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Cooperative problem solving in a social carnivore

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Numerous field researchers have described cooperative hunting in social carnivores, but experimental evidence of cooperative problem solving typically derives from laboratory studies of nonhuman primates. We present the first experimental evidence of cooperation in a social carnivore, the spotted hyaena, *Crocuta crocuta*. Eight captive hyaenas, paired in 13 combinations, coordinated their behaviour temporally and spatially to solve cooperation tasks that modelled group-hunting strategies. Unlike many primates that cooperate infrequently or require extensive shaping, spotted hyaenas displayed a natural aptitude for teamwork: all teams achieved success rapidly, repeatedly, and without specific training. Social influences on cooperative performance included an audience effect that could influence party formation and hunting success in the wild. Performance also varied across dyads, notably with rank-related aggression between partners impairing performance. Efficiency improved as partners increasingly attended to one another and coordinated their actions. Lastly, experienced cooperators modified their behaviour to accommodate a naïve companion, using visual monitoring and tracking to promote coordination. We suggest that social carnivores should be considered relevant models for the study of cooperative problem solving, as their abilities provide a comparative framework for testing theories about the mechanisms of social learning and the evolution of intelligence.

Animal cooperation has held significant interest to evolutionary biologists (Axelrod & Hamilton 1981) and comparative psychologists, particularly with regard to understanding the cognitive implications of cooperation in our own species. In experimental studies of cooperative problem solving, at least two animals must jointly perform similar or complementary actions to obtain a food reward. For animals to be considered 'cooperators' within this paradigm, partners must pursue their common goal while taking account of each other's behaviour (Chalmeau & Gallo 1996). The level of behavioural organization between participants can vary, increasing in temporal and spatial complexity from mere similarity of action, to synchrony (similar acts performed in unison), then coordination (similar acts performed at the same time and place), and finally collaboration (complementary acts performed at the same time and place: Boesch & Boesch 1989). For over seven decades, such studies have focused almost exclusively on nonhuman primates (for an exception in corvids, see Seed et al. 2008), reflecting a general premise that higher-order cognitive functioning in large-brained or highly encephalized animals should enable organized teamwork. Curiously, however, primates are often inefficient at solving cooperation problems in the laboratory, potentially reflecting a weak tendency to cooperate for food in nature. We therefore asked whether species that cooperate for food more routinely in the wild, such as social carnivores, might better meet the criteria of cooperative problem solving in the laboratory. In three successive experiments, we tested captive spotted hyaenas, *Crocuta crocuta*, for evidence of (1) synchrony and coordination during cooperative problem solving, (2) social modulation of cooperative performance and (3) behavioural adjustment between cooperating partners.

Using various cooperation tasks, laboratory studies have produced evidence of teamwork in apes (chimpanzees: Crawford 1937; Savage-Rumbaugh et al. 1978; Chalmeau 1994; Povinelli & O'Neill 2000; Melis et al. 2006; bonobos: Hare et al. 2007; orangutans: Chalmeau et al. 1997b); nevertheless, the interpretation of these findings can be somewhat contradictory. While some researchers have implicated complex cognitive processes during task solution, others have shown that even 'human-enculturated' apes may require extensive training or shaping to work together (Crawford 1937). Success often comes slowly, and, given a choice, many apes preferentially work alone. Given the interactive nature

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of the task, some studies have revealed social constraints on performance, such that when partner preferences are taken into account, success can be achieved more readily (Melis et al. 2006). Monkeys also solve cooperation problems to access and share food (baboons: Beck 1973; capuchins: Westergaard & Suomi 1997; Mendres & de Waal 2000; de Waal & Berger 2000; tamarins: Cronin et al. 2005); however, some studies report that monkeys generally fail to cooperate and, if successful, do not necessarily attend to their partner's behaviour, such that solution may be fortuitous (baboons: Fady 1972; macaques: Mason & Hollis 1962; Burton 1977; Petit et al. 1992; capuchins: Chalmeau et al. 1997a; Visalberghi et al. 2000). To date, there is no evidence of cooperative problem solving in any prosimian primate.

From the perspective of comparative psychology, these mixed results suggest that nonhuman primates may require specific conditions or training to cooperatively solve food acquisition problems. From an ecological or biological perspective, however, the negative findings are broadly consistent with the prototypical primate lifestyle. Specifically, the natural parallel of working together for food in the laboratory is group hunting in the wild; yet, primate foraging typically involves individual acquisition and handling of food items that make up a predominantly vegetarian diet. In other words, most of the 200-odd primate species rarely forage cooperatively or share food in nature, and most do not normally face feeding challenges that necessitate a cooperative resolution. The issue of biological significance or ecological relevance is brought to bear from field observations of primate predatory behaviour and food sharing. Notably, the species that most reliably cooperate in the laboratory (e.g. chimpanzees, bonobos and capuchins) are those that hunt and potentially share food in the wild (e.g. Rose 1997; Surbeck & Hohmann 2008). This relationship between cooperative tendencies, hunting and joint feeding raises the question of why archetypal social hunters are not more often the focus of cooperation studies.

