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THE EVOLUTION OF COOPERATIVE HUNTING

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Cooperative hunting, probably the most widely distributed form of cooperative behavior in animals, is of considerable theoretical interest. First, cooperative hunting may be an important evolutionary cause of sociality. However, sociality can evolve for this reason only when the mutualistic advantages of cooperation are sufficiently high that the per capita rate of food intake within a hunting group exceeds that of a solitary individual (Sibley 1983; Pulliam and Caraco 1984; Clark and Mangel 1986). Second, differing characteristics of the prey may cause predators to show differing propensities to hunt in a truly cooperative manner. If groups of predators specialize on prey that is large and risky to capture, an individual might benefit from refusing to cooperate during the hunt and then scavenging from its companions' kills. When it is impossible to scavenge from companions, however, there is not a similar temptation to cheat.

An extensive body of data is available on the hunting success of solitary and social hunters, and group hunting has been studied in detail in many species of birds, mammals, fish, insects, and spiders. Nonetheless, no rigorous attempt has been made to explain the distribution of cooperative hunting across species. Furthermore, no study has examined the dynamics of group hunting from a theoretical perspective or explored the implication that group hunting is often no more effective than solitary hunting.

We show here that the size and abundance of prey have important consequences for the expected behavior of individuals in hunting groups. We develop a series of simple game-theoretical models that illustrate the conditions under which cooperative hunting should occur and show how such cooperation can be detected. We test these predictions with data from 60 species and 28 different studies of group hunting.

GAME-THEORETICAL MODELS OF COOPERATIVE HUNTING

The propensity of predators to hunt cooperatively varies enormously across species. At one extreme, most mammalian carnivores are solitary, always hunting alone (Ewer 1973). At the other extreme, a number of species hunt in groups and

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are assumed always to hunt cooperatively, at least to the extent that all group members hunt simultaneously (e.g., canids, herons, some spiders, and some falcons). However, most predators are also scavengers, and many species commonly scavenge from conspecifics (e.g., Kruuk 1972; Packer 1986). It is important, therefore, to consider the possibility that some individuals may thrive by scrounging from kills made by conspecifics. However, because most predators hunt as well as scavenge, their behavior lies somewhere between that of a pure hunter and that of a pure scavenger.

In our analyses, we consider four strategies that span this spectrum of possibilities. We define "hunt" as the active pursuit of prey. In all strategies, individuals always feed from their own kills but can feed from their companions' kills only if the prey is sufficiently large.

A *cooperator* always hunts in the presence of a companion. Thus, if the partner is also a cooperator, they hunt as a pair. Otherwise, the cooperator hunts by itself.

A *cheater* will hunt if it is the first to spot the prey but stops if its partner joins in the hunt. A cheater does not hunt if it is the second to spot the prey. Thus, if the partner is another cheater, each hunts by itself half of the time, on the average. If the partner is a cooperator, then the cooperator always hunts by itself and the cheater never hunts. Note that if we redefined a cheater as an individual that hunted only when it was the closest to the prey or the hungriest of the pair, the payoffs would be the same.

A *scavenger* never hunts. A cooperator always hunts by itself when with a scavenger. A cheater hunts by itself half of the time it is with a scavenger, and neither hunts in the other half.

A *solitary* avoids conspecifics and thus always hunts alone. Consequently, if cooperators or cheaters are "paired" with a solitary, they too must remain solitary and hunt alone. A cheater hunts at every opportunity when alone, since it is always the "first" to spot the prey while alone. A scavenger also remains solitary but still does not hunt.

Note that we have defined cheater in such a way that it hunts only when necessary and scavenges whenever possible. A cheater is just as likely to invade a population of cooperators as is an animal with a strategy of pure scavenging, but a population of cheaters is very unlikely to be invaded by a scavenger (see below).

The number of prey captured per predator and the relative body sizes of predator and prey have important effects on the dynamics of group hunting. For certain types of prey, each group member can procure its own prey during a group hunt; but for other types of prey, the entire group may have to pursue the same individual prey. When the prey is sufficiently large, more than one group member can feed from it; but if it is very small, only the successful hunter can feed. We use "large" for prey that is in some way divided, either because it is so large that no one hunter can monopolize it (e.g., lions on antelope) or because it is shared between group members (e.g., falcons provisioning their mate, chimpanzees sharing meat). We regard active sharing of the prey as a separate behavioral decision outside the scope of this paper. A "small" prey is not divided.

By dichotomizing these two variables (multiple prey vs. single prey; large prey vs. small), we develop four simple game-theoretical models of cooperative hunting and outline the conditions under which cooperative hunting could be an evolutionarily stable strategy, or ESS (Maynard Smith 1982). We first restrict these models to cases in which individuals hunt either alone or in pairs and then demonstrate the effect of an increase in group size beyond two.

The payoffs from each of the four strategies depend on the following variables. We provide separate variables according to the number of prey per group because, when group members hunt the same individual prey, the success of one individual hunter depends directly on that of its companion. When group members each hunt their own prey, one individual's success is to a large extent independent of that of its companion.

For all prey:
V = value of captured prey;
E_1 = costs to single hunter from pursuing prey (whether or not the hunt was successful);
E_2 = costs to each member of a pair from pursuing prey;
C_1 = costs to single hunter from subduing captured prey; and
C_2 = costs to each member of a pair from subduing prey.

For single prey:
H_1 = probability that a single hunter will capture the prey;
H_2 = probability that a pair will capture the prey (i.e., success rate per group);
L_1 = prey-encounter rate of a solitary; and
L_2 = prey-encounter rate of a pair (i.e., encounter per group).

For multiple prey:
K_1 = probability that a single hunter will capture the prey;
K_2 = probability that a pair member will capture the prey (i.e., success rate per individual);
M_1 = prey-encounter rate of a solitary; and
M_2 = prey-encounter rate of a pair member (i.e., encounter per individual).

Expected Effects of Group Size on Each Variable

Cooperative hunting can evolve only when it increases individual feeding efficiency. We focus on the effects of cooperative hunting that would be expected to follow from simultaneous (rather than coordinated) action by a group of predators because we wish to specify the conditions under which cooperation would arise in the first place. Once rudimentary cooperation has evolved, then complex group hunting strategies or division of labor might follow. Although the following models do not assume any such highly evolved forms of cooperation, they can be used as an approximate baseline measure of group performance, allowing the presence of such behaviors to be detected.

Because of the contrasting dynamics for each type of prey, we discuss separately the effects of group size on groups that capture single prey and on groups that capture multiple prey.

Groups hunt the same individual prey.—In this situation, each hunter in the

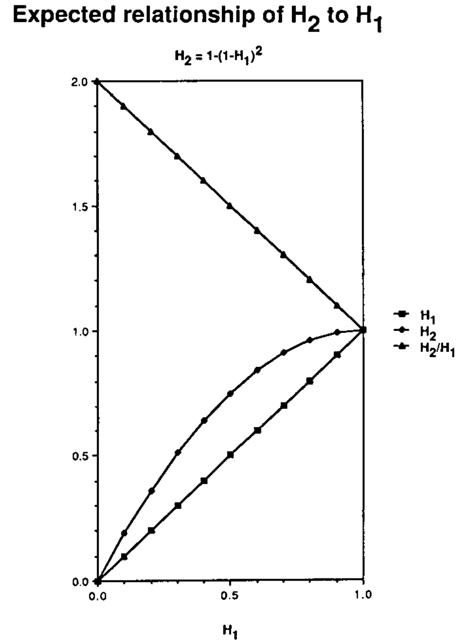

FIG. 1.—Expected hunting success of a pair (H_2) compared to that of a singleton (H_1), and the ratio of H_2 to H_1, if both individuals simultaneously pursue the same prey.

group is likely to contribute to the group's hunting success. Therefore, *group* success should improve as more individuals hunt simultaneously, but hunting success can never exceed 100%. Thus, hunting success increases asymptotically with increasing group size, but it can increase significantly only when individual hunting success (H_1) is small. When individual hunting success is already high, little improvement can be achieved by a group.

The exact relationship between group size and group hunting success depends on at least two sets of factors: the abilities of each predator in the group, and the characteristics of individual prey. In order to generate simple algebraic expressions of cooperative hunting, we assume that group hunting success depends primarily on predator-related factors. In the empirical part of this paper, we assess the validity of this assumption and also try to control for characteristics of the prey by examining hunting success separately for each prey species.

Following Treisman (1975), Rubenstein (1978), and Lendrem (1983), we assume that each group member's performance is independent of the performance of its companions. If a single hunter has a probability H_1 of capturing a particular prey, then it has a probability $1 - H_1$ of missing. Therefore, if two hunters pursue the same prey simultaneously, the probability that they will both miss is $(1 - H_1)^2$. Thus, $H_2 = 1 - (1 - H_1)^2$. Note that this relationship behaves in the precise manner outlined above: H_n approaches one as n becomes large; when H_1 is small, $H_2 \equiv 2H_1$, but at the limit of $H_1 = 1$, $H_2 = H_1$ (fig. 1).

This relationship has important implications for the evolution of cooperative hunting. When H_1 is small, the probability that more than one hunter will be successful simultaneously is virtually zero, and thus $H_n \equiv nH_1$. Therefore, companions do not reduce their individual efficiency by hunting the same prey as a group. However, when H_1 is close to one, then both would often be successful if they hunted separate prey, and they thus dramatically reduce their individual efficiency by hunting the same prey.

The effect of increasing group size on prey-encounter rate is more difficult to estimate. Clark and Mangel (1986) suggested that prey-encounter rate could increase as $L_n = nL_1$. However, this must represent an upper limit. Whenever travel time between prey items is significant or predators must await the arrival of successive prey, the prey-encounter rate can increase only asymptotically with group size to some maximum. Data from two laboratory studies showed a strong positive effect of increasing group size, but in both of these, the travel times were negligible (goldfish and minnows, Pitcher et al. 1982; great tits, Krebs et al. 1972). There are no relevant field data on the relationship between group size and prey-encounter rate per se, and thus a plausible estimate for naturalistic conditions cannot be provided. Conservatively, it seems likely that as more individuals search together, the prey-encounter rate of the group will increase and L_2 will thus be larger than L_1, but L_2 will be less than $2L_1$.

If a prey can inflict only a limited amount of damage while being captured, then on the average each hunter should receive $1/n$ of that damage. Thus, $C_2 = C_1/2$. Similarly, if a single poisonous predator can inject sufficient venom to immobilize its victim, then each member of a pair could inject half as much venom (as for cooperative spiders; Ward and Enders 1985). However, if the prey is capable of killing both of its captors or if the prey could be subdued only by the combined venom of two individuals, then $C_2 = C_1$.

The effects of grouping on the energetic costs of hunting should vary according to the precise hunting strategy employed by a particular taxon. If species stalk and surround their prey, then members of a pair may expend less effort than solitaries. If they chase prey long distances, then each individual may run as far as when hunting alone. However, most predators are presumably adapted to withstand repeated failures, and thus $E_1 \ll V$. Therefore, E_2 will be effectively equivalent to E_1.

Groups hunt multiple prey.—If individuals independently hunt their own prey from a school, flock, or herd, then $K_2 = K_1$. The behavior of one individual will not necessarily influence the individual hunting success of its companion.

Prey-encounter rate may have a complex relationship with group size. If, for example, flocks of predatory birds search together for schools of fish, the probability that a pair will locate a school may increase asymptotically with group size, in the same way as a group detecting a single prey. However, once the school has been located, each bird must detect its own individual prey and $M_2 = M_1$. Thus, overall $2M_1 > M_2 \geq M_1$.

Costs of prey capture are not affected by grouping if each individual captures its own prey; and energetic costs are the same as for single prey.

TABLE 1

PAIRWISE PAYOFF MATRIX FOR SINGLE LARGE PREY

RECIPIENT	RECIPIENT'S PAYOFF AGAINST OTHER MEMBER OF PAIR			
	Cooperator	Cheater	Scavenger	Solitary
Cooperator	$L_2\left[H_2\left(\frac{V}{2} - C_2\right) - E_2\right]$	$L_2\left[H_1\left(\frac{V}{2} - C_1\right) - E_1\right]$	$L_2\left[H_1\left(\frac{V}{2} - C_1\right) - E_1\right]$	$L_1[H_1(V - C_1) - E_1]$
Cheater	$L_2H_1\frac{V}{2}$	$\frac{1}{2}L_2\left[H_1\left(\frac{V}{2} - C_1\right) - E_1\right]$ $+ \frac{1}{2}L_2H_1\frac{V}{2}$	$\frac{1}{2}L_2\left[H_1\left(\frac{V}{2} - C_1\right) - E_1\right]$	$L_1[H_1(V - C_1) - E_1]$
Scavenger	$L_2H_1\frac{V}{2}$	$\frac{1}{2}L_2H_1\frac{V}{2}$	0	0
Solitary	$L_1[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$

MODELS OF COOPERATIVE HUNTING FOR SPECIFIC TYPES OF PREY

Model 1: Groups Capture a Single Prey Large Enough to Be Divided

Predators forage in pairs (payoff matrix given in table 1).—When two cooperators are together, they always hunt as a pair. On the average, each cooperator gains $V/2 - C_2$ from a successful hunt since each feeds from the kill and each incurs some cost from prey capture. Thus, the payoff per hunt is $H_2(V/2 - C_2) - E_2$. Prey is encountered at L_2.

