Chapter 9

ON PREDATION, COMPETITION, AND THE ADVANTAGES OF GROUP LIVING

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I. ABSTRACT

Many evolutionary reasons have been suggested as to why animals live in groups. Based on the costs and benefits associated with group living it appears that the risk of predation and the competitively induced need to forage efficiently are the most important forces responsible for the formation and maintenance of groups.

Most field studies and mathematical models that have investigated the environmental conditions that favor the formation of groups have studied the effects of either predation or competition. After examining some of these studies and their major conclusions, I present a model, based on the theory of games, that focuses on the combined action of predation and competition. Simulations under a variety of environmental conditions reveal that individuals that are poor competitors are more likely to remain in groups when the visibility of the habitat is low, when the level of competitive inequality among group members is low, when the carrying capacity of the habitat is high, and when the presence of neighbors enhances an individual's feeding success.

Models, such as this one, that incorporate the effects of predation and resource competition, while accounting for how differences in age, sex, size, and past experience influence competitive ability, provide insights into the dynamics of social behavior. When other factors, such as kinship relationships and subtle interspecific interactions, are also considered, a general and predictive theory of social organization can be developed.

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II. INTRODUCTION

One of the most studied and most poorly understood concerns of ethology is why animals live in groups. Living in groups has been claimed to aid in the rearing of young, to facilitate mating, to increase foraging success, to reduce the risk of predation, to provide protection from inclement weather, and to increase swimming efficiency. Undoubtedly each of these advantages has contributed to the formation of groups in particular situations. Nevertheless, constructing a simple patchwork of advantages that can be used to justify the existence of groups often differing with respect to habitat and the sex, age, and degree of relatedness of its constituents provides no real understanding of why animals live in groups. If a predictive theory of social organization is to emerge, it will require an understanding of how various selective pressures operate so that an individual's chances of survival or reproductive success are greater when it is living in a particular type of group than when it is living alone or in a different type of group. In particular, ethologists must (1) determine which are the most important selective forces; (2) determine how the action of each force is influenced by characteristics of the environment, attributes of the individual, and species-specific constraints; and (3) determine the ramifications of the combined action of these selective forces. From such an evolutionary understanding of social dynamics, a predictive theory of social organization can be developed.

The purpose of this paper is to examine how much progress has been made toward the achievement of each of the three objectives. Pausing to reflect upon what has already been accomplished will provide insights into what still needs to be investigated.

III. THE MAJOR SELECTIVE FORCES

It is easy to speculate on how natural selection operates, but proving how it operates is one of the most difficult tasks in evolutionary biology. Even if one assumes that a behavior is beneficial and has been favored by natural selection, it is very difficult to prove that selection has favored the behavior because of a particular consequence.

For example, black-headed gulls remove broken eggshells from their nests. Tinbergen and his co-workers (1962) suggested that selection might favor the removal of broken eggshells from the nest because such behavior might reduce the predator's ability to locate the nest, reduce the chances of a chick's cutting itself on sharp edges, reduce the growth of bacteria, or increase the parents' ability to brood the young. Although these authors performed a series of experiments demonstrating that eggshell removal served to maintain the camouflage of the nest, others (e.g., McFarland, 1976) have contended that it is still possible that the other considerations might also exert small selection pressures.

Studying the adaptive value of behavior, such as group living, is even more difficult when experimental manipulations are not possible. Probably the most realistic approach involves listing possible advantages and disadvantages associated with the behavior, then noting the frequencies at which the benefits associated with the advantages and the costs associated with the disadvantages occur. Based on the distribution of costs and the occurrence of benefits, an understanding of the important selective forces and how they operate will emerge.

Using this approach, Alexander (1974) proposed that groups form only when the advantages derived from the presence of others—reduced risk of predation and enhanced feeding efficiency—offset the detriments of group living: automatically intensified competition and increased disease and parasite transmission, as well as potentially increased chances of injury because of competition, increased conspicuousness to predators, and increased chances of misdirected parental care. Based on this statement, predation and the competitively induced need to forage efficiently should be the two major selection pressures that determine whether an individual lives alone or in a group.

Unfortunately, the paucity of field studies measuring both the cost and the benefits of group living makes it difficult to verify that predation and competition are the two major forces responsible for the formation of groups. In one study on colonial nesting bank swallows, Hoogland and Sherman (1976) uncovered several detrimental aspects of group living: increased competition for nest sites, nest material, and mates; increased likelihood of misdirected parental care; and increased parasite transmission. These authors concluded, however, that there was only one advantage of colonial living: predator defense. They noted that increases in colony size resulted in more rapid detection, more vocal harassment, and greater percentages of inhabitants participating in the mobbing of predators. In a few instances, this mobbing resulted in the predator's being driven away. Although Hoogland and Sherman found no evidence that coloniality enhanced feeding success, Emlen (1975) observed that bank swallows of another colony left in groups to forage and suggested that this social foraging led to increased reproductive success.

