

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.

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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: Bown 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 cercopithecae (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

proximity, we predicted that the experienced hyaena would modify its behaviour to maintain proximity with its inexperienced partner and enhance the likelihood of success.

In all three experiments, the basic task involved delivery of hidden food rewards, from an elevated platform, contingent upon an animal raising its head and tugging on a vertically suspended rope. Pulling hard on the rope would release a spring mechanism, causing a trap door to swing downward, thereby dropping food to the floor. The ‘solo task’ modelled a solitary hunting strategy and involved a single rope that could be controlled by one animal acting alone, whereas the ‘cooperation task’ modelled a group-hunting strategy and involved an additional spring controlled by a second rope. Because animals could operate only one rope at a time, food delivery demanded that two hyaenas work together, pulling in unison for the springs to release simultaneously (Fig. 1).

With only one apparatus, as has been the case in all laboratory studies of cooperation to date, animals need only synchronize their behaviour to be successful (Drea 2006). Moreover, joint action may be facilitated by the close quarters of most laboratory studies. By doubling the apparatus and using a large test arena (Fig. 2), we introduced the element of spatial choice (as hunters might face when selecting between two different prey animals). This duplication increased the challenge of the task, as success required both temporal and spatial coordination, and was less likely to occur fortuitously. Thus, we studied cooperation at two levels of complexity: ‘synchrony’ involved one platform (with 2 ropes total) and ‘coordination’ involved two platforms (with 4 ropes total). In addition, we varied the social context of testing, such that animals could be tested in pairs or in groups. In any social condition (i.e. two, three or four animals), only two hyaenas were required to



Figure 1. Spotted hyaenas solving a cooperation task. By simultaneously tugging on two vertically suspended ropes, the trap door of an elevated platform is opened and food is dropped to the floor.

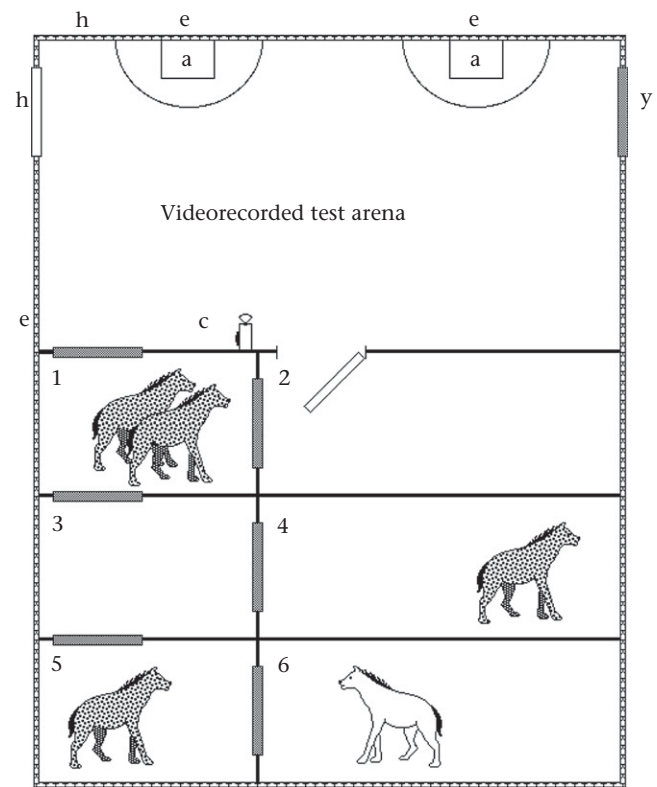


Figure 2. Floor plan of the indoor enclosures and test arena. Depicted (not drawn to scale) is the set-up prior to a pair coordination trial of experiment 2 in which two focal hyaenas in holding pen 1 would be released through pen 2 into the test arena. In this case, each apparatus (‘a’) would be baited, with two ropes hanging down. A semicircle (1 m in radius) delineated proximity to each apparatus. Meanwhile, other hyaenas would be isolated in pens 3–6 from where they could not see the test arena. Experienced cooperators are depicted with spots whereas a cooperation-naïve hyaena is depicted all white. The test arena was monitored by a video camera (‘c’), mounted with a wide-angle lens, and by three experimenters (‘e’) positioned in the hallways (‘h’), two for monitoring the apparatuses and one for recording behaviour. Narrow rectangles represent either personnel doors (white bars) or guillotine doors (shaded bars) that could be controlled from the hallways. Indoor compartments were enclosed by fencing (stippled lines) or by metal walls (solid lines). The outside yard (‘y’) was accessible via a guillotine door in the test arena, but was closed off during tests.

solve the task. Consequently, pair tests imposed a partner constraint that was relaxed during group tests.

EXPERIMENT 1: SYNCHRONY AND COORDINATION IN COOPERATIVE PROBLEM SOLVING

We first examined whether spotted hyaenas could, without training, solve the solo task, followed by cooperative problems at two levels of complexity: synchrony and coordination.

Methods

Subjects and housing

The subjects were the three adolescent members of an all-male social group of spotted hyaenas (cohort A, Table 1). As with all of our subjects, these animals were born and reared at the University of California, Berkeley, Field Station for Behavioral Research (FSBR). The FSBR is fully accredited by the American Association for the Accreditation of Laboratory Animal Care, animal care met with institutional guidelines, and all of the procedures were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of California (protocol no. R091-1092R).

Table 1

Demographics of two cohorts of captive spotted hyaenas that served as subjects in three sequential cooperation experiments involving different partnerships

Experiment	Subjects				Partnerships
	Cohort (size)	Sex and kinship	Age (months)	Rank	
1	A (N = 3)	Twin males (P, C)	16–20	α , β	$\alpha\beta$, $\alpha\gamma$, $\beta\gamma$
		Singleton male (H)	11–15	γ	
2	B (N = 4)	Twin females (N, I)	15–21	α , β	$\alpha\beta$, $\alpha\gamma$, $\alpha\delta$, $\beta\gamma$, $\beta\delta$, $\gamma\delta$
		Twin males (G, V)	15–21	γ , δ	
3	B (N = 5)	Twin females (N, I)	21–22	α , β	$\alpha\Omega$, $\beta\Omega$, $\gamma\Omega$, $\delta\Omega$
		Twin males (G, V)	21–22	γ , δ	
		Singleton male (W)	19–20	Ω	

Age ranges of subjects are provided from start to finish of each experiment. Experiment 1 was conducted 1 year before experiment 2. Experiment 3 was conducted immediately following experiment 2.