When a cheater is with a cooperator, the cooperator always hunts but hunts by itself. The cheater scavenges from the cooperator's kills; thus, each gains $V/2$ per kill. However, the cheater does not incur any costs of hunting, whereas the cooperator incurs C_1 and E_1 (table 1). Prey is captured with a probability of H_1 and is encountered at L_2. (We assume that pairs always encounter prey at the same rate regardless of the hunting strategies followed by pair members.)

When a scavenger is with a cooperator, the payoffs are the same as when a cheater is with a cooperator.

Since a solitary refuses to remain in the vicinity of a cooperator, both hunt alone. Each has the success of a single hunter, and each incurs the costs of hunting alone, but the prey is not divided in half. Each individual encounters prey at L_1. Solitaries always have the same payoffs regardless of the opponent; cheaters gain the same against solitaries as do cooperators.

When two cheaters are together, one of the pair always hunts. Each cheater hunts by itself half of the time (and has its kills scavenged by its companion) and scavenges from its partner's kills in the other half. Thus, each receives half of the payoff of a cheater against a cooperator plus half of the payoff of a cooperator against a cheater.

When a scavenger is with a cheater, the cheater hunts by itself half of the time, and its kills are scavenged by its companion; neither hunts the other half of the time. Thus, the cheater gains half of the payoff of a cooperator against a cheater, and the scavenger gains half of the payoff of a cheater against a cooperator.

When two scavengers are together, or when a scavenger is "with" a solitary, the scavengers never hunt and thus receive nothing.

Cooperation can be the evolutionarily stable strategy (ESS) in this game only under the following circumstances. First, for cooperation to be an ESS against solitary hunting, the increased performance of a cooperative pair must be sufficient to overcome the twofold disadvantage of dividing the prey in half. Otherwise, individuals would do better to hunt alone. This improved performance could come from increased hunting success by pairs ($H_2 > H_1$), increased prey-encounter rates ($L_2 > L_1$), or decreased hunting costs ($C_2 < C_1$ and/or $E_2 < E_1$).

These inequalities will often be met by two individuals simply searching for and pursuing prey simultaneously: when H_1 is small, H_2 may be nearly twice as high as H_1 (fig. 1), and thus hunting together does not hold a twofold disadvantage. Similarly, L_2 may be considerably larger than L_1. If $C_2 = C_1/2$, this can further help to overcome the disadvantage of dividing the prey, but it is by itself insufficient to make up the twofold difference between cooperating pairs and solitaries.

Second, for the cooperative strategy to be an ESS against either the cheater or the scavenger, the hunting success of cooperative pairs must be sufficiently greater than that of singletons to overcome the costs of participating in a cooperative hunt [$H_2 - H_1 > 2(H_2C_2 + E_2)/V$]. Otherwise, there is an advantage to cheating and/or scavenging against a cooperator and thereby avoiding the costs of hunting. This condition is again more likely to be met when H_1 is small.

Note that because animals may often be constrained to live in groups for reasons other than foraging (see below), individuals are unable to play "solitary." Thus, the second condition can be sufficient to lead to the evolution of cooperative hunting.

Larger groups.—Table 2 shows the payoffs to each strategy against a cooperator if the predators forage in groups of n individuals. In a group of n cooperators, each individual would have a hunting success of H_n, suffering costs C_n and E_n and gaining V/n of the kill. If the nth individual played cheater or scavenger, then $n - 1$ would still cooperate, and the nth individual would receive $H_{n-1}(V/n)$ from every hunt. If the nth played solitary, then his payoffs would remain as before.

As n increases, V/n decreases and the groups become increasingly prone to invasion by a solitary, and hence become less stable. Further, with increasing n, $H_n = 1-(1 - H_1)^n$ approaches one, and thus $H_n - H_{n-1}$ approaches zero. Therefore, as n increases, cheating can invade more easily because the improvement in group hunting success resulting from the nth individual's cooperation becomes insufficient to overcome the advantage to the nth individual of avoiding the costs of hunting.

Note, however, that as group size becomes very large, the number of group members may exceed the number able to feed from a particular carcass. Thus, with very large groups, the situation begins to approximate single small prey (see model 3, below).

Model 2: Multiple Prey Large Enough to Be Divided

Foraging by pairs (table 3).—When both members of a pair cooperate, then each tries to capture its own prey, but if one fails and the other succeeds, then that prey is divided. When both are successful simultaneously, each must subdue its prey by itself (thus incurring C_1); when only one prey is captured, both eventually subdue the prey together (each thus incurs C_2). The energetic cost of hunting is the same when one or two prey are captured. Both will be successful K_2^2 of the time, in which case, each will receive $V - C_1$. Only one will be successful $2K_2(1 - K_2)$ of the time, and each then receives $V/2 - C_2$.

The remainder of the matrix is the same as in model 1 since only one large prey is captured at a time in every other combination.

The cooperative strategy is much more likely to be the ESS in this situation since pairs of cooperators often catch two prey, and foraging in pairs thus no longer incurs a twofold disadvantage compared to foraging solitarily. However, when individuals hunt multiple prey, K_2 should equal K_1. Although it is often expected that $C_2 = C_1/2$, each cooperator helps as often as he is helped and thus pays C_1 for every complete carcass. Thus, the initial evolution of cooperation would be most likely to result from an increased prey-encounter rate ($M_2 > M_1$). A

TABLE 2

PAYOFFS TO THE nTH STRATEGIST IN A GROUP OF COOPERATORS HUNTING A SINGLE LARGE PREY

Recipient	Payoff against Cooperator
Cooperator	$L_n\left[H_n\left(\frac{V}{n} - C_n\right) - E_n\right]$
Cheater	$L_nH_{n-1}\frac{V}{n}$
Scavenger	$L_nH_{n-1}\frac{V}{n}$
Solitary	$L_1[H_1(V - C_1) - E_1]$

synergistic effect of coordinated cooperation on hunting success could subsequently become important in maintaining cooperative hunting.

A cheater or a scavenger forgoes opportunities to catch its own prey and only gains half a carcass by scavenging from a cooperator. Therefore, a noncooperative strategy can invade a population of cooperators only when the costs of hunting are high.

Larger groups.—The temptation to cheat increases with increasing group size. If the nth individual cheats rather than cooperates, then on the average he receives $(n - 1)/n$ as much food as if he had cooperated. In table 3, $n = 2$; thus, the cheater receives only half as much as a cooperator, but as n becomes large, $(n - 1)/n$ approaches one. Thus, as group size increases, the cheater could receive almost as much from feeding from companions' kills as he would from his own without incurring any costs of hunting.

Assuming equal numbers of prey and predators, members of larger groups do not gain decreasingly smaller payoffs and hence do not fare poorly compared to a solitary predator. However, once the number of predators exceeds the number of prey, the situation approximates model 1.

Model 3: Single Prey Small Enough to Be Monopolized by Its Captor

Foraging by pairs (table 4).—Since each cooperator has an equal chance of catching the prey, each one feeds and incurs the costs of prey capture in only half of its hunts. The cost of prey capture is C_1 because the unsuccessful partner never touches the prey.

Cheaters and scavengers never feed in the presence of a cooperator since they never hunt with a cooperator and scavenging is now impossible. Thus, their payoffs are zero, whereas the cooperator always gains the prey when its hunts are successful.

The remainder of the payoffs are shown in table 4.

The cooperative strategy is less likely to be the ESS against solitary in this situation than in model 1. Foraging in pairs incurs a similar twofold cost because

TABLE 3

Pairwise Payoff Matrix for Multiple Large Prey

Recipient	Recipient's Payoff against Other Member of Pair			
	Cooperator	Cheater	Scavenger	Solitary
Cooperator	$M_2\left[K_2^2(V - C_1) + 2K_2(1 - K_2)\left(\frac{V}{2} - C_2\right) - E_2\right]$	$M_2\left[K_1\left(\frac{V}{2} - C_1\right) - E_1\right]$	$M_2\left[K_1\left(\frac{V}{2} - C_1\right) - E_1\right]$	$M_1[K_1(V - C_1) - E_1]$
Cheater	$M_2K_1\frac{V}{2}$	$\frac{1}{2}M_2\left[K_1\left(\frac{V}{2} - C_1\right) - E_1\right] + \frac{1}{2}M_2K_1\frac{V}{2}$	$\frac{1}{2}M_2\left[K_1\left(\frac{V}{2} - C_1\right) - E_1\right]$	$M_1[K_1(V - C_1) - E_1]$
Scavenger	$M_2K_1\frac{V}{2}$	$\frac{1}{2}M_2K_1\frac{V}{2}$	0	0
Solitary	$M_1[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$

partners are competing for the same prey, but in this case, the disadvantage must be overcome entirely by an increase in prey-encounter rate ($L_2 > L_1$) or hunting success ($H_2 > H_1$) or a decrease in the energetic costs of foraging ($E_2 < E_1$). Individuals incur the same costs of prey capture (C_1) whether alone or in pairs. Again, the cooperative strategy is more likely to be evolutionarily stable than the solitary strategy when H_1 is very low.

However, there is no temptation to cheat since cheaters and scavengers never feed in the presence of a cooperator. The cooperative strategy is always the ESS when individuals are constrained to live in groups. For this kind of prey, cooperation is the most effective form of intragroup competition.

Larger groups.—As group size increases, the payoff per hunter in a cooperative group is $L_n[H_n(V - C_1)]/n - E_n$, and the relative advantage of foraging solitarily becomes increasingly large. Hence, the foraging groups become increasingly unstable. However, since cheaters and scavengers are never able to feed in the presence of a cooperator, being a cooperator is the only alternative to being a solitary across all group sizes.

Model 4: Multiple Prey Small Enough to Be Monopolized by Respective Captors

Foraging by pairs (table 5).—Payoffs are the same as in model 3 except that the two cooperators are not competing for the same prey and each receives $V - C_1$ rather than $\frac{1}{2}(V - C_1)$.

The cooperative strategy can be the ESS with any increased net performance by pairs; otherwise, the solitary strategy is the ESS. As in model 2, the initial increase would be expected to come from an improvement in prey-encounter rate: it is expected that $K_1 = K_2$ and, as in model 3, each successful hunter always pays C_1.

As in model 3, there is no temptation to cheat, and cooperation is always the ESS when individuals are constrained to be together.

Larger groups.—The assumption that the number of prey always equals the number of predators keeps groups from becoming increasingly unstable as they grow larger. Once the number of predators exceeds the number of prey, the model starts to approximate model 3 and groups do become unstable. There is no advantage to cheating or scavenging in groups of any size.

GENERAL FEATURES OF THE MODELS

Table 6 summarizes the major predictions of the models. Cooperation is relatively unlikely to be the ESS against solitary hunting when foraging groups capture a single prey, whereas cooperation may often be the ESS when groups capture multiple prey. Being a cheater or a scavenger can be an ESS only when groups capture large prey, since only large prey can be scavenged. If animals are constrained to be in groups for some reason besides foraging, solitary hunting is not a possible strategy. Therefore, cooperation is the only possible ESS when individuals are constrained to hunt small prey in groups, but such groups could be composed of cheaters in species that typically capture large prey. Hunting groups

TABLE 4

Payoff Matrix for Single Small Prey

	Recipient's Payoff against Other Member of Pair			
Recipient	Cooperator	Cheater	Scavenger	Solitary
Cooperator	$L_2\{\frac{1}{2}[H_2(V - C_1)] - E_2\}$	$L_2[H_1(V - C_1) - E_1]$	$L_2[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$
Cheater	0	$\frac{1}{2}L_2[H_1(V - C_1) - E_1]$	$\frac{1}{2}L_2[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$
Scavenger	0	0	0	0
Solitary	$L_1[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$	$L_1[H_1(V - C_1) - E_1]$

TABLE 5

Payoff Matrix for Multiple Small Prey

	Recipient's Payoff against Other Member of Pair			
Recipient	Cooperator	Cheater	Scavenger	Solitary
Cooperator	$M_2[K_2(V - C_1) - E_2]$	$M_2[K_1(V - C_1) - E_1]$	$M_2[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$
Cheater	0	$\frac{1}{2}M_2[K_1(V - C_1) - E_1]$	$\frac{1}{2}M_2[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$
Scavenger	0	0	0	0
Solitary	$M_1[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$	$M_1[K_1(V - C_1) - E_1]$

TABLE 6

SUMMARY OF PREDICTIONS FROM THE MODELS

Prey Type	Probability that Cooperative Hunting Leads to Gregariousness	Possible ESS's if Constrained to Be in Groups	Effect of Increase in Group Size
Single large	low	cooperation, TFT, cheating, scavenging	increase cheating, scavenging, and solitary hunting
Multiple large	high	cooperation, TFT, cheating, scavenging	increase cheating and scavenging
Single small	lowest	cooperation	increase solitary hunting
Multiple small	highest	cooperation	none

NOTE.—TFT, tit-for-tat cooperation.

become less stable as group size increases (single prey) and cheating or scavenging becomes more likely (large prey).