Even though this evidence by no means implies that predation and competition are the only important selective pressures responsible for the formation of groups, it does suggest that they do play a major role. The fact that in one area it appears that predation was the chief pressure for bank swallow coloniality whereas in another area it appears that feeding demands were responsible underscores the need for more comparative studies, especially those that compare similar groups under different environmental conditions.

Theoretical studies also play an important role in determining how the action of predation and competition influences the formation of groups. If characteristics of the environment, the species, and the individuals are incorporated into models of predatory and competitive behavior, the actions most beneficial to predators and prey can be predicted. For example, Treisman (1975a) used models that incorporated the perceptual abilities of the predator and the prey to predict under what environmental conditions the prey should live in groups. But if a realistic and predictive theory of social organization is to be achieved, both empirical and theoretical studies must be pursued simultaneously. The models provide an understanding of how predation and competition might operate and thus help focus field studies. Therefore, the remainder of this paper focuses on theoretical studies. Nevertheless, empirical studies provide basic biological data that, by making the assumptions underlying the models realistic, help ensure that the predictions will be biologically meaningful.

IV. PREDATION AND RESOURCE COMPETITION: INFLUENCES OF ENVIRONMENT, INDIVIDUALS, AND SPECIES

A. Predation

Animals can reduce the risk of predation by increasing their probability of detecting the predator and responding—by concealment, avoidance, or defense—before the predator can detect and attack them. Thus, we might ask: Are animals in groups more likely to be successful at reducing the risk of predation than are solitary animals? And if so, under what circumstances?

Based on some simple assumptions, Pulliam (1973) demonstrated theoretically that birds in flocks could benefit from the scanning behavior of neighbors. By assuming that birds cock their heads to scan for predators, that there is a mean head-cocking rate, and that the attacking predators are exposed for some mean time period, he showed that birds in a group are more likely than solitary birds to detect a predator and fly to safety before being killed. In addition, he showed that birds in flocks could derive the same level of predator protection as do solitary birds, even if each individual lowered its level of vigilance.

Even if animals are randomly assembled when a predator appears, Hamilton (1971) has shown that the formation of a group offers immediate benefits. His simplest hypothetical example depicts a snake emerging from a pond about which frogs are distributed at random. If the predator were to strike the nearest frog, Hamilton showed that a frog could reduce its chances of being the nearest to the predator by jumping into the gap between two other frogs. As every frog performed these calisthenics, the arrangement would become less random, and eventually a densely packed aggregation would be produced. (Similar conclusions were reached when the geometric model was expanded to include animals living on the plain.) One of the elegant features of the model is that the formation of a group requires only that animals behave in their own self-interest.

Pulliam (1973) has claimed, however, that purely selfish behavior does not lead to the formation of an aggregation. In spite of all the realignments that take place, some individuals still remain on the periphery, subject to a greater risk of predation than those in the interior. Pulliam implicitly assumed that because the risk of predation on the periphery is greater than that of living alone, the outermost individuals should abandon the group. And because each successive inner layer eventually becomes the peripheral layer, the group should eventually deteriorate. Thus, unless the risk of predation for the peripheral individuals can be lowered, Pulliam argued that groups should not form.

Pulliam was certainly correct in elaborating on how Hamilton's scheme accentuates individual inequalities. But although an individual on the outside of a group suffers the greatest risk of predation during any particular encounter with the predator, it is not valid to assume that over a number of such encounters an individual's average risk is automatically higher than the risk suffered by animals living alone. If the same individuals always acquired the central spots, then the average risk to the peripheral individuals probably would be higher than that of a solitary individual. Thus, groups would not form unless the peripheral individuals received ancillary benefits. But if all the individuals had an equal chance of being in the center, then the average predation risk might be lower for peripheral individuals than for animals living alone. In this case, then, simple geometric considerations would lead to the formation of a group.

In certain respects, it does not really matter if Hamilton's theory of the selfish herd is sufficient to account for the formation of groups. According to Alexander (1974), behavior providing ancillary benefits that make group living even more attractive should subsequently evolve for two reasons. First, social behavior may evolve to minimize the disadvantages inherent in group living. For example, social grooming in mammals might have evolved to reduce parasite transmission; communicatory and dominance systems might have evolved to limit the intensity of competition. Second, social behavior may evolve to enhance the original advantage that was responsible for the formation of the group. Thus, if a group formed as a means of reducing each individual's risk of being preyed upon, it is likely that additional types of behavior that further reduce this risk, such as collective predator detection, would be favored by natural selection.

The major weakness of Hamilton's idea of the selfish herd is that it is based on the assumption that the predator instantly appears among the prey. Probably very few predators are able to do so. More likely, they wander about the habitat detecting and attacking prey from outside the perimeter of the population. Therefore, Vine (1971) believed that in order to determine how effective different arrangements of prey are at reducing the risk of predation, one must consider the perceptual abilities of the predator. His model is based on the idea that the predator's ability to detect prey visually increases as the magnitude of the prey's minimum dimension increases. Because he considered height to be an ungulate's minimum dimension, he concluded that a group would be no easier to perceive than solitary individuals. But because animals in a group are localized in one point in space, the predator would, on average, have to turn its head through a greater angle to detect prey in a group than to detect those randomly scattered about the environment. Thus, it would take longer for a predator to locate animals in a group. If this mean time to detection exceeded the time allotted by the predator to scanning the environment, the group would escape being preyed upon. Thus, Vine concluded, group living could be advantageous, because groups are difficult for the predator to detect.