Each cohort was housed socially in outdoor yards (6.9 × 18.6 m) with access to an indoor enclosure (4.5 × 8.7 m), as well as to several smaller holding pens (Fig. 2). The indoor enclosure served as the test arena. On test days, we withheld regular feeding of Nebraska Brand carnivore zoo diet and pork bones until after trials, so that the subjects would be moderately food motivated.

All of our subjects were relatively young (Table 1) and had not previously participated in any cognitive study. Hyaenas are virtually full-grown at 11–22 months of age, but males are peripubertal, and females, which mature slightly later, are subadult (Kruuk 1972). Although the prime hunting years for hyaenas in nature may occur later in life (Holekamp et al. 1997), animals do hunt at the ages under study (Kruuk 1972) and must be prepared to engage in socially facilitated cooperative predation. Also, by this age, spotted hyaenas have clearly defined, stable dominance relations (Holekamp & Smale 1993), which we determined for all pairs of subjects within a cohort, using previously described methods for twins (Drea et al. 1996) and unrelated group members (Jenks et al. 1995). Cohort A contained twin males, C and P (ranked α and β , respectively), and a singleton unrelated male, H (γ).

Apparatus, reward and habituation

All tasks involved one or two elevated (2.5 m) metal platforms (95 × 70 cm), each with one or two ropes (2.5 cm across, 1.5 m long) hanging from it that was connected to a spring-release mechanism controlling a trap door (22 × 60 cm). Although prey are not stationary, the actions required to solve the basic task mimic motions displayed by hunters biting at the flanks of prey to pull it down in nature.

We placed the same amount of food (two bone chips about the size of small pork chops and two meatballs of Hill's prescription feline diet) on any trap door used. If the hyaenas opened the trap door, food would be dispersed on the ground in a manner that typically allowed each animal to obtain some of the reward: whereas hyaenas could quickly gobble up bone chips, meatballs would stick to the floor upon impact and therefore required a little more handling time. These differences promoted an equitable distribution of rewards such that solution of the cooperation task typically involved the 'sharing' of food. Unlike in similar studies on primates, the food on the platforms was not visible to the hyaenas. Therefore, to enhance the signal of food availability in experiment 1, we associated platforms with black and white symbols, placed both at the site of food delivery and food consumption (Fig. 1). Upon solution of the task or after 10 min, we retracted the vertical ropes to prevent further pulling. The distribution of food and our retraction of the ropes served to minimize the occurrence of unrewarded pulling.

Hyaenas are neophobic, so to habituate the animals to the apparatus, we permanently installed the platforms (positioned 2.1 m apart) 1 month before the onset of testing. Using food incentives, we then trained the subjects to shuttle between holding

pens on command, and habituated them to spending time in various social contexts, including alone, in all possible pairings or as a group. Once habituated to those procedures, we allowed animals to discover how to solve the task.

General testing procedures

We used the following general protocol in all three experiments (procedural variations are described in turn). First, we presented each hyaena with the solo task. Subsequently, we tested hyaenas on variants of the cooperation task that involved either different levels of complexity (synchrony versus coordination) or different social contexts (pair versus group). We tested the hyaenas between 1000 and 1300 hours on trials that lasted 10 min (maximum). If they were unsuccessful within this time frame, we raised the ropes; otherwise, success latency determined trial duration. When testing involved one platform only, we varied the baited side randomly between the left and right positions. Whether singly or in dyads, we tested animals in random order on parallel trials. For instance, during pair testing, all dyads rotated through trial 1 before advancing to trial 2. Thus, when testing, for example, three hyaenas in their three possible dyads, each hyaena would be exposed to the same task twice for any given trial, but each time with a different partner. We thereby could examine social effects (and maximize the number of dyads tested), while keeping the level of experience, per dyad and per individual, consistent across trials. This procedure also circumvented analysis problems otherwise introduced by the nonindependence of subjects.

Specific testing procedures

We presented the hyaenas of cohort A with the solo task, first as a group of three (70 trials total) and then per hyaena alone (70 trials each or 210 trials total). We conducted numerous trials in which only one hyaena pulling was needed to open the door, primarily because prior studies on chimpanzees had shown that even enculturated subjects required extensive pretraining and shaping, including modelling by a human, to solve such a task (Crawford 1937). We also wanted to fully habituate the animals to the basic task presented under different social testing conditions.

For cooperative testing, we next partnered subjects (as CP, CH and PH, reflecting the following rank relationships: $\alpha\beta$, $\alpha\gamma$ and $\beta\gamma$) first for the coordination task (3 trials per dyad), then for the synchrony task (14 trials per dyad). Our order of cooperation trials specifically placed the most complex condition first to assess ability independent of shaping. The subsequent focus on simpler synchrony tasks was to provide information on performance at a level of cooperative complexity comparable to that of primate studies.

Data collection and analyses

We collected data in real time (using a portable computer that time-tags each entry with an accuracy of 1 s) and from

videotaped records of all trials (Fig. 2). As this experiment focused on cooperative ability, our main performance measures included success (percentage of trials that a trap door was opened to deliver food) and efficiency (latency in minutes to open the trap door).

Results

Although our hyaenas had never participated in any behavioural study, they eagerly solved the solo task with 100% success, regardless of the social context (group versus alone). No shaping, specific training or human modelling was necessary for individual hyaenas to reliably pull on the rope and obtain food. Despite the complexity introduced by requisite joint action, all three dyads were 100% successful across all pair coordination trials, displaying remarkable efficiency even on their initial exposure (latency to open the first trap door on trial 1: $\alpha\beta$, 1.52 min; $\alpha\gamma$, 4.41 min; $\beta\gamma$, 0.27 min). During the less exacting pair synchrony trials, success remained at 100% and, on average, efficiency increased even further (mean \pm SE latency to open the single trap door across all trials: $\alpha\beta$, 1.05 ± 0.47 min; $\alpha\gamma$, 1.00 ± 0.28 min; $\beta\gamma$, 1.27 ± 0.42 min). Therefore, after much experience solving a solo task, partnered hyaenas spontaneously displayed cooperative behaviour (Fig. 1), both at the level of synchrony (which is comparable to that displayed by some primates), and at the level of coordination (which remains to be tested in other species).