In all pairwise models, a mixed ESS is impossible. In models 1 and 2, cooperation is never the only ESS; cheating is also an ESS. However, when cooperation is an ESS, the payoff to a cooperator against another cooperator is greater than the payoff to a cheater against another cheater, and cooperation thus has a greater zone of attraction than cheating. When solitary hunting is the ESS, it is the only ESS. Models 3 and 4 never have more than one ESS. Also, in all models, scavenging can never replace cheating when hunting as a member of a pair yields a positive payoff. When the payoff is negative, scavenging replaces cheating.

In larger groups, solitary hunting and cooperation can be a mixed ESS in models 1 and 3. Thus, under the appropriate conditions, some proportion of a finite population would be expected to hunt in groups, whereas the remainder would be solitary. A stable mixture of cooperators and cheaters can occur only with single large prey. In this model, the transition from complete cooperation to complete cheating with increasing group size is generally abrupt; but under some parameter values, the transition involves a mixed ESS over a narrow range of intermediate group sizes.

EMPIRICAL TESTS OF THE MODELS

Cooperative Hunting versus Solitary Hunting: The Distribution of Cooperative Hunting across Species

Because of the asymptotic nature of *group* hunting success with increasing group size for predators that hunt single prey, species showing low values of solo hunting success (H_1) should be more likely to hunt cooperatively. Cooperation could more often be the ESS when H_1 is small (when H_n/H_1 should be high). The increase in group hunting success can therefore overcome the n-fold disadvantage

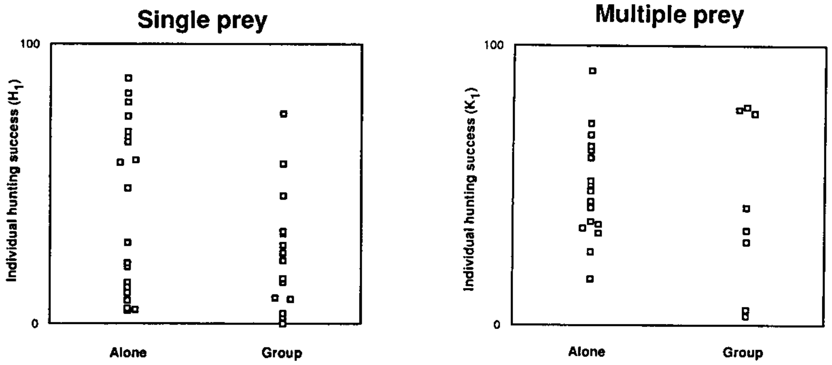

FIG. 2.—Hunting success of singletons across species. Sources, sample sizes, and conditions of study for each species are given in the Appendix. Solitary species are categorized as taking single prey or multiple prey according to the classification of group hunters that capture similar prey. Data from laboratory studies are included because they do not show a consistently higher or lower hunting success than do field studies. *Left*, Hunting success of singletons in species that capture a single prey per group (H_1). There is no statistically significant difference in H_1 between solitary species and group-hunting species ($U = 129$, $n_1 = 16$, $n_2 = 20$, $P > 0.20$). *Right*, Hunting success of singletons in species that capture multiple prey per group (K_1). There is no difference between solitary species and group-hunting species ($U = 76$, $n_1 = 17$, $n_2 = 8$, $P > 0.20$).

of dividing the prey among n hunters. Solitary hunting would more often be the ESS when H_1 is high (when H_n/H_1 is close to 1). In contrast, in species that capture multiple prey during group hunts, a similar effect is not expected because there is not an n-fold disadvantage to being in a group of n, and *individual* hunting success should be similar across group sizes regardless of the value of K_1. Thus, K_1 and group hunting should not be related.

We focus on hunting success here because data are available for a large number of species. The relationship of group size and prey-encounter rate may be an important factor, but very few studies have attempted to measure L_1 or M_1. It would also be difficult to make meaningful comparisons of prey-encounter rate between species that capture vastly different types of prey. *Observed* encounter rates may also be affected by a tendency for animals to distribute themselves in an ideal-free manner (Fretwell 1972).

The predicted relationship between group hunting and H_1 is not supported by the available data (fig. 2, *left*). For species that frequently hunt in groups, H_1 is only slightly lower than it is for solitary foragers. As expected, group foraging and K_1 are not related in species that capture multiple small prey (fig. 2, *right*), but this is not convincing given a similar trend for single prey.

These data suggest that cooperative hunting has not been a widespread cause of grouping in species that capture single prey, although the lack of a strong relationship between H_1 and group hunting may have three other causes.

First, we can only test the effect of one parameter, hunting success, whereas our models emphasize the importance of several other variables. Species may hunt in groups when prey is much more efficiently encountered by a group or when costs of prey capture are high. However, virtually no good data are available for these variables.

Second, definitions of hunting success vary from study to study. In some cases, attempted hunts involve conspicuous behaviors such as dives (seabirds), strikes (frogs, herons), and chases (carnivores). In others, they merely involve orientation to the prey (invertebrates, some carnivores). Such variation in definitions inevitably obscures trends across species.

Third, although it is always possible to tell whether species that hunt in groups typically capture single or multiple prey, it is difficult to be certain whether solitary species would take multiple prey if they were social. We have categorized solitary predators into single- or multiple-prey categories when their prey is clustered in the same way as prey of group hunters that take single or multiple prey. If we have mistakenly categorized some species, then the predicted trends will be obscured, since the data that we have called H_1 would be in fact K_1.

One way to deal with this last problem is to compare K_1 with H_1 in the group hunters. Often, K_1 should be higher than H_1 because a high value of K_1 does not constrain group foraging the same as does a high value of H_1. Although K_1 does show some tendency to be higher than H_1 (fig. 2), the tendency is not statistically significant (Mann-Whitney U-test, $U = 41$, $n_1 = 16$, $n_2 = 8$, $P > 0.05$).

Do species that capture a *single* prey per group hunt in groups even though they would do better to hunt solitarily? The data in the left graph of figure 2 provide only tentative evidence for this possibility. However, this suggestion is supported by many behavioral studies suggesting that such species often hunt in groups for reasons besides feeding. Most reviews of social carnivores conclude that sociality is not the result of advantages of cooperative hunting (Kruuk 1975; MacDonald 1983; Packer 1986). Similarly, cooperative hunting is often considered to have evolved secondarily in social spiders (Rypstra 1985) and raptors (Hector 1986; but see Bednarz 1988). More data are required to confirm the generality of these conclusions, but thus far it appears that cooperative hunting in most species is more likely to be a consequence of gregariousness than its cause.

In contrast, species that capture *multiple* prey may often gain an increase in feeding performance sufficient to make cooperative hunting an important cause of grouping. Our analyses emphasize that cooperative hunting rather than solitary hunting is more likely to be the ESS when groups hunt multiple small prey (table 6). It is worth noting that most species showing a strong positive relationship between group size and individual feeding rates take such prey (Krebs 1974; Götmark et al. 1986; see also below).

Cooperation versus Noncooperation: Behavior during Group Hunts

Group hunting may occur either because cooperative hunting yields higher payoffs than solitary foraging or because animals are constrained to live in groups for reasons other than foraging and thus must pursue prey simultaneously. Regardless of the reason that animals form foraging groups, once they are observed to hunt in groups, we can specify the conditions under which group members should hunt cooperatively or noncooperatively. We assume that the only option for individuals in this case is either cooperation or cheating. They cannot play "solitary" while in a group, nor can they play scavenger if they are ever observed hunting. If all group members played scavenger, no hunting would be observed.

Among species that capture a single large prey, our models predict that cooperation is more likely to be the ESS against cheating when solo hunting success (H_1) is low and group size is small (table 6), except when groups become so large that not all group members can feed. In games between cooperator and cheater, H_1 is the most important variable. The prey-encounter rate of a group is expected to be independent of each individual's tendency to cooperate during prey capture, and the increase in hunting success from cooperation is most likely to overcome the costs of hunting when H_1 is low.

In species that capture multiple large prey, cooperation is more likely to be the ESS whenever the *costs* of prey capture are small. The value of K_1 should not affect a species' tendency to be cooperative.

Species that capture small prey should always be cooperative in a group, irrespective of H_1, K_1, and group size (table 6).

A large number of studies provide data on group-size-specific hunting success. Most have interpreted changes in hunting success as evidence of either a synergistic effect of cooperation or interference between group hunters. However, none has considered the possibility that individuals may not actually be cooperating even though they may seem to be pursuing the same individual or group of prey. It may be difficult to determine whether each group member is actually trying to assist in capturing the prey, is merely remaining nearby so that it can gain access to the kill, or is deflecting the prey toward a companion so that the companion must catch it. Our game-theoretical analyses suggest that group hunting is not always expected to be cooperative, and we now show how cooperative groups can be distinguished from noncooperative groups.

Data on the hunting success of different-sized groups (H_n) can be used to infer whether individuals are cooperating (fig. 3). If all group members show simultaneous cooperation in hunting a single prey (i.e., cooperation is the ESS), the hunting success of a group should increase approximately as $H_n = 1 - (1-H_1)^n$. However, if all group members are cheaters, then only one individual per group will make an effort to capture the prey, and hunting success across all group sizes will equal that of a single hunter ($H_n = H_1$).

If groups capture multiple prey, individual hunting success should remain the same across group sizes ($K_n = K_1$) whether all group members play cooperator or cheater. If all play cheater, however, then the proportion hunting would be $1/n$: the group would capture only a single prey. Therefore, by definition, species that typically capture multiple prey are playing cooperator rather than cheater.

Our analysis makes predictions about the particular distributions that group-size-specific hunting success should follow. In certain cases, it should increase approximately as $H_n = 1-(1-H_1)^n$, and in others it should remain constant as $H_n = H_1$ or $K_n = K_1$. In practice, there may well be synergistic effects of coordinated cooperation or reduced hunting efficiency from interference. However, effects from factors such as interference should be distributed randomly

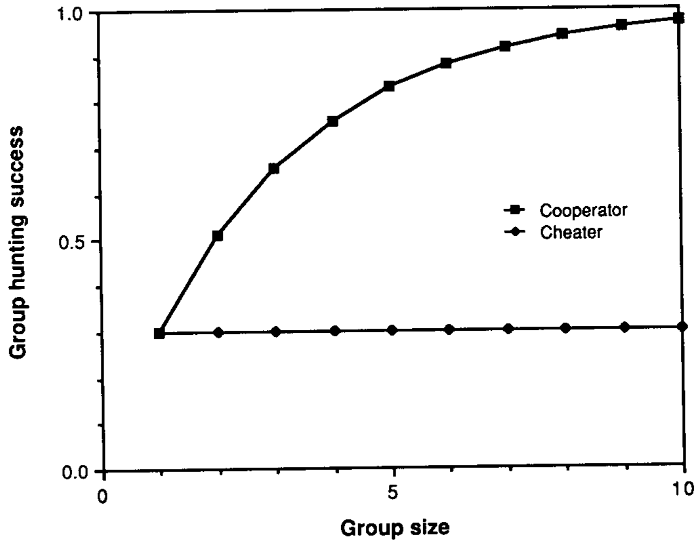

FIG. 3.—Expected group-size-specific hunting success (H_n) of groups composed entirely of cooperators ($H_n = 1 - (1 - H_1)^n$) and groups composed entirely of cheaters ($H_n = H_1$) when $H_1 = 0.30$.

across different prey types. If cheating is in fact widespread, it should be restricted to species that capture large prey.

We first present data on observed hunting success for groups that hunt single prey. The predictions for single small prey are straightforward, and the contrast with single large prey illustrates each of the above predictions. We then discuss data from species that typically capture multiple prey. We believe that these are all of the data available on group-size-specific hunting success where group members hunt simultaneously. We have excluded studies in which only one or two group hunts were observed (Mills 1978) and have combined data from adjacent group sizes when only one or two hunts were observed for a particular group size.