Although Vine's conceptualization of the problem has influenced many other studies, his model suffers from some unrealistic assumptions about predators' foraging habits and the mechanisms of visual perception. Most predators probably do not leave an area when no prey are detected during a single scan of the environment. As Treisman (1975a) has indicated, animals often possess territories or home ranges that provide them with information about the habitat and habits of the prey. Because of this familiarity, they probably do not leave an area after one negative scan. Instead, Treisman suggested that predators stay in an area until the cost of staying and rescanning the habitat exceeds the cost of leaving. The actual number of rescans that occur before the habitat is deemed unprofitable depends on the amount of effort required of the predator to scan the habitat, the abundance of prey in the habitat, and the predator's ability to detect the prey, given that they are present. Certainly, this last consideration is affected by the predator's perceptual abilities. But it is also affected by the perceptual abilities of the prey, which, as we have seen, can be influenced by their pattern of social dispersion.

Treisman (1975a) also objected to the idea that a prey animal's ability to be detected depends on the magnitude of its minimum dimension. Based on human sensory data, he proposed instead that the ability of predators and prey to detect objects visually increases as the area of the object increases, the probability of detection being lowest when no object is present and reaching a maximum past a critical area.

Given that the predator scans the environment some optimal number of times, that its ability to detect prey depends on the size of the prey aggregation, and the additional assumption that concealment is the only benefit that the prey derive from living in a group (i.e., they can not escape once they detect a predator), Treisman showed that regardless of the number of prey in the habitat, the probability of detecting prey scattered randomly about the habitat is always greater than the probability of detecting prey living in a group. Because the prey cannot escape once they are detected, however, the per capita probability of being killed is greater for animals living in a group than for animals living alone. Thus, if the prey's only defense is concealment, natural selection favors individuals living alone.

Animals capable of escaping from a predator are involved, with the predator, in a contest for priority of detection. In such situations, Treisman showed that regardless of the size of the group, the collective ability to detect the predator always exceeds the increased conspicuousness of the group. Therefore, when prey can flee from a predator, natural selection favors animals living in groups.

But as Treisman indicated, these models are somewhat artificial. For example, they predict that there should be no limit to the size of the group. Even though they incorporate the perceptual abilities of both the predator and the prey, they fail to account for other activities that compete for the prey animal's time. Some of these activities, such as acquiring food, are just as important for survival as is the need to avoid predators. Thus, we should ask: Are animals in groups more likely to enhance their feeding success than solitary animals? And, if so, under what circumstances?

B. Resource Competition

Changes in social structure often accompany changes in the distribution and abundance of resources. For example, Brown (1964) accounted for the existence of territories by the principle that a resource is defended only when the energetic costs of defense are exceeded by the energetic gains associated with the exclusive use of that resource. Field evidence, such as that provided by Gill and Wolf (1975) on African sunbird energetics, supports the principle of economic defensibility. At normal nectar concentration, individual sunbirds defended feeding territories. But as the nectar quality improved, the cost of repelling invaders disproportionately increased. Eventually, the energetic costs of defense exceeded the energetic gains derived from the exclusive use of the flowers, and the birds abandoned their territories.

There is also evidence that economic considerations determine when groups should form. Zahavi (1971) altered the pattern of social organization of wintering wagtails by manipulating the dispersion of their food. When the food was distributed in small patches, the birds established territories, but when the food was presented in large clumps, which were unevenly distributed, the birds formed flocks.

More detailed field studies comparing the foraging success of individuals, in and out of flocks, also suggest that birds in groups enhance their foraging efficiency. Murton (1971a,b) showed that solitary wood pigeons pecked more slowly than did those in flocks, and Rubenstein and his coworkers (1977) showed that although all finches pecked at the same rate, those finches in flocks (both mixed- and single-species flocks) fed for longer uninterrupted feeding episodes than did solitary finches. Krebs (1974) also demonstrated that the amount of food eaten by individual great blue herons increased as flock size increased.

But why do individuals in groups have enhanced feeding success? Horn (1968) suggested that birds nesting in colonies minimize their daily foraging route. Based on a simple model, he concluded that in order to minimize the distance traveled while foraging, birds should disperse their nests about the habitat when food is evenly spaced but that birds should clump their nests when food is present in patches that are unevenly distributed in space and time. His field observation revealed that Brewer's blackbirds, which nest colonially, fed on prey that were indeed distributed in patches that appeared randomly throughout the habitat. But as Horn noted, because he did not study the feeding habits of birds that lived alone, he was unable to give conclusive support to his generalizations.