Cooperative hunting occurs in various animals, including aerial predators (e.g. hawks: Bednarz 1988) and marine mammals (e.g. killer whales: Smith et al. 1981; Florez-Gonzales et al. 1994), but most notably characterizes social terrestrial carnivores (e.g. lions: Schaller 1972; Scheel & Packer 1991; wild dogs: Estes & Goddard 1967; Creel & Creel 1995; wolves: Mech 1970; coyotes: Bowen 1981; spotted hyaenas: Kruuk 1972; Mills 1990). Based on field descriptions, communal hunting in social carnivores ranges in complexity from seemingly opportunistic actions to highly organized attacks, where unique hunting styles reliably identify packs (wild dogs: Malcolm & van Lawick 1975; wolves: Haber 1996). Even the pinnacle of cooperative complexity, collaboration, is evidenced during lion hunts when individuals assume different, but complementary, roles (lions: Stander 1992). Social carnivores additionally have elaborate expressions of food solicitation and food sharing, ranging from simple co-feeding, to provisioning, regurgitation and allonursing (Estes & Goddard 1967; Mills 1990; Packer et al. 1992). Based on feeding ecology alone, social carnivores presumably would have experienced stronger selection pressures for perfecting cooperative hunting skills, including understanding their partner's role, than would most primates.

Despite the biological relevance of cooperation for social hunters, no experimental study (of the sort available for primates) has demonstrated that the various defining features of cooperative problem solving are present in carnivores. Likewise, there is no information on the social modulation of performance in carnivores. Therefore, our understanding of cooperation could profit from a more broadly comparative analysis. Spotted hyaenas are prime candidates for such studies because they are formidable pack hunters that obtain most of their diet through predation (Kruuk 1972; Cooper 1990). They additionally lend themselves to studies of interindividual behaviour because their social complexity rivals that of primates (Drea & Frank 2003). They live in stable, matriarchal clans that are characterized by female philopatry, year-round male residency, and overlapping generations (Kruuk 1972; Frank 1986a). Moreover, adherence to strict rules of social conduct is aggressively enforced along linear dominance hierarchies in which females outrank adult males (Frank 1986b; Smale et al. 1995). Because the social and behavioural arrangement of spotted hyaenas is similar to that of many cercopithecine (Frank 1986a, b) and prosimian (Kappeler 1993; Drea 2007) primates, there is ample precedent for a hyaena/primate comparison (Holekamp et al. 1999; Drea & Frank 2003) to validate a similarly comparative study of cooperation.

Hyaena forays have no leaders and often involve long pursuits that culminate in hunters fanning out to encircle their quarry (Kruuk 1972). Thus, using the scale developed by Boesch & Boesch (1989), it would appear that hyaenas show similarity, synchrony and coordination, but perhaps not collaboration, when cooperatively hunting in the wild. Consequently, we predicted that captive hyaenas could complete a cooperation task that required, at most, temporal and spatial coordination. In experiment 1, we examined whether hyaenas would show evidence of cooperation on tasks that (1) modelled salient features of the hunting strategies applied in nature and (2) varied in complexity, demanding either temporal synchrony of behaviour alone or temporal synchrony in combination with spatial coordination.

Hyaena hunting parties bring down large ungulates and defend their kills against theft by lions, but the participants also display fierce competition over the spoils. In large parties, rivalry is evidenced by the ravenous speed at which hyaenas devour their kill (Kruuk 1972; Mills 1990), and in smaller parties, by rank-related priority of access to the carcass (Tilson & Hamilton 1984; Frank 1986b). This juxtaposition of social cohesion and competition (Smale et al. 1995; Glickman et al. 1997; Drea & Frank 2003) sets the stage, in experiment 2, for a study of the social modulation of cooperation. The predominance of social facilitation in spotted hyaena behaviour (Glickman et al. 1997), coupled with the positive correlation between party size and difficulty of prey capture (Kruuk 1972), led us to anticipate an audience effect on performance. In particular, we predicted that success in solving a cooperation task would improve by the mere addition of subjects. Moreover, because dominance relations play a crucial role in spotted hyaena society (Drea & Frank 2003) and the social marginalization of subordinates can negatively affect the performance of otherwise proficient animals (Drea & Wallen 1999), we anticipated an effect of social status on hyaena performance. In particular, because hyaenas might be less inclined to cooperate in partnerships of disparate rank, we predicted that team success would vary in relation to the hierarchical composition of partnerships.

Lastly, if spotted hyaenas were biologically prepared to cooperate, we would expect the species to fulfil the requirements of cooperation as defined in primate studies, in particular, that partners would attend to each other's actions. We therefore expected that the coordination of behaviour between partners would improve with experience. Likewise, because gaze orientation is often used as a measure of intentionality or understanding in primate studies (Leavens & Hopkins 1998; Tomasello et al. 1998; Mendres & de Waal 2000), we predicted that hyaenas would increase their rate of visual monitoring (of both the apparatus and their partner) over time. Lastly, as in a study of chimpanzee cooperation (Povinelli & O'Neill 2000), we reasoned that a partner's naiveté would motivate an experienced animal to alter its behaviour in a manner that might facilitate cooperation. Thus, in experiment 3, we paired each experienced cooperator of experiment 2 with a 'naïve' subordinate. Because success requires physical