Single small prey.—Figure 4 shows the observed group-size-specific hunting success for three different species. Each graph also shows the predicted hunting success if all individuals cooperate and the predicted success if all cheat. In all cases, cooperation is the predicted ESS (table 6), and in all cases, group hunting success more closely matches the predicted curve for cooperation than that for cheating. Hunting success consistently tends to increase with group size, at least to the extent predicted by $H_n = 1-(1-H_1)^n$. Veliid bugs also show some evidence of a synergistic effect from cooperation, but such synergism would presumably occur only if all group members were at least trying to capture the prey simultaneously.

Single large prey.—When a group captures a single large prey, cheating may often be the ESS. At some group sizes, the ESS may be cheating, but at other sizes, the ESS may be cooperation. Thus, group hunting success may often switch

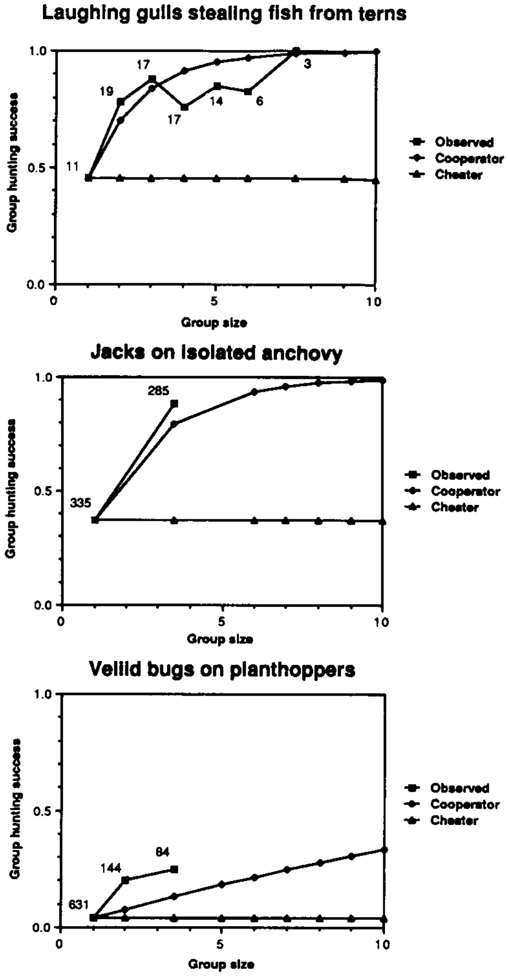

FIG. 4.—Hunting success of groups that capture a single small prey. The expected group-size-specific hunting success for each species is generated by the observed value of H_1 for that species. Data on laughing gulls are from Hatch 1970; on veliid bugs, Nakasuji and Dyck 1984. Data on jacks on isolated anchovy are from Major 1978; H_n has been recalculated from his data since he reported his results in terms of K_n.

between that for cooperation ($H_n = 1-(1-H_1)^n$) and that for cheating ($H_n = H_1$). We first describe data for each individual species separately and then summarize all the data.

Extensive data are available on the hunting success of spotted hyenas in two different areas (fig. 5). In the Kalahari Desert, the H_1 of hyenas hunting gemsbok calves is much higher than the H_1 while hunting other ungulates. In this case, model 1 predicts that cheating is the ESS when hyenas hunt gemsbok calves, whereas cooperation should be the ESS when they hunt other ungulates (at least in small group sizes). Group hunting success should not increase with group size

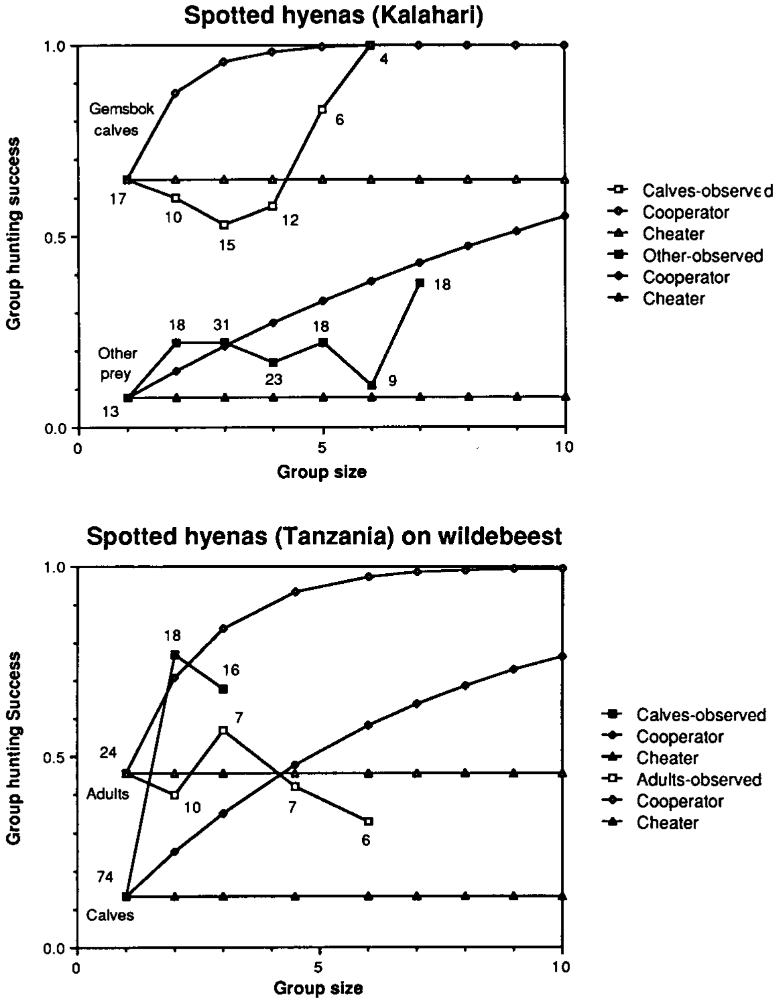

FIG. 5.—Group hunting success (H_n) of hyenas on single large prey (Kalahari, Mills 1985; Tanzania, Kruuk 1972).

for hyenas hunting gemsbok calves until group size is so large that only a few hunters can feed. Hence, the situation approximates that for a single small prey. Hyenas are such rapid feeders that latecomers in large groups are often unable to feed (Kruuk 1972) and cannot benefit from cheating. In contrast, hunting success on the other ungulates should initially increase as $H_n = 1 - (1 - H_1)^n$ but should tend toward $H_n = H_1$ at larger group sizes until group size is finally so large that latecomers would again be unable to feed.

In northern Tanzania, hyenas are far better at capturing adult wildebeest than wildebeest calves; thus, in contrast to hyenas in the Kalahari, these animals should cooperate to catch calves but play cheater while hunting adult wildebeest.

All the predicted trends are apparent in the data (fig. 5). An important feature in this comparison is that the only difference between the two areas is the hyenas'

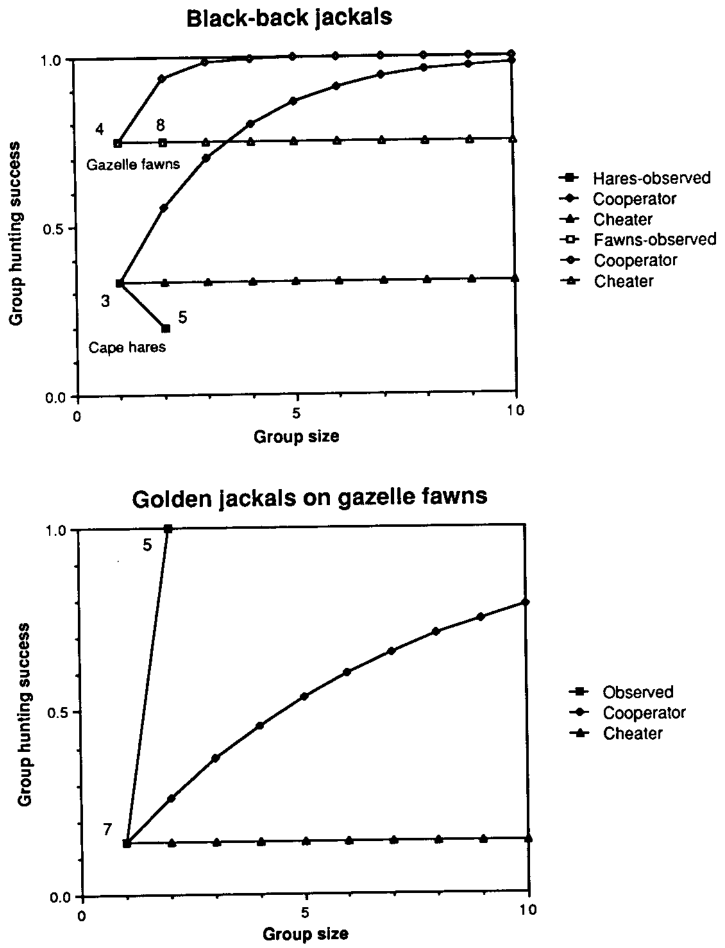

FIG. 6.—Group hunting success of black-back jackals and golden jackals (Lamprecht 1977).

relative ability to capture calves compared to adults. Cooperation at small group size is associated with a low value of H_1. In the case of hyenas hunting wildebeest calves in Tanzania, Kruuk's descriptions show clearly that the pair really are cooperating: a solitary hyena cannot separate a calf from its mother because of the mother's defensive behavior. When two hyenas hunt together, one engages the mother while the other catches the calf.

Another matched pair of studies on jackals (fig. 6) is again consistent with our predictions. Two species of jackal in the Serengeti vary in their ability to capture gazelle fawns. Golden jackals have a lower value of H_1 and show a striking tendency to cooperate when hunting in pairs, whereas black-back jackals apparently play cheater. (Note that black-back jackals also show little evidence of

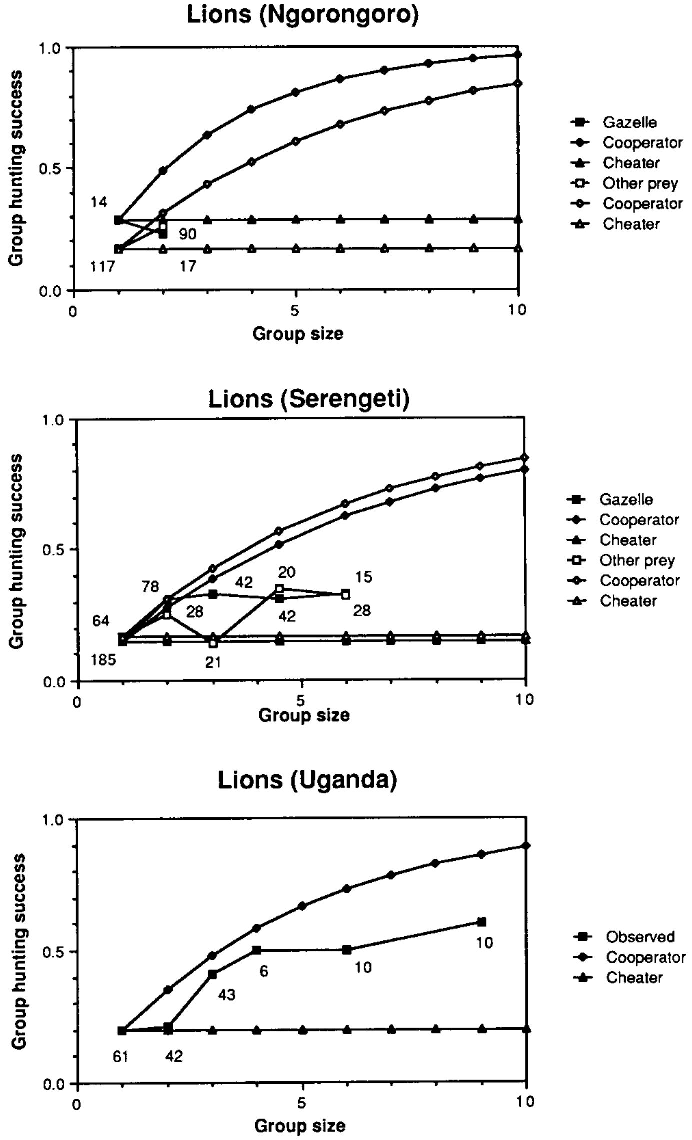

FIG. 7.—Group hunting success of lions (Ngorongoro Crater, Elliott et al. 1977; Serengeti, Schaller 1972; Uganda, Van Orsdol 1981).

cooperating while hunting hares; their H_1 for hares is also rather high compared to that for most cooperative hunters; see below.)

Lions have been studied in several areas (fig. 7). In Ngorongoro Crater, lions acting alone are better at catching gazelles than other ungulates. They also show a greater tendency to cooperate in capturing the prey for which they have the lower H_1. In the Serengeti, they are as good at capturing gazelles as any other ungulates. Serengeti lions should thus show more-similar tendencies to cooperate when hunting either type of prey. The data support this prediction. In a study in Uganda, hunting success on different types of prey was not separated.