Others argue that individuals in groups enhance feeding success by acquiring certain types of information from neighbors. Ward and Zahavi (1973) examined the feeding patterns of many species of colonial nesting birds and concluded, on the basis of circumstantial evidence, that colonies act as "information centres." They claimed that birds that were unsuccessful at locating unevenly dispersed food resources could enhance their feeding success by following already successful individuals to the feeding areas.

It was Krebs (1974), however, studying a population of colonial nesting great blue herons, who provided convincing evidence that colonies can in fact serve as information centers. He showed that birds faced with an unpredictable food source left the colony on foraging trips synchronously and that nearest neighbors showed the most similarity with respect to time of departure and feeding destination.

For birds that aggregate only to feed, other types of information can be transferred among group members. Krebs and his co-workers (1972) have shown that chickadees in aviaries increased their foraging success by copying feeding actions of their flockmates. Field studies of the feeding behavior of finches also revealed the occurrence and beneficial effects of social learning (Rubenstein *et al.,* 1977).

Other studies suggest that the physical presence of neighbors facilitates foraging. Often group cooperation is necessary to capture large prey. This appears to be the case for many mammal species (Kruuk, 1972; Schaller, 1972). At other times, group activity, because of high levels of disturbance, flushes prey from under cover. Many tropical flocks of birds forage in this manner (Willis, 1966; Morse, 1970).

Although these advantages often accrue to individuals living in groups, not all animals live in or feed in groups. In these instances, the costs of intensified competition most likely offset the potential gains, thus making group living, based solely on dietary consideration, uneconomical. Using a mathematical model based on a bird's ability to locate food, the abundance of food in the habitat, and the costs associated with aggression, Pulliam (1976) outlined some of the conditions under which animals should form feeding groups. He concluded that at low levels of food abundance the feeding rate of a dominant individual (one who can drive away a competitor) and a submissive individual would be higher than that of an individual feeding alone. Thus, under low levels of food abundance, natural selection would favor individuals foraging in a group. At higher food concentrations, however, Pulliam predicted a different outcome. At higher food levels, the dominant bird reaches its maximum feeding rate and begins to use its excess time to chase the subordinate bird. Because the subordinate is spending time fleeing from the dominant, its feeding rate is reduced. When the dominant bird's aggression reaches a level where the subordinate bird's feeding rate falls below that of a solitary bird, the subordinate leaves the group. Thus, based on Pulliam's model, animals are induced to form feeding groups only when food abundance is low.

Both empirical and theoretical studies indicate that the economics of foraging plays a major role in determining patterns of social organization. Different species, however, appear to respond to different aspects of the resource. For example, whereas decreased levels of food abundance seem to favor the formation of flocks in granivorous birds, increased food patchiness and unpredictability seem to favor flock formation in Brewer's blackbirds and wagtails. Thus, any real understanding of how feeding considerations affect an individual's decision to live either alone or in a group requires a knowledge of what the individual preys upon and the prey's overall relationship with the habitat.

V. PREDATION AND RESOURCE COMPETITION: THEIR COMBINED ACTION

From the preceding discussions, it appears that either the influence of predators or the competitively induced need to forage efficiently could alone provide individuals with advantages that under certain conditions could induce them to form groups. In fact, many biologists contend that one force or the other is solely responsible for the evolution of group living and that the other force is responsible for generating secondary adaptations. For example, Alexander (1974) has proposed that predation is solely responsible for the formation and maintenance of groups, whereas Ward and Zahavi (1973) have claimed that "the primary importance of predation in the evolution of information centres lies in its 'shaping' the assemblies (which are formed for the efficient exploitation of a patchy food supply) so that the resultant vulnerability to predation is minimized" (p. 532). Although this is not a trivial debate, it has polarized the study of sociality and has diverted attention away from the fact that animals living in groups must simultaneously contend with the conflicting needs of defense and nourishment. Certainly, variations with respect to the environment, the individuals, and the species affect the relative importance of each force. But any theory that claims to account for why animals living in groups remain in those groups must account for the combined effects of both selective forces.

A. Games against Nature

Any level of vigilance exhibited by a prey animal has a cost associated with it. Obviously, the more time a prey animal spends searching for a predator, the less time it can devote to other activities, such as feeding, grooming, or finding and securing mates. But in addition, Treisman (1975a) has shown that a prey animal can increase its probability of detecting a predator only by increasing its probability of mistakenly detecting a predator (i.e., by increasing its level of skittishness). Paradoxically, the more vigilant a prey, the more it will be in flight.

Because of these costs associated with vigilance, Treisman (1975b) has developed an economic model of social organization, which I call a *game against nature.* In this game against nature, the fitness of a prey animal depends not only on its ability to determine when a predator is present but also on its ability to determine when a predator is not present. Depending on the accuracy of the prey animal's perception, four possible situations can occur, each potentially providing a different fitness payoff ($V_{..}$). The following matrix depicts one possible payoff scheme.