EXPERIMENT 2: SOCIAL MODULATION OF COOPERATION

Having established that spotted hyaenas can effectively solve cooperation problems, we turned our attention to questions pertaining to the social modulation (facilitation or inhibition) of performance. The focus here is not on how animals learn to cooperate, but on whether and how their performance is modulated by social context.

Methods

Subjects

The subjects were the four top-ranking members of a mixed-sex social group of five adolescent captive-born spotted hyaenas (cohort B, Table 1). They included twin females (N and I) and twin males (G and V), ranked as α , β , γ and δ , respectively. While continuously housed with cohort B, we secluded the lowest-ranked member, the singleton male (W), in one of the holding pens during all trials of experiment 2 (see experiment 3). Whereas the hyaenas of cohort A were control animals, all five hyaenas of cohort B had received prenatal antiandrogens that had modified the morphology of their external genitalia (Drea et al. 1998). Nevertheless, group dynamics, rank relations (in which females retain social dominance over males), and ultimately, reproductive and maternal behaviour of these treated subjects were similar to those of control animals (Drea et al. 2002). Therefore, we suggest that any effect of treatment on cooperative behaviour was negligible. Housing, habituation and feeding regimens were as in experiment 1.

Apparatus and testing procedure

We used the same apparatus as in experiment 1, but without the symbols, as these considerations proved unnecessary. In experiments 2 and 3, ropes hanging down from the apparatus provided the only visual cue of potential food availability.

We refer to each phase of experiment 2 (illustrated in Fig. 3a–g) using a compound label that denotes first the social context of testing (alone, $N = 4$; pair, $N = 6$; group, $N = 1$) and then the type of task (solo, synchrony, or coordination). We distinguish replicate

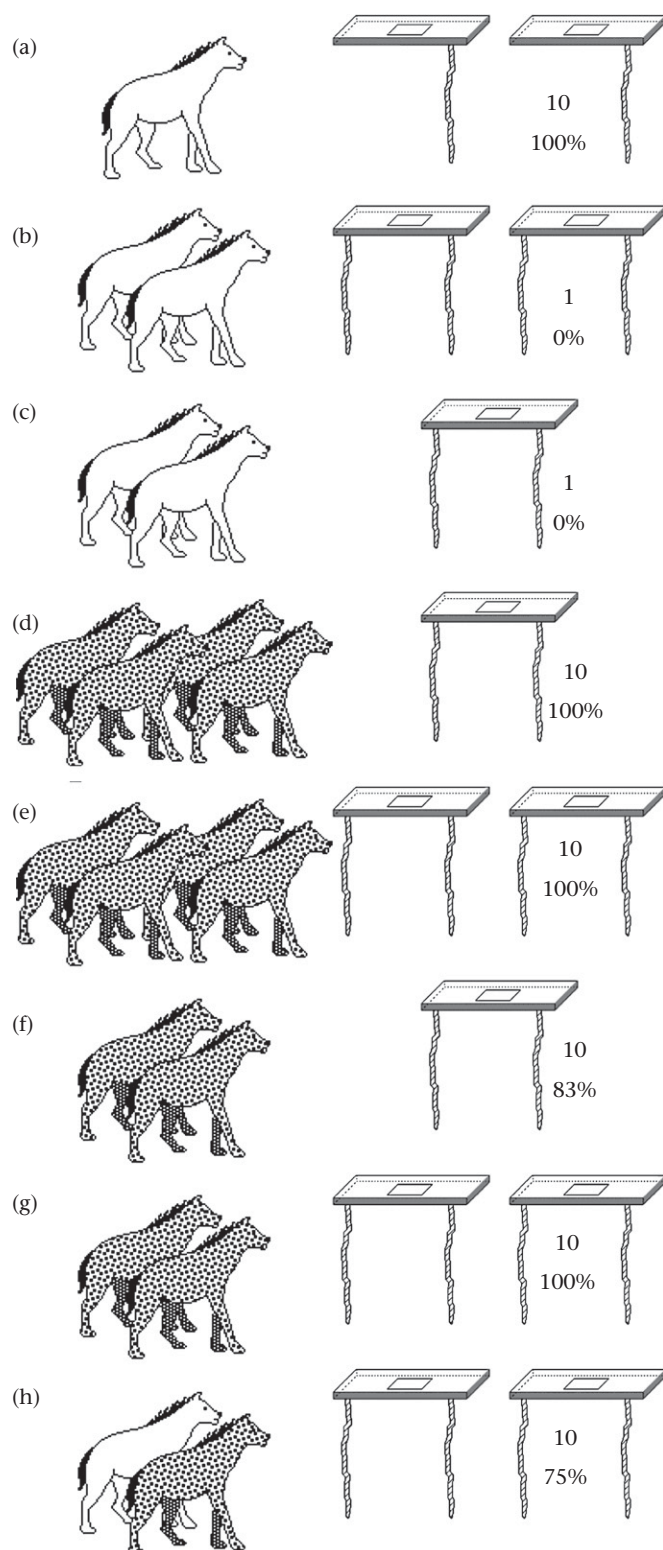


Figure 3. Experimental design: (a–g) experiment 2 and (a, h) experiment 3. The left panel shows the social context of testing (alone, pair, or group), as well as the naïveté (white) or experience (spots) of the participating hyaenas. The right panel shows the number of platforms and ropes that define the type of task (solo, synchrony, or coordination). The values reported to the far right indicate the total number of trials per animal, pair or group, per study phase (top), and the mean percentage success for all animals opening the first trap during trial 1 of that study phase (bottom). Experimental phases were as follows: (a) alone solo; (b) pair coordination, baseline; (c) pair synchrony, baseline; (d) group synchrony; (e) group coordination; (f) pair synchrony, test; (g) pair coordination, test; (h) pair coordination, naïve.

phases by a final qualifier (baseline, test, or naïve) that reflects differences in the hyaena's level of experience with the task (see experiment 3 for more on the 'naïve' condition).