Across all five distributions from the three sites, the increase in hunting success by pairs of lions (i.e., their tendency to cooperate) is inversely related to H_1 (Spearman test, $r_s = -1.0$, $n = 5$). Note, however, that in the Serengeti and in Uganda, H_n is mostly at an intermediate level between the two predicted distributions. In the Ugandan study, this probably results from combining data on prey that the lions hunt cooperatively with data on prey that they do not hunt cooperatively. Successful hunts by solitary lions were mostly on antelope calves, which lions usually hunted alone (Van Orsdol, pers. comm.). In the Serengeti, however, it appears that in large groups, two individuals hunt cooperatively and the remainder of the group are cheaters. This result is not predicted by the above models and is considered more fully below.

Similar data on peregrine falcons are also consistent with the predicted trends (fig. 8). Although pairs of peregrines do not always feed from the same carcass, they commonly provision each other, and a cheater thus gains from its partner's kills. Peregrines in Quebec have moderate individual success hunting jays, swallows, and blackbirds; and peregrines in Cornwall have high success in catching pigeons and razorbills. Those in Tunisia, however, have much lower success hunting passerines, doves, and swallows. Figure 8 shows that only the Tunisian peregrines appear to cooperate while hunting in pairs.

Figure 9 shows all of the remaining available data for hunting success on single large prey. Some species, such as the wild dog and cheetah, show a tendency to cooperate in small groups but to cheat at larger group sizes (in these species, unlike in hyenas, carcasses are divided equitably even at large group sizes). Chimpanzees resemble the Serengeti lions in showing an intermediate level of hunting success. Only in *Stegodyphus* spiders do pairs show clear evidence of cooperation in spite of a high value of H_1. However, this is also the only laboratory study of a species taking a single large prey. Stegodyphids may have a low H_1 in the wild and are inappropriately showing cooperation in artificial circumstances.

For each of the distributions in figures 5–9, we have logistically transformed the data and calculated the regression slope of hunting success against group size. If cooperation is mostly restricted to cases in which solo hunting success is low, the slopes of the regressions and H_1 should have a negative relationship. For pairs and trios, the correlation between the slope of success and H_1 is highly negative (pairs, $r_s = -0.68$, $n = 22$, $P < 0.01$; 1–3 individuals, $r_s = -0.72$, $n = 10$, $P < 0.05$). However, larger group sizes show no relationship (1–4, $r_s = -0.33$, $n = 8$; 1–6, $r_s = 0.30$, $n = 8$). Thus, for small group sizes, more cooperation is seen when solo hunting success is low, but the relationship disappears at larger group sizes.

We predicted that cheating should become more likely as group size increases (table 6), but in practice cooperation may be more likely if the captured prey is not evenly divided, and a single large prey thus begins to approximate a single small prey. It is impossible to say at which group size these switches should occur without detailed data on the behavior of each species. It is encouraging that hyenas, which are known for the rapidity of their feeding, switch as predicted to

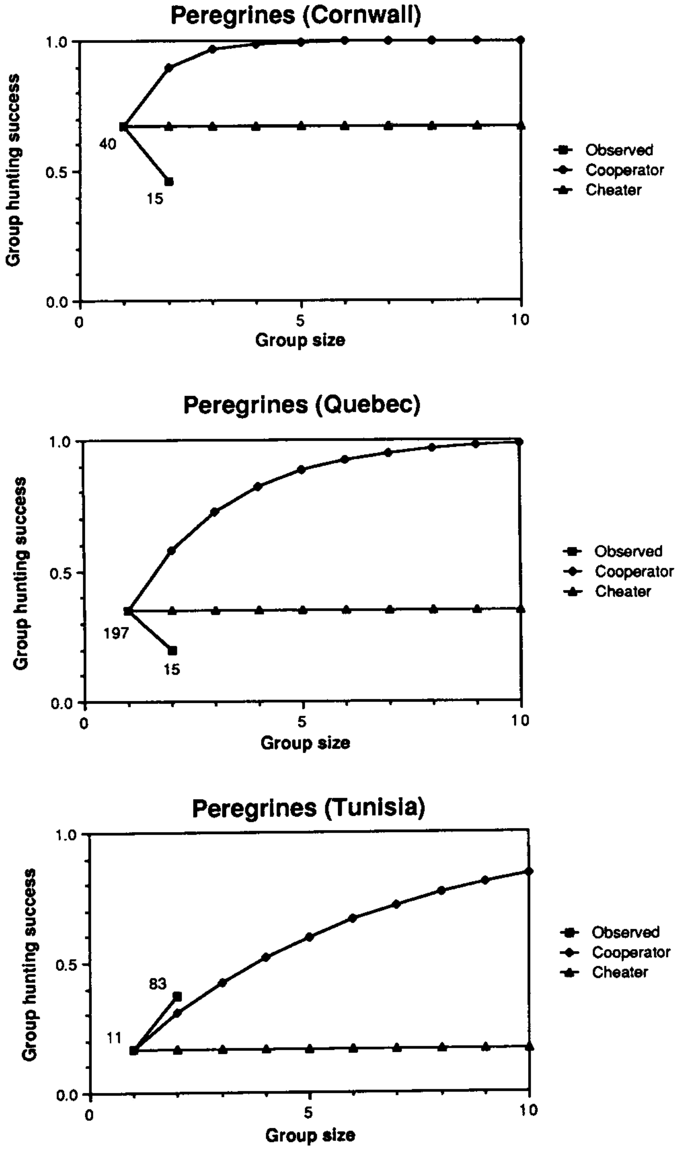

FIG. 8.—Group hunting success of peregrine falcons (Cornwall, Treleaven 1980; Quebec, Bird and Aubrey 1982; Tunisia, Thiollay 1982).

cooperative behavior at a large group size, and the more relaxed feeders (cheetah and wild dogs) switch in the opposite direction. Data are needed from large feeding groups in many more species before the generality of these latter predictions can be confirmed.

Multiple small prey.—As outlined above, any species that typically captures multiple prey is in fact playing cooperator since the cheater strategy would result in only one hunter per group and hence a single prey. Many species do, in fact,

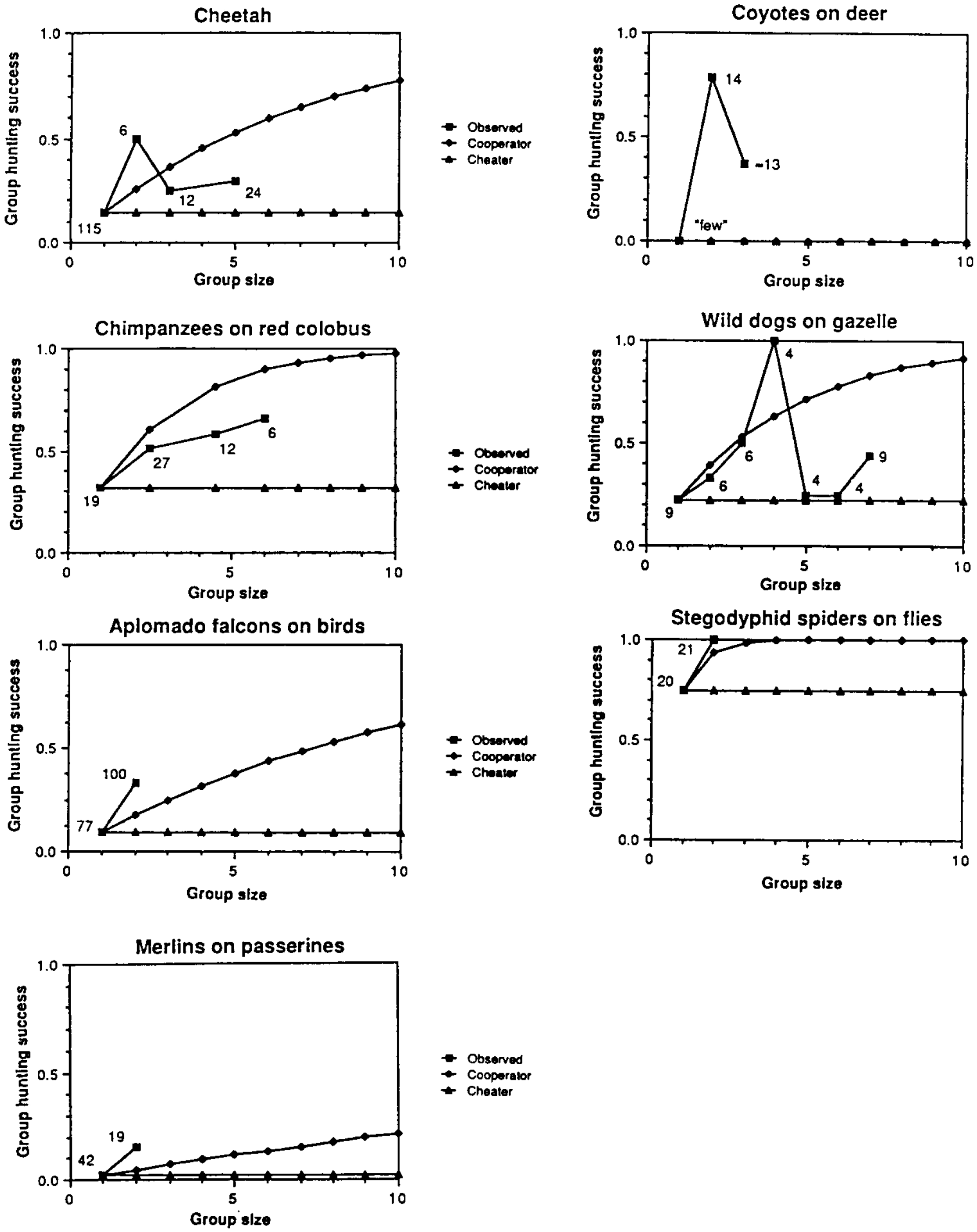

FIG. 9.—Group hunting success: Aplomado falcons, Hector 1986; merlins, Bengtson 1975; cheetah, Eaton 1970; chimpanzees, Busse 1978; coyotes (percentage of pursuits), Hilton 1978; wild dogs, FitzGibbon & Fanshawe, MS; and *Stegodyphus* spiders, Ward and Enders 1985).

take multiple small prey. Group-size-specific hunting success for these species is given in figure 10. It is expected that $K_n = K_1$ regardless of whether group members play cooperator or cheater. An increase in hunting success with group size therefore indicates synergism from cooperation, whereas a decrease indicates some form of interference. We present these data to show how often group hunting involves either factor (see below). Note that although synergism may provide strong advantages to grouping (and almost all these species do show some synergism), species that live in groups and capture small prey should forage cooperatively regardless of any such effect.

Multiple large prey.—We know of no species that typically captures multiple prey large enough to feed more than one group member (except possibly ants or humans). Although several species that typically capture single large prey occasionally catch multiple prey (e.g., lions; Schaller 1972), it is not known how often multiple prey are captured simultaneously (as our models specify) or in rapid succession by the group as a whole (in which case they are always catching a single prey). Because the likelihood of cheating increases with increasing group size (table 6), we predict that multiple kills should be disproportionately common in small hunting groups. Schaller (1972) stated that most multiple kills were made by groups of four or more lions, but we cannot use his data to estimate the relative frequency of multiple kills across hunting-group sizes.

Overall, group-size-specific hunting success is consistent with the predictions of our simple models. Animals that hunt small prey always show evidence of cooperation, whereas those that hunt large prey often appear to cheat. Species that capture single large prey cooperate in small groups when H_1 is low but often appear to cheat when H_1 is high. Several species that take a single large prey switch from one strategy to another as group size increases. Two species that conform to the conditions of a single large prey at all group sizes cooperate in small groups but not in large ones. One species that forms groups sufficiently large that the prey effectively becomes a single small prey switches from cheating to cooperation at large group size. Many species show synergistic hunting success and hence evidence of coordinated cooperation. However, synergism mostly occurs when group members are predicted to show rudimentary cooperation of the type outlined in our models.

Are there alternative explanations for these findings? Most authors have interpreted a failure of hunting success to improve with increasing group size as evidence of interference. However, for no reason should interference be virtually restricted to situations in which our models predict cheating (e.g., divisible prey and either a high value of H_1 or a large group size). If anything, interference should be most frequent when individual hunters are inept since they would be most likely to get in each other's way. Instead, the data show the opposite trend: inept individual hunters have a higher combined success. Interference should also be apparent when predators take small prey, but such species almost always match or exceed the success rates predicted from cooperation (figs. 4, 10).