		Prey's response	
		Detect	Not detect
Predator:	Present	$V_{PD} = -1$	$V_{PN} = -10$
	Absent	$V_{AD} = -1$	$V_{AN} = +1$

It reveals that if a prey animal detects a predator when a predator is present, it will interrupt whatever activity it is engaged in and flee the habitat, incurring a small cost. If it "detects" a predator when a predator is not present, then it also flees the habitat and incurs the same small cost. But if it fails to detect a predator when one is present, then it is killed, incurring a much larger cost. Conversely, if a prey animal correctly perceives that there is no predator in the habitat, it will continue whatever activity it is engaged in, thus receiving an increase in fitness.

These relative payoffs play an important role in determining a prey animal's overall expected fitness, but they are influenced by the probability of a predator's being present, the probability of a prey animal's detecting a predator, and the probability of a prey animal's incorrectly detecting a predator. Once an animal's expected fitness is determined, we can answer questions such as whether an animal living in a group receives a higher fitness than an animal living alone and, if so, for what environmental conditions, group sizes and levels of vigilance.

Treisman's game against nature not surprisingly shows that the expected fitness of prey animals living in a group increases as the probability of either the predator's being present or the prey's detecting the predator increases. But it also reveals that forming larger and larger groups does not automatically lead to increased expected gains. Instead, the model shows that there are group sizes that maximize an individual's expected gains. Optimal group sizes result from the fact that although the group's collective ability to detect predators increases as group size increases, the group's collective probability of false detection disproportionately increases as group size increases. Thus, as group size increases, the costs associated with large false detection levels eventually exceed the benefits associated with true detection levels, and the expected gains begin to decrease.

When the probability of predation changes, Treisman suggested that there are a number of ways that animals in groups can adjust their behavior to maximize their expected fitness. If the risk of predation increases, then individuals of species unable to adjust sensory capabilities can increase their fitness by living in larger groups. But individuals of species capable of adjusting sensory capabilities can also reduce the risk of predation by increasing their levels of vigilance and by living in smaller groups. Thus, it appears that similar environmental forces can affect behavior in different ways for different species.

Treisman addressed the issue of whether animals living in groups have higher expected gains than animals living alone by using a version of the game-against-nature model that includes the predator's detection capabilities. He found that prey animals in groups do not always have an advantage over their solitary counterparts. For most realistic parameter values of the model, it appears that when the number of prey animals in a habitat is low, animals do better when assembled into a group. But when the population of prey animals is large, the greatest protection from predators occurs when prey are distributed randomly about the habitat.

Treisman's game against nature has provided a powerful means of investigating how and under what conditions predation induces individuals to live in groups. It effectively shows how subtle variations in the accuracy of both the predator's and the prey's sensory capabilities can have dramatic impacts on social dynamics by altering an individual's chances of survival. In spite of these attributes, the model ignores some important biological considerations. Because he was concerned primarily with the influence of predation, Treisman deliberately ignored the direct influence of feeding considerations. Nevertheless, any theory of social organization should incorporate the influence of both forces. In addition, he assumed, probably for mathematical simplicity, that all individuals in a group receive the same expected fitness payoff. This assumption is certainly unrealistic because evolution occurs precisely because individuals compete and derive unequal benefits.

In the next section, I present a model, in the form of a game, that directly analyzes the conflict between the need for defense and the need for nourishment, without assuming that all individuals in a population receive the same expected payoff.

B. Social Games

If the benefits of group living are not shared equally among group members, then under certain conditions it might be advantageous for the individuals receiving the fewest benefits to abandon a group and live alone. Thus, we might ask: Could this type of behavior occur? And, if so, under what circumstances?

The theory of games provides a convenient means by which we can predict when animals should choose one strategy over another. The simplest social game would contain only two strategies: to live in a group or to live alone. In general, an animal adopts the strategy that produces the highest fitness. But because the fitness associated with each strategy depends not only on environmental conditions but also on individual attributes such as age, sex, size and past experience, the "best" strategy is often difficult to predict. In the following social games, we assume for convenience that both animals are of equal age, and we call the individual best at acquiring resources the *dominant* and the other individual the *subordinate.*

An individual's fitness during a time interval, x to $x + 1$, can be represented (as a first approximation) as:

$$V_x = p_x m_x$$

where p_x is the probability of living through the interval and m_x is the number of offspring produced during the interval. (A glossary of terms appears in the appendix.) Let the probabilities of a dominant and a subordinate individual living through the interval, while either living alone or in a group, be P_{xR}, p_{xr}, P_{xG}, and p_{xg}, respectively. In a similar fashion, let the number of offspring produced during the interval by a dominant or a subordinate individual, either living alone or in a group, be M_{xR}, m_{xr}, M_{xG}, and m_{xg}, respectively. Then the following matrix depicts the strategies of both the dominant and the subordinate animal, as well as the fitness payoffs that each would expect to receive.