Because this experiment focused on the social modulation of performance rather than on demonstrating cooperative abilities, per se, we first established a baseline of solo performance without extensive pretraining. Thus, rather than replicate the numerous solo trials of experiment 1, we began with only 10 solo trials per hyaena (Fig. 3a), reflecting our conservative criterion that each animal, presented alone with two platforms, had to open a trap door 20 times and consume the food dispensed before progressing to social testing. Thereafter, to establish a baseline of performance at each level of cooperation, we presented each dyad (NI, NG, NV, IG, IV and GV, ranked as $\alpha\beta$, $\alpha\gamma$, $\alpha\delta$, $\beta\gamma$, $\beta\delta$ and $\gamma\delta$, respectively) with a single coordination trial (Fig. 3b), followed by a single synchrony trial (Fig. 3c). To potentially test for an audience effect, we continued testing with all four animals present during 10 group synchrony trials (Fig. 3d), followed by 10 group coordination trials (Fig. 3e). Lastly, to examine social influences on the performance of 'cooperation-experienced' animals (specifically to test for rank effects), we again conducted pair synchrony trials (10 per dyad; Fig. 3f), followed by pair coordination trials (10 per dyad; Fig. 3g).

Data collection and analyses

As in experiment 1, we collected data in real time and from videotaped records of all trials. Again, main performance measures included success and efficiency (as defined in experiment 1). In addition, we scored all behaviour directed by the animals towards the apparatus, including proximity to and visual or olfactory investigation of a platform, biting and pulling on a rope, opening a trap, and eating the reward (for behavioural definitions, see Supplementary Material Table S1). We also scored all behaviour directed by the animals towards other hyaenas, with the most pertinent social interactions including aggression (i.e. threatening or biting), subordination (i.e. appeasing or withdrawing) and social monitoring (i.e. watching the partner or alternating gaze between the partner and the apparatus). Operational definitions for most of these interactions have been reported elsewhere (Zabel et al. 1992; Jenks et al. 1995; Drea et al. 1996; Tomasello et al. 1998), but additional details are provided in Supplementary Material Table S2. Lastly, we calculated measures of coordinated action (e.g. percentage of responses allocated to the apparatus when the partner was present versus absent) from integrated time course analyses, for instance, by matching the latencies and localities of approaches and leaves for two hyaenas.

We used AWK programming and UNIX/STAT compact programs (Perlman 1986) for data validation, extraction and analyses. One observer (C.M.D.) performed all real-time data collection. In addition, at the end of the study, both observers (C.M.D. and A.N.C.) viewed the videotapes in their entirety, sometimes frame by frame, to retrieve any behaviour missed during real-time observation. Data validation (e.g. matching the number of approaches of an apparatus with the number of departures, verifying the requisite sequence of behaviour, such as a bite preceding a pull, etc.) provided a first tier of 'quality control' or observer reliability, as we corrected for any mismatch or omission by re-reviewing the tape.

For intraobserver reliability estimates, each observer twice scored a given tape (which represented several trials), once at the beginning and once at the end of data collection. For interobserver reliability estimates, both observers scored another tape. We considered differences in the chronology or labelling of events for a given subject as disagreements, such that the likelihood of chance agreement was negligible. Consequently, we calculated indexes of concordance for each behavioural measure reported herein as the percentage agreement between two data sets (Martin & Bateson

1993). The indexes for behaviour directed towards the apparatus were as follows: proximity (approach and leave) = 97%; investigate = 92%; bite rope = 96%; pull (and let go) = 99%; open = 100%; eat = 100%. The indexes for behaviour directed towards another hyaena were as follows: threaten = 97%; bite hyaena = 96%; appease = 99%; withdraw = 96%; watch = 91%; alternate gaze = 93%. Because coordinated action was derived primarily from sequential analyses of recorded behaviour, we do not present independent reliability scores for these measures.

During trials, human observers managed the ropes and recorded behaviour, but because experimenters varied between five different people, it was unlikely that a 'Clever Hans' effect (Sebeok & Rosenthal 1981) could account for hyaena cooperative behaviour. Nevertheless, we tested for this possibility by inserting control trials at various stages of testing. During these trials, the subjects' behaviour was filmed without any experimenters present. Equivalent behaviour and success rates were obtained during control trials, indicating that hyaena performance was unaffected by human presence.

Results

Performance across the various cooperation tasks

Following only a few trials on the solo task (Fig. 3a), all six dyads showed 0% success in the single baseline trials of pair coordination (Fig. 3b) and pair synchrony (Fig. 3c). Nevertheless, when cooperation testing continued with all four animals present (Fig. 3d, e), pairwise performance improved dramatically. Regardless of partnerships, hyaenas solved the cooperation problems in all group synchrony trials (success: 100%; mean \pm SE latency: 4.06 ± 0.95 min) and all group coordination trials (success: 100%; mean \pm SE latencies: 1.67 ± 0.38 min and 3.43 ± 0.72 min for the first and second trap doors, respectively), with every possible dyad within the group opening at least one door. Thus, the addition of animals enhanced performance on identical tasks.

After experiencing group testing (Fig. 3d, e), paired hyaenas continued to cooperate at both levels of complexity (Fig. 3f, g). That is, most dyads solved the synchrony task on trial 1 (Fig. 4a) and maintained a high standard of success throughout all 10 synchrony trials (Fig. 4b). Likewise, all dyads solved the coordination task on trial 1 (Fig. 4c) and also maintained a high standard of success throughout all 10 coordination trials (Fig. 4d). Consequently, early and relatively brief group exposure to a cooperation task (experiment 2) had enhancing effects on pairwise performance, similar to the more prolonged exposure on a solitary task (experiment 1).

Social modulation of performance: audience and partnership effects

By examining hyaena behaviour across the various stages of testing in experiment 2, we could test for the social modulation (facilitation or inhibition) of performance, specifically by comparing behaviour across tasks (e.g. $\alpha\beta$ during group synchrony versus pair synchrony) or across partnerships (e.g. $\alpha\beta$ versus $\gamma\delta$ during pair synchrony). Such comparisons revealed that hyaena performance was socially modulated by party size and pair membership. For instance, social context (i.e. group versus pair) affected efficiency in that any given dyad showed a decrement in performance following removal of other group members, this despite having gained more experience on the task: during coordination trials (cf. Fig. 3e and Fig. 3g), successful partners took less time, on average, to open the first trap door in the 'earlier' group condition than they did in the 'later' pair condition (mean \pm SE: group coordination latency: 1.84 ± 0.46 min; pair coordination latency: 3.10 ± 0.49 min; $t_5 = 2.94$, $P < 0.05$).