Similarly, if hunting success depends more on features relating to the prey than to the predator (e.g., a proportion of prey are impossible to catch, whereas the remainder may always be caught), then hunting success would not be expected to

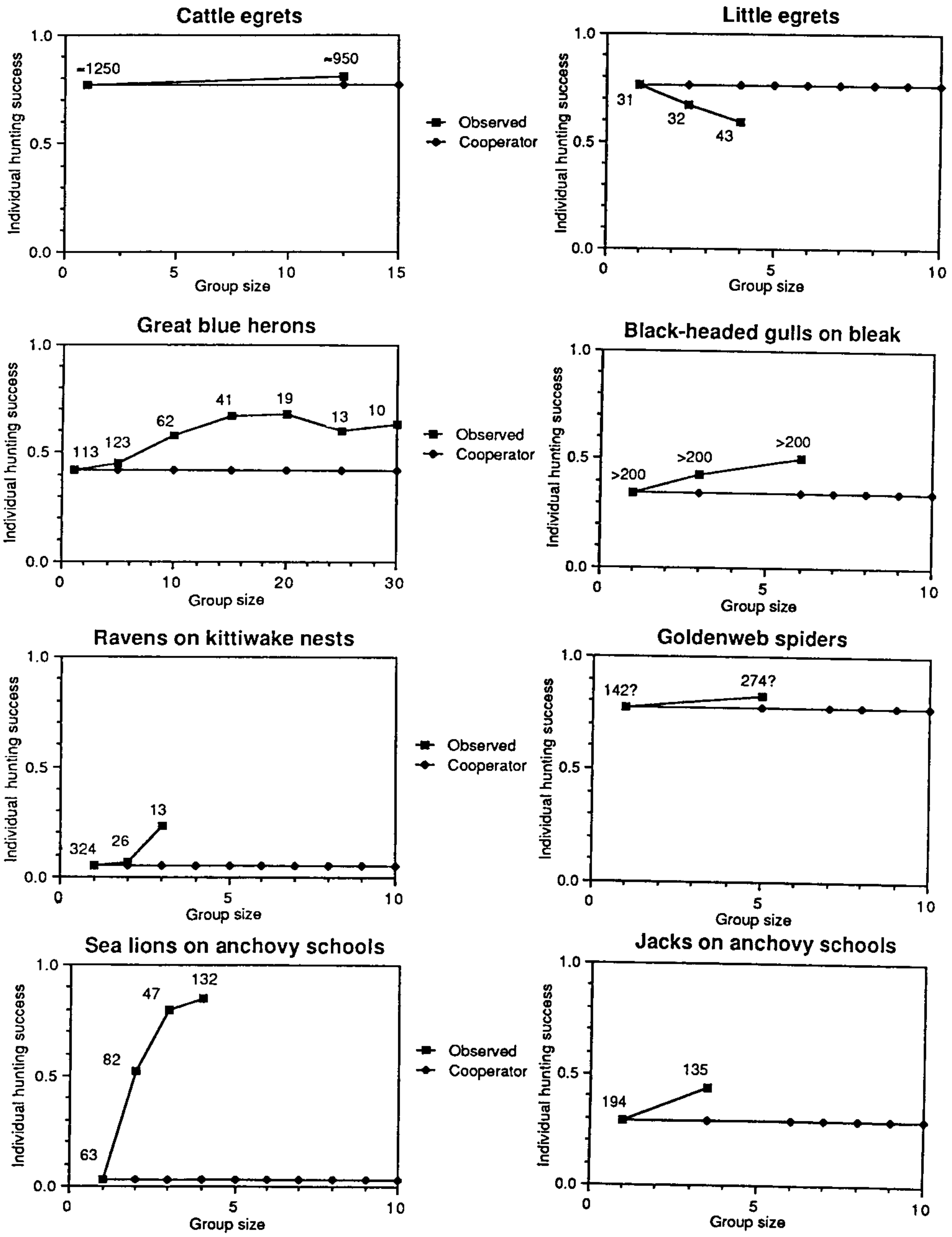

FIG. 10.—Individual hunting success (K_n) of species that capture multiple small prey: cattle egrets, Scott 1984; little egrets, Erwin et al. 1985; great blue herons, Krebs 1974; black-headed gulls, Götmark et al. 1986; golden-web spiders, Rypstra 1985; ravens, Montevecchi 1979; jacks, Major 1978; California sea lions, R. Pierotti, pers. comm.

improve with increasing predator-group size. However, this should be equally likely for all types of prey, at all group sizes, and regardless of individual hunting success.

We therefore consider neither of these hypotheses strong alternatives to the predictions of our models. We suggest that interference may be less widespread than previously supposed and may in fact be less common than cheating. We also feel justified in assuming that group hunting success primarily results from factors associated with the combined ability of the predatory group. We hope that future studies will attempt to provide direct evidence of cheating by distinguishing between these alternatives. The evidence that we provide here is purely circumstantial, and it is clearly important to use direct observation to establish the existence of cheating.

THE INFLUENCE OF KINSHIP ON COOPERATIVE HUNTING OF SINGLE LARGE PREY

When hunting partners are close kin, an individual's strategy affects its inclusive fitness through the consequence of that strategy on its hunting partner (Grafen 1979; Hines and Maynard Smith 1979). Kinship has two major effects on the behavior of predators that capture a single large prey. First, cooperation can be the ESS at a level of H_1 higher than that permitted if the hunting partners are unrelated. Second, cooperation will be the ESS at a group size larger than that if the partners are unrelated. Therefore, in a given species, close kin should hunt a wider variety of prey cooperatively than do non-kin, and cooperative groups should be larger when they are composed entirely of kin. None of the data in figures 5–9 can be used to test either hypothesis. However, it is noteworthy that recent studies have suggested that social spiders are typically highly endogamous, and hence group members are extremely closely related (Lubin and Robinson 1982; Roeloff and Riechert 1988). Field studies of *Stegodyphus mimosarum* suggest that this unusually cooperative species (see fig. 9) has a similar social organization (Wickler 1973). It is also relevant that cooperative coalitions of four or more male lions are always composed only of kin, whereas smaller coalitions are commonly composed of nonrelatives (Packer and Pusey 1982; Packer 1986; Pusey and Packer 1987).

Cooperating pairs of close kin within larger groups might also account for the intermediate levels of cooperation in the Serengeti lions (fig. 7) and chimpanzees (fig. 9). Further observations on these species could show whether kin within the same group cooperate and non-kin act as cheaters.

WHY NOT HUNT SINGLE LARGE PREY TIT-FOR-TAT?

The above analyses focus on the outcome of individual hunts, but group members may forage together repeatedly. The payoff matrix for single large prey (table 1) often follows the conditions of the iterated prisoner's dilemma: when two cooperators meet they receive a reward (R) from cooperation, but there is often a temptation to cheat (T) and thereby to avoid the costs of prey capture, which consequently fall entirely on the sole cooperator (S). If two cheaters meet, each gains a punishment (P) that is less than if both cooperated. By our definition of cheater, each cheater receives T and S on alternate encounters: $P = (T + S)/2$. Whenever cheating is the ESS in a single encounter, $T > R > P > S$ and $R > (T + S)/2$.

These are precisely the conditions under which a tit-for-tat form of cooperation (TFT) would be expected to occur (Axelrod and Hamilton 1981). An individual playing TFT would cooperate in the initial hunt and then play the partner's preceding strategy in the following hunt. By Axelrod and Hamilton's analysis, TFT is an unbeatable strategy when the probability (w) is high that the same two individuals will hunt together again. More precisely, TFT is expected when $w > (T - R)/(T - P)$ and $w > (T - R)/(R - S)$. With most reasonable values of V, C, H, and E and following the expected relationships between pairs of variables (e.g., $H_n = 1 - (1 - H_1)^n$) as specified above, TFT would be the ESS if the same pair hunted together at least 10–50 times.

Since most predators hunt daily, w must be sufficiently large that cooperation would always be expected in social hunters that take single large prey. They should show "pure" cooperation when H_1 is sufficiently low and TFT cooperation when it is high. The data in figures 5–9 suggest, however, that several species may cheat instead of playing TFT. Why don't these predators cooperate tit-for-tat?

TFT is most likely to evolve when interactions are between pairs, but it becomes increasingly unlikely as group size increases (Boyd and Richerson, in press). However, several species that apparently play cheater live in monogamous pairs (jackals, fig. 6; peregrine falcons, fig. 8).

Do predators lack the cognitive skills to distinguish between cheaters and cooperators? Two sorts of information must be monitored simultaneously by each hunter: the behavior of each partner and the type of prey. An individual must be able to determine which group members are cheaters and which are cooperators. Moreover, the appropriate hunting strategy may vary according to the species of prey (e.g., fig. 5; hyenas should play cooperator when hunting wildebeest calves and cheater when hunting gemsbok calves). If the type of prey varies from hunt to hunt, then it may be very difficult to remember which partners played which strategy on a particular prey species during the preceding hunt. However, limitations of memory would seem less important for monogamous pairs since they only hunt with each other and only need to recall their partner's behavior during the preceding hunt. Amusingly, the species in figures 5–9 that seems most likely to be cooperating TFT is the *Stegodyphus* spider, since it is the only cooperative hunter of single large prey with a high value of H_1 (fig. 9).

Are predators simply unable to distinguish between a cheater and an unlucky cooperator? Individual hunting success is typically low (see fig. 2), and by chance an individual may miss several times in a row. If cheaters attempt to mimic cooperation but still refuse to take a risk in subduing the prey, then it may be difficult to differentiate cheaters from cooperators. Indeed, we suggest that most observers have been unable to make the distinction in the studies presented in figures 5–9. This idea is obviously speculative, but if nothing else, we hope that this paper inspires field-workers to watch hunting groups with a more cynical eye.

Alternative explanations must be considered because monogamous pairs ap-

TABLE 7

Double-Payoff Matrix for Single Large Prey When the Dominant Member of a Pair Gains a Disproportionate Share of the Kill

	Dominant	
Subordinate	Cooperate	Cheat
Cooperate	$H_2(pV - C_2) - E_2$ $H_2[(1 - p)V - C_2] - E_2$	H_1pV $H_1[(1 - p)V - C_1] - E_1$
Cheat	$H_1(pV - C_1) - E_1$ $H_1(1 - p)V$	$\frac{1}{2}[H_1(pV - C_1) - E_1] + \frac{1}{2}H_1 pV$ $\frac{1}{2}H_1(1 - p)V + \frac{1}{2}\{H_1[(1 - p)V - C_1] - E_1\}$

Note.—The dominant receives the payoffs in the upper right-hand corner of each cell. For simplicity we have left out L_2 since each combination of strategies has the same prey-encounter rate.

parently do not engage in TFT. Such pairs not only would be expected to play TFT, but should also be less inclined to cheat since the reproductive success of one depends on the success of its mate. It is therefore surprising that jackals and peregrines tend to cheat just as much as lions and hyenas. If these two monogamous species are significantly promiscuous, then males may have alternative breeding opportunities (Maynard Smith 1977) and may maximize their reproductive success by letting their mates catch their supper. Alternatively, if these species are long-lived and pair again, an individual could maximize its own survival by avoiding the costs of prey capture. The first of these possibilities predicts a male bias in cheating; the second predicts no sex bias.

Although it might seem that mating partners should be less likely than any other two individuals to cheat during group hunts, sex differences can have important consequences on the evolution of cooperation between spouses. First, individuals of one sex may have greater access to the prey once it has been captured. In many species, sexual dimorphism allows one sex to dominate the other during feeding. Table 7 shows the payoff matrix for partners with unequal feeding success, where p is the proportion of each carcass eaten by the dominant member of the pair (in the original model, each hunter was assumed to receive half of each kill; $p = \frac{1}{2}$). For a single-encounter game in which one member of the pair gains more than half of the food, if cooperation is the ESS, H_1 must be even lower than when the two partners gain equal access. Since the subordinate receives less of the reward than the dominant, the subordinate regains the costs of participating in a cooperative hunt only if H_1 is concomitantly lower. Thus, the subordinate is the first to cheat, and in response the dominant must also cheat. As in the original analysis, however, TFT could be an ESS in an iterated game over all values of H_1 when simple cooperation is not the ESS.