		Subordinate lives:	
		In group	Alone
Dominant lives:	In group	$p_{xg}m_{xg}$ $P_{xG}M_{xG}$	$p_{xr}m_{xr}$ $P_{xG}M_{xG}$
	Alone	$p_{xg}m_{xg}$ $P_{xR}M_{xR}$	$p_{xr}m_{xr}$ $P_{xR}M_{xR}$

An individual maximizes its fitness only if it adopts an evolutionary stable strategy (ESS). According to Maynard Smith (1976, 1977), a strategy is evolutionarily stable only if a pair of individual strategies (S_D, S_s) exists so that it does not pay the dominant individual to diverge from its strategy S_D, when the subordinate adopts strategy S_s, and it does not pay the subordinate to diverge from strategy S_s as long as the dominant adopts strategy S_D. In the simple social game, there are four possible ESSs:

1. Dominant and subordinate live in a group: requires that $P_G M_G > P_R M_R$ (otherwise the dominant will live alone) and that $p_g m_g > p_r m_r$ (otherwise the subordinate will live alone).
2. Dominant in group and subordinate alone: requires that $P_G M_G > P_R M_R$ (otherwise the dominant will live alone) and $p_r m_r > p_g m_g$ (otherwise the subordinate will live in a group).
3. Dominant alone and subordinate in group: requires that $P_R M_R > P_G M_G$ (otherwise the dominant will live in a group) and that $p_g m_g > p_r m_r$ (otherwise the subordinate will live alone).
4. Dominant and subordinate live alone: requires that $P_R M_R > P_G M_G$ (otherwise the dominant will live in a group) and $p_r m_r > p_g m_g$ (otherwise the subordinate will live in a group). To determine under what conditions a potential ESS becomes an actual ESS, more precise descriptions of the $p_{x.}$ and $m_{x.}$ functions are required.

The functions that describe the probability of survival (p_x) are based on the idea that once an animal acquires its maintenance energy, the major factor affecting its probability of survival is its ability to detect a predator before the predator detects it. Thus, in general, the probability that an individual that lives alone will survive from age x to $x + 1$ is:

$$P_{xR} = p_{xr} = \alpha_x \cdot f_1[C_i(N), D_i(N)]$$

where α_x is the probability that an animal aged x will live to age $x + 1$, given that there are no predators in the habitat, and $f_1(C_i(N), D_i(N))$ is a discrete function describing the probability of an individual's not being killed by a predator during the interval x to $x + 1$. This function increases monotonically as the size of the population (N) increases and is influenced by the predator's ability to detect prey (C_i) and the prey's ability to detect a predator (D_i).

The probability that an individual living in a group will survive from age x to age $x + 1$ is:

$$P_{xG} = p_{xg} = \alpha_x \cdot f_2[C_G(N), D_G(N)]$$

where $f_2[C_G(N), D_G(N)]$ again is a function describing the probability of an animal's not being killed by a predator. It increases monotonically because both the probability of a predator's detecting a group (C_G) and the ability of prey in a group to detect a predator (D_G) increases as the size of a group increases.

The functions describing an animal's fecundity are based on the idea that the number of offspring that an animal can produce is related to the amount of energy that it can acquire and devote to reproduction. For an animal living alone, the number of offspring that it can produce during the interval x to $x + 1$ is:

$$M_{xR} = m_{xr} = \beta_x \cdot \gamma_x \cdot g_1 (r, N)$$

where β_x is a conversion factor that represents the ability of an animal aged x to convert calories into offspring, γ_x is the maximum amount of calories that an animal aged x can acquire for reproduction given that there are no competitors present, and $g_1 (r, N)$ represents the proportion of food actually acquired for reproduction as a result of an individual's competitive ability (r) and the number of competitors (N). This function decreases as either an individual's competitive ability decreases or as population size increases.

For an animal living in a group, the number of offspring that it can produce during the interval x to $x + 1$ is:

$$M_{xG} = m_{xg} = \beta_x \cdot \gamma_x \cdot g_1 (r, N) \cdot g_2(N)$$

where $g_2(N)$ represents the proportion of food eaten as the result of beneficial effects of neighbors. This function increases monotonically as group size increases.

Thus, in general, an animal aged x living in a group will have a fitness of

$$V_{xG} = V_{xg} = \alpha_x \cdot f_2 (C_G(N), D_G(N)) \cdot \beta_x \cdot \gamma_x \cdot g_1 (r, N) \cdot g_2(N)$$

whereas an equally old individual living alone will have a fitness of

$$V_{xR} = V_{xr} = \alpha_x \cdot f_1 (C_i(N), D_i (N)) \cdot \beta_x \cdot \gamma_x \cdot g_1 (r, N)$$

In order to predict which strategy an animal should choose, one must calculate fitness values for each strategy. Therefore, specific functions for $f_1 (\cdot)$, $f_2 (\cdot)$ $g_1 (\cdot)$, and $g_2 (\cdot)$ must be derived. The following $g_1 (\cdot)$ and $g_2 (\cdot)$ functions were chosen because they are simple and because the parameters governing their shape are sensitive to ecological consideration; functions based on physiological considerations would have been selected had enough data been available.