Moreover, proficiency in experienced pairs of cooperating animals (Fig. 3f, g) varied across partnerships (Fig. 4b, d). Notably,

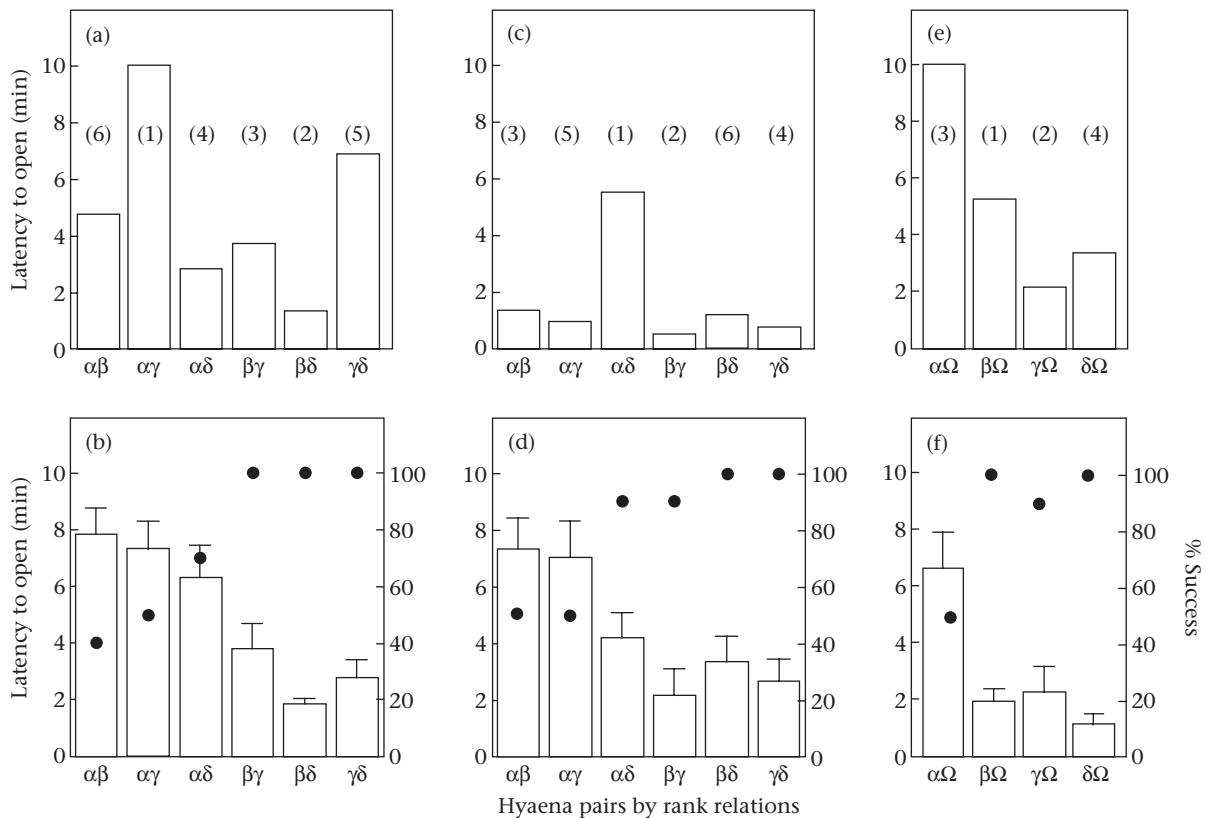


Figure 4. Pairwise performance of cooperating spotted hyaenas: (a–d) experiment 2 and (e–f) experiment 3. Performance is reflected by two measures: mean \pm SE latency (\square) and percentage success (\bullet) in opening the first of two trap doors (i.e. during coordination) or the only trap door (i.e. during synchrony). A latency of 10 min indicates failure to cooperate. The phases of testing represented are as follows: (a, b) pair synchrony, test (see Fig. 3f); (c, d) pair coordination, test (see Fig. 3g); (e, f) pair coordination, naïve (see Fig. 3h). (a, c, e) Top panel shows first-trial latency (with the order of pair testing in parentheses). (b, d, f) Bottom panel shows mean latency and percentage success across 10 trials. Note that first-trial performance allows comparison with the sole trials of baseline testing (e.g. Fig. 3b, c).

dyads involving the most dominant member (α) were relatively inefficient and did not always open the trap door within the allotted time. By contrast, lower-ranking animals paired together were faster and successful every time. Variation in performance correlated with differences in received aggression. For example, during pair coordination (Fig. 3g), rates of aggression (threats and bites) by the dominant team member combined with submission (appeasement and withdrawal) by the subordinate team member were four times greater in the two least successful pairs ($\alpha\beta + \alpha\gamma$; $N = 59$) than in the two most successful pairs ($\beta\delta + \gamma\delta$; $N = 14$) and were positively correlated with success latency (Pearson correlation: $r = 0.94$). Thus, hyaena performance was facilitated by greater numbers of animals present, but inhibited by the aggressive dominance relations between partners.

Taking account of the partner's behaviour: social monitoring and coordination

To begin to address whether spotted hyaenas took account of each other's actions, we examined whether partners were differentially attentive to each other or the apparatus across stages of testing. Specifically, we compared the rates (frequency per min) of visual monitoring during early and late stages of cooperation testing. In this analysis, we combined the sole trials of pair coordination and pair synchrony (Fig. 3b, c) for the 'baseline' condition, and combined the first trials each of pair synchrony and pair coordination (Fig. 3f, g) for the 'test' condition, for a total of two trials per condition per dyad. The mean \pm SE rate at which partners watched one another remained constant throughout the study, but hyaenas looked at the apparatus more often and showed gaze alternation only during test trials (Table 2).