Second, individuals of one sex may be more proficient hunters than those of the

TABLE 8

Double-Payoff Matrix for Single Large Prey When One Hunter Is Better than Its Partner

	Better	
Worse	Cooperate	Cheat
Cooperate	$H_2\left(\frac{V}{2} - C_2\right) - E_2$ $H_2\left(\frac{V}{2} - C_2\right) - E_2$	$H_w\frac{V}{2}$ $H_w\left(\frac{V}{2} - C_1\right) - E_1$
Cheat	$H_b\left(\frac{V}{2} - C_1\right) - E_1$ $H_b\frac{V}{2}$	$\frac{1}{2}\left[H_b\left(\frac{V}{2} - C_1\right) - E_1\right] + \frac{1}{2}H_w\frac{V}{2}$ $\frac{1}{2}H_b\frac{V}{2} + \frac{1}{2}\left[H_w\left(\frac{V}{2} - C_1\right) - E_1\right]$

Note.—Format as in table 7.

opposite sex. In lions and jumping spiders, the hunting success of females is higher than that of males (Schaller 1972; Givens 1978), whereas in peregrines, males may be better hunters than females (Bird and Aubry 1982). The payoff matrix for partners with unequal hunting success is given in table 8, which introduces two new variables: H_b, which is the solo hunting success of the better hunter; and H_w, the solo success of the worse hunter. With unequal hunting success, we assume that $H_2 = 1 - (1 - H_b)(1 - H_w)$.

The consequences of unequal hunting success are somewhat surprising. The value of H_b at which pure cooperation will be an ESS in a single-encounter game decreases as the relative abilities of the two become more disparate (as H_b/H_w increases). In fact, if the relative abilities of the two are sufficiently extreme, then cooperation never occurs. That is, if the hunting success of the worse hunter is sufficiently low, then his cooperation will make virtually no difference to the better hunter's chances of success, and the consequent increase in the pair's hunting success would not be sufficient to overcome his own costs of participating in the hunt. In contrast, the better hunter always does best to cooperate (even if his partner cheats) because he gains more from hunting than from relying on his incompetent partner. In these cases, the ESS is cooperation by the better hunter and cheating by the worse hunter. Consequently, the better hunter will do all the hunting alone.

These payoffs no longer describe a symmetrical prisoner's dilemma: although it is still true that $T > R > P > S$ for the worse hunter, $R > S > P > T$ for the better hunter. In an iterated game, the most likely outcome is for the better hunter always to cooperate and the worse hunter always to cheat. Because $S > P$ for the better hunter, he gains a higher payoff from cooperating with a cheater than from playing TFT. However, because $R > P$ for both hunters, TFT can still be an unbeatable strategy, but only if most good and bad hunters initially play TFT. A high initial proportion of individuals playing TFT is required in the symmetrical prisoner's dilemma (Axelrod and Hamilton 1981), but this asymmetry greatly increases the required initial frequency of TFT. Thus, TFT is far less likely to evolve in a species in which the partners initially showed differential hunting ability.

If both hunting success and feeding access vary, the two variables can reinforce each other. If the better hunter also has greater access to the captured prey, then it becomes the sole hunter of the pair at a lower disparity in hunting success than when the prey is equally divided. However, if a subordinate is a sufficiently better hunter than its companion, it may still become the sole hunter but only if its share of the kill is not too small. Although female lions are subordinate at kills, they are better hunters than males and do most of the hunting (Schaller 1972).

These final analyses illustrate that the range of possible values under which cooperation could evolve may sometimes be rather small. The available data are inadequate to show whether either factor is generally important, but we hope that future studies will investigate that possibility.

SUMMARY

Using a series of game-theoretical models, we develop two major predictions concerning the evolution of cooperative hunting. First, we specify the conditions under which individuals should hunt in groups rather than solitarily. When a group captures only a single prey per hunt, the expected benefits from cooperation rarely outweigh the advantages of hunting alone, since the prey must be divided between group members. Cooperation to capture the same prey can confer sufficient mutual benefit only when solitaries have low foraging efficiency; otherwise, each individual would do better to hunt separate prey. In contrast, species that capture multiple prey in a single hunt are not faced with similar disadvantages from grouping and should not be similarly constrained to hunt alone by high individual foraging efficiency. However, these predictions are not well supported by comparisons of individual hunting success in species that hunt alone and in groups. Consistent with previous reviewers, we consider that cooperative hunting in many species is more often a consequence of gregariousness than its evolutionary cause. However, cooperative hunting does often appear to be an important cause of grouping in species that take multiple prey.

Second, we specify the conditions under which group members should hunt cooperatively. A temptation to cheat is prevalent in species that capture prey large enough to be scavenged by noncooperative companions. Cheaters can thereby avoid the costs of hunting and prey capture. Cooperation is most likely when an individual has a low probability of capturing a large prey by itself. Under these conditions, a second hunter can sufficiently increase the pair's chances of capturing the prey to overcome his own costs of participating in the hunt. However, the temptation to cheat increases with group size, since each additional

hunter is decreasingly likely to overcome his costs of hunting. In contrast, there is no temptation to cheat when prey size is so small that only the successful hunter can feed from the captured prey. Data from 28 studies of group hunting generally conform to these predictions. Group members always cooperate when hunting small prey. When groups hunt large prey, cooperation mostly occurs when solo hunting success is very low, whereas cheating appears to be common when solo hunting success is high and group size is large.

Although repeated hunting of a single large prey often conforms to the conditions of the iterated prisoner's dilemma, we have little evidence that cooperation has evolved from a "tit-for-tat" hunting strategy. We specify the theoretical effects of kinship, individual differences in hunting ability, and behavioral dominance on the evolution of cooperative hunting of single large prey. We show that "tit-for-tat" is unlikely to be found where there are extreme individual differences in hunting ability.

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APPENDIX

Hunting Success of Singletons across Species

Predator	Hunting Strategy	Prey	H_1/K_1*	% Success	n	Lab/ Wild	Source
Mammals							
Black-back jackal *Canis mesomelas*	group	mammals	H_1	57.1	7	wild	Lamprecht 1977
Black bear *Ursus americanus*	alone	fishes	K_1	25.8	1481	wild	Frame 1974
Brown hyena *Hyaena brunnea*	group	vertebrates	H_1	8.7	103	wild	Mills 1978
Cheetah *Acinonyx jubatus*	group	mammals	H_1	14.8	115	wild	Eaton 1970
Chimpanzee *Pan troglodytes*	group	red *Colobus*	H_1	32.0	19	wild	Busse 1978
Coyote *Canis latrans*	group	deer	H_1	.0	44	wild	Hilton 1978
Golden jackal *Canis aureus*	group	mammals	H_1	25.0	12	wild	Lamprecht 1977
Leopard *Panthera pardus*	alone	mammals	H_1	4.7	64	wild	Bertram 1982
Lion *Panthera leo*	group	mammals	H_1	16.0	44.1	wild	Elliott et al. 1977; Schaller 1972; Van Orsdol 1981
Lynx *Lynx canadensis*	alone	vertebrates	H_1	14.6	151	wild	Nellis & Keith 1968
Puma *Felis concolor*	alone	elk/mule deer	H_1	82.0	45	wild	Hornocker 1970
Sea lion *Zalophus californianus*	group	fishes	K_1	3.1	63	wild	R. Pierotti, pers. comm.
Serval *Leptailurus serval*	alone	rodent/reptile	H_1	48.6	1922	wild	Geertsema 1985

(continued)

APPENDIX (*Continued*)

Predator	Hunting Strategy	Prey	H_1/K_1*	% Success	*n*	Lab/ Wild	Source
MAMMALS (*cont'd.*)							
Spotted hyena *Crocuta crocuta*	group	mammals	H_1	28.0	128	wild	Kruuk 1972; Mills 1985
Tiger *Panthera tigris*	alone	mammals	H_1	8.0	12	wild	Schaller 1967
Wild dog *Lycaon pictus*	group	mammals	H_1	22.2	9	wild	FitzGibbon & Fanshawe, MS
BIRDS							
Aplomado falcon *Falco femoralis*	group	birds	H_1	9.0	77	wild	Hector 1986
Black-backed gull *Larus marinus*	alone	tern chicks	K_1	~35.9	~103	wild	Hatch 1970
Black-headed gull *Larus ridibundus*	group	fishes	K_1	34.0	7200	lab	Götmark et al. 1986
Blue-gray gnatcatcher *Polioptila caerulea*	alone	invertebrates	H_1	21.3	n.a.	wild	Root 1967, cited in Salt & Willard 1971
Cattle egret *Bubulcus ibis*	group	invertebrates	K_1	78.0	123	wild	Scott 1984
Eastern bluebird *Sialia sialis*	alone	invertebrates	H_1	66.7	189	wild	Goldman 1975
Golden eagle *Aquila chrysaetos*	alone	birds	H_1	20.0†	115	wild	Collopy 1983
Goshawk *Accipiter gentilis*	alone	birds	H_1	28.9	90	wild	Kenward 1978
Great blue heron *Ardea herodias*	group	fishes	K_1	42.0	113	wild	Krebs 1974
Grey heron *Ardea cinerea*	alone	fishes	K_1	50.0	114	wild	D. Cook 1978

Herring gull *Larus argentatus*	alone	tern chicks	K_1	~44.1	~28	wild	Hatch 1970
Kestrel *Falco sparverius*	alone	birds/insects	H_1	58.3	1610	wild	Jenkins 1970; Balgooyen 1976; Collopy 1973
Lanner *Falco biarmicus*	alone	birds	H_1	13.0	n.a.	wild	Mebs 1959
Laughing gull *Larus atricilla*	group	stolen fish	H_1	45.5	11	wild	Hatch 1970
Little blue heron *Florida caerulea*	alone	aquatic animals	K_1	67.9	1529	wild	Recher & Recher 1969; Kent 1986
Little egret *Egretta garzetta*	group	aquatic animals	K_1	76.0	31	wild	Erwin et al. 1985
Loggerhead shrike *Lanius ludovicianus*	alone	invertebrates	H_1	65.0	2946	wild	Craig 1978
Merlin *Falco columbarius*	group	birds	H_1	2.4	42	wild	Bengtson 1975
Osprey *Pandion haliaetus*	alone	fishes	K_1	62.7	834	wild	Ueoka & Koplin 1973
Peregrine falcon *Falco peregrinus*	group	birds	H_1	32.9	351	wild	Bird & Aubrey 1982; Thiollay 1982; Treleaven 1980
Raven *Corvus corax*	group	gull eggs/chicks	K_1	5.5	324	wild	Montevecchi 1979
Red-tailed hawk *Buteo jamaicensis*	alone?	mammals/birds	H_1	78.8	169	wild	Orde & Harrell 1977
Reef heron *Egretta sacra*	alone	aquatic animals	K_1	47.8	2268	wild	Recher & Recher 1972
Sea eagle *Haliaeetus albicilla*	alone?	birds	H_1‡	5.0	60	wild	Rudebeck 1951
Sparrow hawk *Accipiter nisus*	alone?	birds	H_1‡	10.8	213	wild	Rudebeck 1951
Tricolored heron *Egretta tricolor*	alone	aquatic animals	K_1	33.0	121	wild	Kent 1986
Western reef heron *Egretta gularis*	alone	aquatic animals	K_1	51.5	565	wild	Davis 1985

(continued)

APPENDIX (*Continued*)

Predator	Hunting Strategy	Prey	H_1/K_1*	% Success	*n*	Lab/ Wild	Source
Other Vertebrates							
Bass *Micropterus salmoides*	alone	aquatic animals	K_1	34.6	315	lab	Landeau & Terborgh 1986; Nyberg 1971
Jack *Caranx ignobilis*	group	fishes	K_1	29.9	194	lab	Major 1978
Sunfish *Lepomis cyanellus*	group?	*Notonecta* spp.	H_1	57.3	143	lab	W. Cook & Streams 1984
Green treefrog *Hyla cinerea*	alone	insects	H_1	73.9	280	lab	Freed 1980
Invertebrates							
Crab spider *Misumena vatia*	alone	insects	H_1	5.7	439	wild	Morse 1981
Funnel-web spider *Agelenopsis aperta*	alone	insects	K_1	60.0	718	wild	Riechert & Tracy 1975
Golden-web spider *Nephila clavipes*	group	invertebrates	K_1	77.1	152	wild	Rypstra 1985
Jumping spider *Phidippus audax*	alone	insects	H_1	68.6	35	lab	Givens 1978
Orb-weaver *Araneus* *Araneus trifolium*	alone	insects	K_1	42.2	204	lab	Olive 1980
Orb-weaver *Argiope* *Argiope trifasciata*	alone	insects	K_1	36.8	204	lab	Olive 1980
Stegodyphid spider *Stegodyphus mimosarum*	group	insects	H_1	75.0	20	lab	Ward & Enders 1985

Chaoborus larvae *Chaoborus trivittatus*	alone?	*Daphnia*	K_1	16.4	632	lab	Pastorak 1981
Clerid beetle *Thanasimus dubius*	alone?	insects	K_1	72.0	n.a.	lab	Frazier et al. 1981
Praying mantis *Hierodula crassa*	alone	insects	H_1	57.5	1010	lab	Holling 1966
Veliid bug *Microvelia douglasi atrolineata*	group	planthoppers	H_1	3.8	235	lab	Nakasuji & Dyck 1984
Water stick insect *Ranatra linearis*	alone	*Daphnia*	K_1	64.0	~1000	lab	Cloarec 1982
Cuttlefish *Sepia officinalis*	alone	invertebrates	H_1	87.7	197	lab	Duvall et al. 1984
Cuttlefish *Sepia officinalis*	alone	arthropods	K_1	91.0	n.a.	lab	Messenger 1968

NOTE.—It is uncertain whether some species always hunt alone or in groups.