The maximum number of prey that are potentially supportable by a habitat is ultimately determined by the total amount of energy available in the habitat. If no competition occurred between members of the population, then each individual would be capable of acquiring the maximum amount of energy for reproduction (γ_x). As a result, only $N = T/\gamma_x$ individuals could coexist in the habitat. (T represents the total amount of available energy in the habitat.) Even if an inequitable distribution of resources occurred because of competition, it is assumed for the purposes of this model that the habitat can still support only N individuals. The excess energy is either lost through aggression or used by subordinate individuals to meet increased maintenance costs associated with increased levels of stress. Thus, with the size of the population fixed by external conditions, the negative effects of competition depend only on an animal's competitive ability (rank for animals in a group), the size of the population, and the level of competitive inequality that exists among the individuals in the population. One of the simplest functions incorporating these considerations is

$$g_1 = 1 - [(r - 1)/N]^a$$

where r stands for an individual's rank (competitive ability), N stands for the size of the population, and a is a coefficient that reflects the magnitude of competitive inequality in the population ($0 < a < \infty$). For example, when $a = 1$, the proportion of γ_x that an animal receives decreases linearly as its rank decreases (increase in r). When $a < 1$, the inequality in resource distribution is accentuated and the relationship becomes concave. Conversely, when $a > 1$, the inequality in resource distribution is diminished and the relationship becomes convex. An important property of the function is that for animals living in a group, even if animals are of equivalent rank, it takes on different values depending on the size of the group. For example, given two animals of equal rank, the one living in the smaller group will receive a greater proportion of γ_x than the one living in the larger group. Thus, regardless of competitive ability, this function indicates that animals do worse in large groups, where competition is more intense.

For animals living in groups, the presence of neighbors often enhances an individual's feeding success. The simplest increasing function that accounts for this effect is

$$g_2 = 1 + [b(N - 1)^c]$$

where b and c are parameters that govern the shape of this relationship. Values of b and c can range from ($0 <$ b or c, < 1); when b is small, increasing the number of neighbors (N) enhances feeding success very little. When c is also small, this effect is reduced even further, especially at larger group sizes.

The parameters a, b, and c can take on values that reflect a variety of environmental situations. For example, the value of parameter a could be increased to reflect increasing similarity in the competitive abilities of group members or an increasingly even distribution of food resources. In both cases, the higher value of parameter *a* would simulate a lower level of competitive inequality among the members of the group. Similarly, the values of parameters *b* and *c* could be increased to reflect increasingly concentrated or more patchily distributed food resources. In either case, higher values of the parameters would simulate greater feeding benefits to be derived from neighbors. This flexibility of the model's parameters provides a means of interpreting how various attributes of the resource under contention affect an individual's decision to live alone or in a group.

Because Treisman (1975a) provided realistic functions describing a prey's probability of being killed by a predator, I have modified them slightly so that they can serve as the $f_1(\cdot)$ and $f_2(\cdot)$ functions.

Treisman (1975a) proposed that the probability of a solitary prey animal's detecting a predator is $D_i = zA_i + P_f$, where z is a coefficient, A_i is the area of an object (e.g., a predator), and P_f is the probability of the prey's mistakenly detecting a predator when none is present. Similarly, he proposed that $C_i = zA_i + P_f$ is the probability of a predator's detecting a solitary prey. When N prey are present in the habitat, the probability of the predator's detecting at least one of the prey animals becomes

$$C_R = 1 - (1 - C_i)^N$$

which is one minus the probability of the predator's not detecting any prey. The probability of the predator's killing at least one prey animal is

$$K_{NR} = 1 - (1 - K_R)^N$$

where K_R is the per capita probability of a prey animal's being killed. In turn

$$K_R = \frac{(C_R/N)(1 - D_i)}{(C_R/N)(1 - D_i) + D_i}$$

where C_R/N is an individual's risk of being discovered. Thus, the probability of any individual's not being killed by a predator on any given search of the habitat is

$$f_1 = 1 - K_{NR}$$

If we can assume that a prey animal's risk of being killed on a particular search is indicative of its risk of being killed during the interval x to $x + 1$, then the probability that an animal that lives alone will survive from age x to age $x + 1$ is

$$P_{xR} = p_{xr} = \alpha_x \cdot (1 - K_{NR})$$

Animals in groups benefit from the scanning behavior of neighbors. As a result, the probability that an individual living in a group will detect a predator is

$$D_G = 1 - (1 - D_i)^{N \cdot a'}$$

where a' is a parameter that governs the actual number of individuals scanning for the predator ($a' = \min(a, 1)$). The value of parameter a' depends on the value of parameter a because it is assumed that animals receiving few resources either make ineffective lookouts or disturb otherwise competent lookouts. Thus, when the inequalities in competitive payoffs are severe (low values of parameter a), the number of effective watchers in a group will be small (low values of parameter a').