Next, we asked whether successful hyaenas adjusted their behaviour to one another along temporal and spatial dimensions or whether they merely increased their rates of responding. Specifically, we examined the spatial distribution of partners and the timing of rope pulling during different phases of pair coordination (Fig. 3b versus Fig. 3g). At any time during such trials, the location of partners could be distributed in one of four ways: both animals could be outside the proximity zones of either platform; one hyaena could be near a platform while the other was far away from either platform; each hyaena could be near different platforms; or both could be near the same platform (see Fig. 2). Successful coordination required that both animals be in the same location at the same time. During baseline, partners spent approximately 20% of the trial either in different zones or in the same zone, whereas during the test trial, partners differentiated their spatial allocations: by comparison to their baseline behaviour, partners in the test trial tended to spend less time in different zones (paired t test: $t_5 = 2.01$, $P = 0.10$), while significantly increasing time spent in the same zone (paired t test: $t_5 = 2.56$, $P = 0.05$). Thus, experienced

Table 2

Changes in rates of visual monitoring by captive spotted hyaenas across baseline and test trials of cooperation testing

Behaviour	Baseline trial rate	Test trial rate	Paired t_{11}	P
Look at apparatus	2.05 \pm 0.27	3.30 \pm 0.21	3.14	<0.01
Watch each other	1.33 \pm 0.11	1.07 \pm 0.16	1.57	NS
Alternate gaze	0.0 \pm 0.0	0.14 \pm 0.06	2.93	<0.02

Definitions of behaviour are provided in the Methods. Rates are means \pm SE frequency per minute.

partners were more likely than naïve partners to be in the same zone at the same time (Fig. 5a).

Similarly, if the hyaenas were coordinating their behaviour, rope pulling should have increased only when partners were nearby. This analysis required that all four ropes be available, so we assessed behaviour prior to the opening of the first trap door. During baseline trials, the hyaenas avoided their partner, and preferentially pulled on ropes when their partner was not in the same zone ($\chi^2_1 = 29.2$, $P < 0.001$; Fig. 5b). By contrast, during test trials, the hyaenas pulled on ropes more often when their companion was nearby and available to fulfil its partnership role ($\chi^2_1 = 6.33$, $P < 0.025$; Fig. 5b). Only the appropriate response of coordinated rope pulling increased in rate.

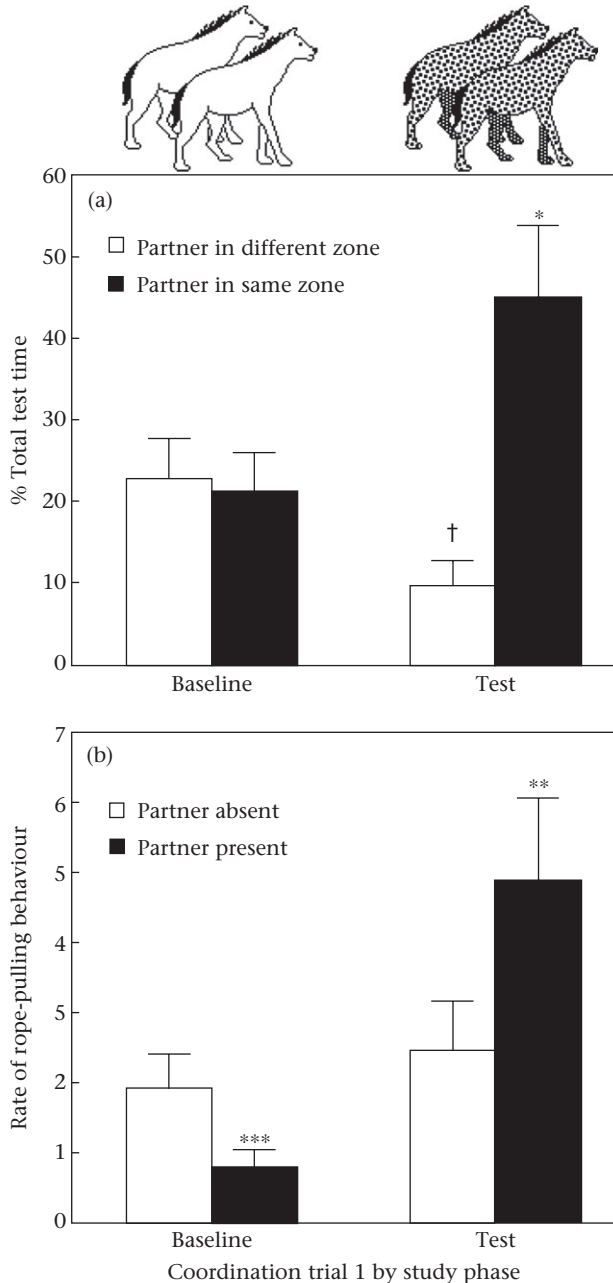


Figure 5. Temporal and spatial coordination of spotted hyaena pairs ($N = 6$), as reflected by (a) partner location and (b) rope pulling. Data are from the single 'baseline' trial (see Fig. 3b) and the first of 10 'test' trials (see Fig. 3g) of the pair coordination task, when hyaenas were cooperation-naïve (white) and cooperation-experienced (spots), respectively. † $P = 0.10$, * $P = 0.05$; ** $P < 0.025$; *** $P < 0.001$.

EXPERIMENT 3: ACCOMMODATING A NAÏVE PARTNER

To examine further whether hyaenas take account of one another's behaviour, we investigated the effects on cooperative performance of pairing experienced cooperators with a naïve companion.

Methods

Subjects

The subjects were all five adolescent members of cohort B (Table 1), including the singleton male, W (ranked Ω), who had remained cooperation-naïve until this point.

Testing procedure

This experiment involved only two contexts for testing W (alone, $N = 1$; pair, $N = 4$). Hyaena W had remained isolated in one of the holding pens during trials of experiment 2 (Fig. 2) and, prior to testing, had reached criterion on the solo task (Fig. 3a). We then paired each of the experienced cooperators of experiment 2 with this 'naïve' partner and presented each new dyad (NW, IW, GW and VW, ranked as $\alpha\Omega$, $\beta\Omega$, $\gamma\Omega$ and $\delta\Omega$, respectively) with the coordination task (10 trials per dyad; Fig. 3h). We use the term 'naïve' to distinguish W's level of experience from that of the other subjects, but recognize that his naiveté diminished across trials. Nevertheless, all first trials involved a new partnership. Moreover, our focus was less on W than on the behaviour of the four subjects paired with W.

Data collection and analyses

We calculated an additional measure of coordinated action or accommodation (i.e. following or joining the partner at the apparatus; Supplementary Material Table S2) from integrated time course analyses. As before, because following and joining were derived primarily from sequential analyses of recorded behaviour, we do not present independent reliability scores for these measures.

