative defense of food and space, breeding, and protection from predators, as well as fission-fusion dynamics, in the Order Carnivora suggest that this taxonomic group continues to offer underexploited opportunities for testing hypotheses relevant to the evolution of hominins.

Large-scale comparative analysis of extant species of Carnivora indicates that multiple traits coevolved with the ability to cooperate; these correlates include a reduced sexual dimorphism,

increased reproductive investment, high population density, fission-fusion dynamics, endurance hunting of big game in open habitats, and large brains (Smith et al. 2012). Similar traits may have also coevolved with cooperation in early hominins. Thus, studying the patterns of cooperation in social carnivores will surely continue to yield new and important insights that will contribute to our understanding of the evolution of cooperation more broadly for years to come.

Cross-Reference

- ▶ Convergent Evolution of Hyena and Primate Social Systems
- ▶ Cooperation
- ▶ Cooperation Among Birds
- ▶ Cooperation Among Fishes
- ▶ Cooperation Among Non-Chimpanzee
- ▶ Cooperation Among Non-Human Primates
- ▶ Cooperation Among Non-Humans
- ▶ Cooperation Among Non-Primate Mammals
- ▶ Cooperation and Cheater-Detection
- ▶ Cooperation and Social Cognition
- ▶ Cooperation in Social Carnivores
- ▶ Cooperation in Social Insects
- ▶ Cooperation Varies with Genetic Relatedness
- ▶ Cooperative Alliances
- ▶ Cooperative Breeding
- ▶ Cooperative Coalitions
- ▶ Cooperative Foraging
- ▶ Cooperative Grooming
- ▶ Cooperative Hunting
- ▶ Division of Labor
- ▶ Non-Human Primates
- ▶ The Evolution of Cooperation
- ▶ The Evolution of Human Sociality

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