* Prey single (H_1) or multiple (K_1).

† Collopy (1983) referred to some hunting attempts as "tandem hunting," but in these cases each individual hunted alone sequentially.

‡ It is uncertain whether this is actually H_1. We excluded numerous other papers that reported hunting success but did not specify hunting-group size. The data presented here may include a few cases of individuals hunting in groups (H_n) as well as hunting alone.

LITERATURE CITED

Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. Science (Wash., D.C.) 211:1390–1396.

Bailey, K. M., and R. S. Batty. 1984. Laboratory study of predation by *Aurelia aurita* on larvae of cod, flounder, plaice and herring: development and vulnerability to capture. Mar. Biol. (Berl.) 83:287–291.

Balgooyen, T. G. 1976. Behavior and ecology of the American kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. Univ. Calif. Publ. Zool. 103:1–88.

Bednarz, J. C. 1988. Cooperative hunting in Harris' hawks (*Parbuteo unicinctus*). Science (Wash., D.C.) 239:1525–1527.

Bengtson, S.-A. 1975. Jakbeteende och bytesval hos en islandsk population av stenfalk. Fauna Flora (Stockh.) 70:8–12.

Bertram, B. 1982. Leopard ecology as studied by radio tracking. Symp. Zool. Soc. Lond. 49:341–352.

Bird, D. M., and Y. Aubrey. 1982. Reproductive and hunting behavior in peregrine falcons, *Falco peregrinus*, in southern Quebec. Can. Field-Nat. 96:167–171.

Boyd, R., and P. J. Richerson. In press. The evolution of reciprocity in sizable groups. J. Theor. Biol.

Busse, C. D. 1978. Do chimpanzees hunt cooperatively? Am. Nat. 112:767–771.

Clark, C. W., and M. Mangel. 1986. The evolutionary advantages of group foraging. Theor. Popul. Biol. 30:45–75.

Cloarec, A. 1982. Predatory success in the water stick insect: the role of visual and mechanical stimulations after moulting. Anim. Behav. 30:549–556.

Collopy, M. W. 1973. Predatory efficiency of American kestrels wintering in northwestern California. Raptor Res. 7:25–31.

———. 1983. Foraging behavior and success of golden eagles. Auk 100:747–749.

Cook, D. C. 1978. Foraging behavior and food of grey herons *Ardea cinerea* on the Ythan estuary. Bird Study 25:17–22.

Cook, W. I., and F. A. Streams. 1984. Fish predation on *Notonecta* (Hemiptera): relationship between prey risk and habitat utilization. Oecologia (Berl.) 64:177–183.

Craig, R. B. 1978. An analysis of the predatory behavior of the loggerhead shrike. Auk 95:221–234.

Davis, W. E. 1985. Foraging behavior of a western reef heron in North America. Colon. Waterbirds 8:70–73.

Duvall, P., M.-P. Chicery, and R. Chicery. 1984. Prey capture by the cuttlefish (*Sepia officinalis* L.): an experimental study of two strategies. Behav. Processes 9:13–21.

Eaton, R. L. 1970. Hunting behavior of the cheetah. J. Wildl. Manage. 34:56–67.

Elliott, J. P., I. M. Cowan, and C. S. Holling. 1977. Prey capture by the African lion. Can. J. Zool. 55:1811–1828.

Erwin, R. M., H. Hafner, and P. Dugan. 1985. Differences in the feeding behavior of little egrets (*Egretta garzetta*) in two habitats in the Camargue, France. Wilson Bull. 97:534–538.

Ewer, R. F. 1973. The carnivores. Cornell University Press, Ithaca, N.Y.

Frame, G. W. 1974. Black bear predation on salmon at Olson Creek, Alaska. Z. Tierpsychol. 35: 23–88.

Frazier, J. L., T. E. Nebeker, R. F. Mizell, and W. H. Calvert. 1981. Predatory behavior of the clerid beetle *Thanasimus dubius* (Coleoptera: Cleridae) on the southern pine beetle (Coleoptera: Scolytidae). Can. Entomol. 113:35–43.

Freed, A. N. 1980. Prey selection and feeding behavior of the green treefrog (*Hyla cinerea*). Ecology 61:461–465.

Fretwell, S. D. 1972. Seasonal environments. Princeton University Press, Princeton, N.J.

Geertsema, A. A. 1985. Aspects of the ecology of the serval *Leptailurus serval* in the Ngorongoro Crater, Tanzania. Neth. J. Zool. 35:527–610.

Givens, R. P. 1978. Dimorphic foraging strategies of a salticid spider (*Phidippus audax*). Ecology 59:309–321.

Goldman, P. 1975. Hunting behavior of eastern bluebirds. Auk 92:798–801.

Götmark, F., D. W. Winkler, and M. Andersson. 1986. Flock-feeding on fish schools increases individual success in gulls. Nature (Lond.) 319:589–591.

Grafen, A. 1979. The hawk-dove game played between relatives. Anim. Behav. 27:905–907.

Hatch, J. J. 1970. Predation and piracy at a ternery in Maine. Auk 87:244–254.

Hector, D. P. 1986. Cooperative hunting and its relationship to foraging success and prey size in an avian predator. Ethology 73:247–257.

Hilton, H. 1978. Systematics and ecology of the eastern coyote. Pages 209–228 *in* M. Bekoff, ed. Coyotes: biology, behavior and management. Academic Press, New York.

Hines, W. S. G., and J. Maynard Smith. 1979. Games between relatives. J. Theor. Biol. 79:19–30.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildl. Monogr. 21:3–39.

Jenkins, R. E. 1970. Food habits of wintering sparrow hawks in Costa Rica. Wilson Bull. 82:97–98.

Kent, D. M. 1986. Foraging efficiency of sympatric egrets. Colon. Waterbirds 9:81–85.

Kenward, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. J. Anim. Ecol. 47:449–460.

Krebs, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). Behaviour 51:99–134.

Krebs, J. R., M. H. MacRoberts, and J. M. Cullen. 1972. Flocking and feeding in the great tit *Parus major*—an experimental study. Ibis 114:507–530.

Kruuk, H. 1972. The spotted hyena. University of Chicago Press, Chicago.

———. 1975. Functional aspects of social hunting in carnivores. Pages 119–141 *in* G. Baerends, C. Beer, and A. Manning, eds. Function and evolution in behaviour. Oxford University Press, Oxford.

Lamprecht, J. 1977. On diet, foraging behavior and interspecific food competition of jackals in the Serengeti National Park, East Africa. Z. Saeugetierkd. 43:210–223.

Landeau, L., and J. Terborgh. 1986. Oddity and the 'confusion effect' in predation. Anim. Behav. 34:1372–1380.

Lendrem, D. W. 1983. Predation risk and vigilance in the blue tit (*Parus caeruleus*). Behav. Ecol. Sociobiol. 13:9–13.

Lubin, Y. D., and M. H. Robinson. 1982. Dispersal by swarming in a social spider. Science (Wash., D.C.) 216:319–321.

MacDonald, D. W. 1983. The ecology of carnivore social behaviour. Nature (Lond.) 301:379–384.

Major, P. F. 1978. Predator-prey interactions in two schooling fishes, *Caranx ignobilis* and *Stolephorus purpureus*. Anim. Behav. 26:760–777.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. Anim. Behav. 25:1–9.

———. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge.

Mebs, T. 1959. Beitrag zur biologie des feldeggsfalken (*Falcon biarmicus feldiggi*). Vogelwelt 80: 142–149.

Messenger, J. B. 1968. The visual attack of the cuttlefish, *Sepia officinalis*. Anim. Behav. 16:342–357.

Mills, M. G. L. 1978. Foraging behavior of the brown hyena (*Hyaena brunnea* Thunberg, 1820) in the southern Kalahari. Z. Tierpsychol. 48:113–141.

———. 1985. Related spotted hyaenas forage together but do not cooperate in rearing young. Nature (Lond.) 316:61–62.

Montevecchi, W. A. 1979. Predator-prey interactions between ravens and kittiwakes. Z. Tierpsychol. 49:136–141.

Morse, D. H. 1981. Prey capture by the crab spider *Misumena vatia* (Clerk) (Thomisidae) on three common native flowers. Am. Midl. Nat. 105:358–367.

Nakasuji, F., and V. A. Dyck. 1984. Evaluation of the role of *Microvelia douglasi atrolineata* (Bergroth) (Heteroptera: Veliidae) as predator of the brown planthopper *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). Res. Popul. Ecol. (Kyoto) 26:134–149.

Nellis, C. H., and L. B. Keith. 1968. Hunting activities and success of lynxes in Alberta. J. Wildl. Manage. 32:718–722.

Nyberg, D. W. 1971. Prey capture in the largemouth bass. Am. Midl. Nat. 86:128–144.

Olive, C. W. 1980. Foraging specializations in orb-weaving spiders. Ecology 61:1133–1144.

Orde, C. J., and B. E. Harrell. 1977. Hunting techniques and predatory efficiency of nesting red-tailed hawks. Raptor Res. 11:82–85.

Packer, C. 1986. The ecology of sociality in felids. Pages 429–451 *in* D. I. Rubenstein and R. W. Wrangham, eds. Ecological aspects of social evolution: birds and mammals. Princeton University Press, Princeton, N.J.

Packer, C., and A. E. Pusey. 1982. Cooperation and competition within coalitions of male lions: kin selection or game theory? Nature (Lond.) 296:740–742.

Pastorak, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology 62:1311-1324.

Pitcher, T. J., A. E. Magurran, and I. J. Winfield. 1982. Fish in larger shoals find food faster. Behav. Ecol. Sociobiol. 10:149–151.

Pulliam, H. R., and T. Caraco. 1984. Living in groups: is there an optimal group size? Pages 122–147 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 2d ed. Sinauer, Sunderland, Mass.

Pusey, A. E., and C. Packer. 1987. The evolution of sex-biased dispersal in lions. Behaviour 101: 275–310.

Recher, H. F., and J. A. Recher. 1969. Comparative foraging efficiency of adult and immature little blue herons (*Florida caerulea*). Anim. Behav. 17:320–322.

———. 1972. The foraging behavior of the reef heron. Emu 72:8–90.

Riechert, S. E., and C. R. Tracy. 1975. Thermal balance and prey availability: basis for a model relating web-site characteristics to spider reproductive success. Ecology 56:265–284.

Roeloff, R., and S. E. Riechert. 1988. Dispersal and population-genetic structure of the cooperative spider, *Agelena consociata*, in West African rainforest. Evolution 42:173–183.

Rubenstein, D. I. 1978. On predation, competition and the advantages of group living. Perspectives in Ethology 3:205–231.

Rudebeck, G. 1951. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. Oikos 3:200–231.

Rypstra, A. L. 1985. Aggregations of *Nephila clavipes* (L.) (Araneae, Araneidae) in relation to prey availability. J. Arachnol. 13:71–78.

Salt, G. W., and D. E. Willard. 1971. The hunting behavior and success of Forster's tern. Ecology 52:989–998.

Schaller, G. B. 1967. The deer and the tiger. University of Chicago Press, Chicago.

———. 1972. The Serengeti lion. University of Chicago Press, Chicago.

Scott, D. 1984. The feeding success of cattle egrets in flocks. Anim. Behav. 32:1089–1100.

Sibly, R. M. 1983. Optimal group size is unstable. Anim. Behav. 31:947–948.

Thiollay, J.-M. 1982. Les resources alimentaires. Facteur limitant la reproduction d'une population insulaire de falcons pelerins, *Falco peregrinus brookei*. Alauda 50:1–44.

Treisman, M. 1975. Predation and the evolution of gregariousness. II. An economic model for predator-prey interaction. Anim. Behav. 23:801–825.

Treleaven, R. 1980. High and low intensity hunting in raptors. Z. Tierpsychol. 54:339–345.

Ueoka, M. L., and J. R. Koplin. 1973. Foraging behavior of ospreys in northwestern California. Raptor Res. 7:32–38.

Van Orsdol, K. G. 1981. Lion predation in Rwenzori National Park, Uganda. Ph.D. diss. Cambridge University, Cambridge.

Wakely, J. S. 1974. Activity periods, hunting methods and efficiency of the ferruginous hawk. Raptor Res. 8:67–72.

Ward, P. I., and M. M. Enders. 1985. Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. Behaviour 94:167–182.

Wickler, W. 1973. Colony formation and social bonding in *Stegodyphus mimosarum* and other social spiders. Z. Tierpsychol. 32:522–531.