Results

When presented with a complex coordination task (Fig. 3h), three of the four new pairs consisting of an experienced cooperator and a naïve partner were successful on trial 1. Overall, these new pairs were also moderately efficient on trial 1 (mean \pm SE latency: 5.17 ± 1.73 min; Fig. 4e). Their performance ranked between that of two naïve animals (Fig. 3b) and two experienced animals (Fig. 3g) solving the same task: whereas two naïve hyaenas had shown 0% success and the maximum latency during baseline coordination, two experienced hyaenas had shown 100% success and a mean \pm SE latency of 1.69 ± 0.77 min (Fig. 4c).

What may have accounted for the initial achievement by the mixed partnerships? The prerequisite of coordination involved being at the same platform at the same time. Therefore, cooperation would have been facilitated by the experienced hyaena (1) monitoring the naïve partner and (2) adjusting its own behaviour to ensure proximity. Throughout trials of experiment 3, visual monitoring (watch + alternate gaze) occurred at a mean rate of 2.6 times per min. Moreover, experienced hyaenas modified their behaviour to accommodate their subordinate partner's inexperience by assuming 'follower' roles with the naïve 'leader' (Fig. 6a) and initially joining him (>70%) at whichever platform he had approached (Fig. 6b). They ceased joining him, however, after he had gained experience. In fact, the pattern was reversed in later trials, when the formerly naïve animal preferentially joined his higher-ranking partners (>80%; Fig. 6b). Despite initial accommodation, the pattern of rank-related social influences on partner

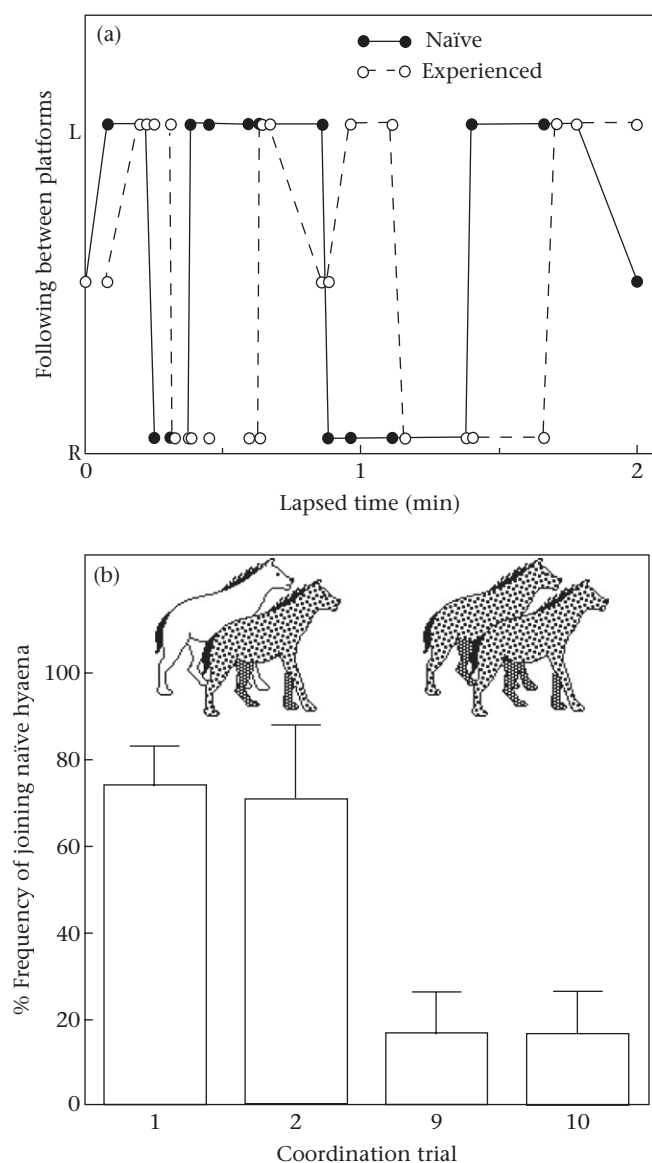


Figure 6. Tracking of a naïve hyaena by experienced cooperators by (a) following and (b) joining. (a) The highest-ranking, cooperation-experienced female initially assumed an uncharacteristic role by following the lowest-ranking, cooperation-naïve male between the L (left) and R (right) platforms, with a delay of 4–19 s (data are presented for the first 2 min of coordination trial 1). Midpoints along the Y axis represent movement away from either platform. (b) The four highest-ranking, cooperation-experienced animals preferentially joined (i.e. approached within 1 m) their naïve, subordinate partner while the naïve partner was already near an apparatus during two early coordination trials, but not during two later trials (after the naïve animal had gained experience), when the ‘joiner’ roles were reversed. Because success terminated trials, data are presented for the first 3 min only to standardize for differences in success latencies across trials. Values are means \pm SE.

performance (evident across trials of experiment 2; Fig. 4b, d) also emerged across trials in the new pairings of experiment 3 (Fig. 4f).

DISCUSSION

In the enduring pursuit to characterize human or even primate uniqueness, evolutionary anthropologists have identified a set of skills, including cooperation, that potentially reflect an animal's possession of special cognitive abilities. Recent years, however, have seen a flurry of studies challenging this general premise by

showing equal, if not superior, performance of these same skills by nonprimates, including, for instance, teaching in meerkats (Thornton & McAuliffe 2006), culture in cetaceans (Noad et al. 2000; Rendall & Whitehead 2001), tool use in corvids (Hunt 1999; Weir et al. 2002) and transitive inference in fish (Grosenick et al. 2007). To this growing list, we can now add cooperative problem solving in spotted hyaenas.

Despite the added complexity of our cooperation tasks, spotted hyaenas proved to be exceptionally skilled cooperators. Young spotted hyaenas rapidly (i.e. within as little as one trial) and readily (i.e. without specific training or shaping) worked together with a partner to obtain food that was otherwise unavailable to them individually. Numerous solo trials prior to pair testing perhaps supported the immediate expression of cooperative problem solving in experiment 1. With less solo experience, the subjects of experiment 2 nevertheless evinced rapid pairwise cooperation, but only following group exposure to the task, suggesting a role for repetition and/or social facilitation in the acquisition of cooperative behaviour. Thus, despite procedural differences between our experiments, the outcome was consistent: all hyaena pairs efficiently solved tasks that required a sophisticated level of organizational complexity. Their performance on temporal synchrony and spatial coordination tasks surpassed that of well-trained chimpanzees solving simpler synchrony tasks (Crawford 1937; Chalmeau 1994). Moreover, data from experiments 2 and 3 on social monitoring, behavioural alignment and partner-dependent adjustment showed that cooperating spotted hyaenas took account of their partner's behaviour, at least in a manner comparable to that reported for some primates. The implication of such behaviour with regard to the attribution of mental state, however, remains uncertain (Tomasello & Call 1997).

Beyond being proficient cooperators, team members were sensitive to their social circumstances and partnerships, modifying their behaviour according to group size, rank relations between teammates and partner expertise. In experiment 2, for instance, a simple increase in party size improved the efficiency with which hyaenas solved identical tasks. This audience effect is in accord with the ubiquitous appearance in hyaenas of socially facilitated behaviour (Glickman et al. 1997), a first step towards cooperation. That teams involving the alpha animal were also characterized by diminished performance suggests that the increased aggression associated with these partnerships significantly impaired cooperation, similar to accounts of the differences in performance shown by socially tolerant bonobos versus more aggressive chimpanzees (Hare et al. 2007). Moreover, similar to the social modulation of performance in group-tested cercopithecine primates (Drea & Wallen 1999), the presence of dominant animals predicted performance better than did the test subject's prior experience at solving the same task. The intricacy of hyaena social interactions during cooperation in captivity, involving the balance between conflict and cohesion, leads to testable hypotheses on hunting behaviour in the field. Specifically, in addition to the relation between social status and hunting rates (Holekamp et al. 1997), we predict that spotted hyaena hunting parties are less likely to comprise animals of disparate rank.

The relative ease with which spotted hyaenas solved complex cooperation tasks may partially reflect a strong biological ‘preparedness’ (reviewed in Cummins & Cummins 1999) for cooperative hunting that is seemingly absent or less well developed in nonhuman primates. As obligate meat-eaters, spotted hyaenas routinely hunt to obtain food and often cannot kill larger, exceptionally combative prey without teamwork (Kruuk 1972). Although their hunting efficiency improves with experience (Holekamp et al. 1997), both sexes participate in hunts from an early age and ultimately pursue a wide variety of game, regardless of habitat (Kruuk

1972; Cooper 1990). By contrast, nonhuman primates that hunt (either cooperatively or en masse) target specific prey species that, by comparison to the hunters, are smaller and individually less powerful (Butynski 1982). Thus, prey defensiveness notwithstanding, primate hunters (other than humans) do not require strength in numbers to overcome their victim: the numbers participating in the hunt may influence capture success, but the kill is generally made by one animal, and even a smaller-sized female is physically capable of prey capture (Boesch & Boesch 1989). Moreover, the group-hunting skills of male chimpanzees require many years to perfect (Goodall 1986; Boesch & Boesch 1989; Uehara 1997) and are variable between populations, with some studies describing hunts as opportunistic affairs (Busse 1978; Stanford et al. 1994; Mitani & Watts 1999).

Despite these differences, social carnivores share with pre-agricultural humans many forms of behavioural plasticity, particularly community organization, occupation of central living and rearing sites, group defence, as well as cooperative hunting and food sharing (Schaller & Lowther 1969). Based on these similarities, some have considered the hunting behaviour of social carnivores to be a relevant model for reconstructing early hominid hunting behaviour (Schaller & Lowther 1969; Thompson 1975; King 1980). Our data on the cooperative problem-solving abilities of hyaenas support this proposition. We suggest, therefore, that a better understanding of human cooperative behaviour may require a more broadly comparative perspective than traditionally has been adopted.

A biological basis for hunting notwithstanding, hyaena cooperation is also malleable, shaped by learning experiences and social circumstance. Our data therefore also call for greater taxonomic representation in tests of the social intelligence hypothesis, which posits that social complexity drives the evolution of intelligence (Byrne & Whiten 1988). Given that spotted hyaenas are socially complex animals that share many of the hallmark behavioural and life history traits of primates, hyaenas and primates might be expected to display similar cognitive competencies (Drea & Frank 2003). Increasingly, behavioural data (Engh et al. 2005) and relative brain size estimates (Holekamp et al. 2007) in spotted hyaenas, coupled with the present findings, support this argument.

While similar social factors may contribute to shape cognitive skills in carnivores and primates, it is also likely that different evolutionary forces may drive cooperation in different species (Packer & Rutten 1988). Whereas the group hunting of spotted hyaenas probably reflects selection pressures associated with the need for team effort, food sharing and defence of hunted resources, the group hunting of certain primates may have arisen as a by-product of gregarious living, in combination with selection pressures operating on other features, such as manipulative abilities. The cognitive skills associated with predicting and managing social relationships, when coupled with manipulative skills associated with tool use and extractive foraging, may well serve to enhance vertebrate capture (Fedigan 1990; Rose 1997; Westergaard & Suomi 1997; Visalberghi et al. 2000). If performance differences between taxonomic groups merely mirror different ecological demands, however, it may indicate that certain laboratory tasks are unrealistically arbitrary when uniformly applied across species, as they may fail to adequately model natural situations that would necessitate cooperation. Thus, in nonpredatory primates, such as most cercopithecines, more consistent evidence of cooperation may be associated with social behaviour per se (e.g. alliance formation in aggressive encounters) than with food acquisition.

Descriptions of group hunting by spotted hyaenas portray clusters of animals engaged in coordinated pursuit, following a common route of travel and displaying similar patterns for the capture and consumption of prey (Kruuk 1972). We have not

located any accounts of hyaena hunting behaviour that describe animals moving in different directions to encircle prey, although such accounts have been provided for hunting by lions (Stander 1992). Consequently, although spotted hyaenas solved cooperative tasks requiring synchrony and coordination with relative ease, a strict biological preparedness framework suggests that tasks requiring collaboration might prove challenging for hyaenas. Lions, in turn, might be efficient at some forms of collaboration. Finally, from such a perspective, the cognitive abilities of chimpanzees would not be reflected in the ease with which they would synchronize and coordinate, but in the ultimate complexity of the cooperation that they could display, even if acquisition of such cooperative skills requires many years of practise. Without specific preparedness, such skills could be demonstrated only in a long-lived, highly encephalized species.

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Supplementary Material

Supplementary data associated with this article can be found in the online version, at doi: [doi:10.1016/j.anbehav.2009.06.030](https://doi.org/10.1016/j.anbehav.2009.06.030).

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