Because a group presents a larger area to a predator, the probability of its detecting a group is $C_G = z \min(NA_i, X) + P_f$, where X represents a threshold after which further increases in area no longer increase a predator's detection abilities. The probability that a predator will kill a prey animal living in a group during a scan is

$$K_G = \frac{C_G(1 - D_G)}{C_G(1 - D_G) + D_G}$$

Hence, the probability that a prey animal that lives in a group will not be killed is $f_2 = (1 - K_G)$. Its chances of living from age x to age $x + 1$ are

$$P_{xG} = P_{xg} = \alpha_x \cdot (1 - K_G)$$

For animals playing the social game based on the above functions, the fitness of an individual living in a group is

$$V_{xG} = V_{xg} = \alpha_x \cdot (1 - K_G) \cdot \beta_x \cdot \gamma_x \cdot (1 - [(r - 1)/N]^a) \cdot b(N)^c$$

whereas for an individual living alone it is

$$V_{xR} = V_{xr} = \alpha_x \cdot (1 - K_{NR}) \cdot \beta_x \cdot \gamma_x \cdot (1 - [(r - 1)/N]^a)$$

For the following simulations, let us assume that competition for resources is sometimes more intense among animals in groups than among solitary animals. This assumption is not unreasonable because animals in groups experience both exploitation and interference competition, whereas animals randomly dispersed (no territoriality) and separated by large distances are less likely to experience interference competition. Therefore, the values of parameter a for animals living in a group should be less than or equal to the values of a for prey distributed randomly throughout the habitat. Also, let us assume that animals living alone are less able to assess each other's competitive ability than animals living in a group. Therefore, as a first approximation, an animal leaving a group will do so with the "expectation" of deriving the benefits of the "average" solitary individual.

The results of simulations in which the parameters *a*, *b*, and *c* were varied are shown in Figs. 1–4. Each figure depicts fitness (V_x) as a function of population size. A solid isocline shows how the fitness of equally ranked individuals changes as the group size changes. The bottom of the hatched area shows how the fitness of an "average" ($r = 0.5\ N$) solitary individual changes as the number of animals living alone changes. The top of the hatched area similarly depicts the fitness changes of the "best" solitary competitor.

In all the simulations, fitness of group members varies according to rank. Not surprisingly, the magnitude of these fitness differences reflects the level of competitive inequality. When the intensity of competition is high (Fig. 1), the difference in the fitness of the dominant and most subordinate individual is larger than when the level of competitive inequality is low (Fig. 2).

Regardless of environmental conditions, the dominant individual always derives a higher fitness by being in a group of *N* individuals than by living alone as 1 of *N* randomly dispersed individuals. Thus, based on this specific form of the model, Strategy 3 (where the dominant lives alone and the subordinate lives in a group) and Strategy 4 (where both the dominant and subordinate live alone) of the social game cannot be evolutionarily stable.

The simulations reveal that the best strategy for a subordinate individual, given that the dominant lives in a group, does depend, however, on a number of environmental considerations. For example, when the visibility of the habitat is low, the level of competitive inequality among group members is high, the beneficial affects of neighbors is small (Fig. 1), and the habitat can support only 9 or fewer individuals, then the most subordinate individual in the group is always better off as 1 of 9 or fewer randomly dispersed individuals. As a result, it should leave the group. If the habitat can support more than 9 individuals, each individual by living in a group will receive a higher fitness than by living as one of 10 or more solitary individuals. But this comparison is somewhat misleading. Imagine that the habitat can support only 10 individuals; then, if the most subordinate individual were to leave the group and become the lone solitary individual, it could derive a large increase in its fitness. On the basis of this comparison, the most subordinate individual should leave the group. Should the 9th-ranking individual also leave the group? It should do so only if its fitness, as 1 of only 2 solitary individuals, will be higher than its fitness will be if it remains in a group of 9. Based on the assumption that an animal's percentile rank does not change when poorer competitors leave the group, we could sight along the 90th percentile isocline and determine what its fitness would be in a group of 9 individuals ($V_x = 0.24$) and then compare this value with the fitness of an "average" solitary individual ($V_x = 2.94$) belonging to a population consisting of 2 individuals. In this case, it appears that the 9th-ranking member should also leave the group. By the time the 6th member is faced with the choice of leaving the group, the payoffs have changed, so that it should leave the group if it could be 1 of only 4 randomly dispersed individuals. But if the 6th individual left the group, it would be 1 of 5 randomly dispersed individuals ($V_x = 0.52$), and under these circumstances, it should remain in the group, where its fitness is higher ($V_x = 0.76$). Thus, under the conditions of this simulation, for a habitat able to support 10 individuals, 6 would live in a group and 4 would live alone.

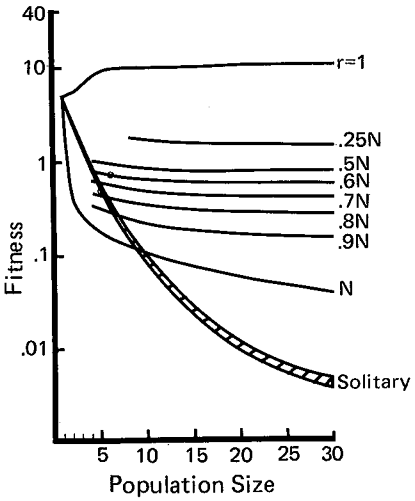

Fig. 1

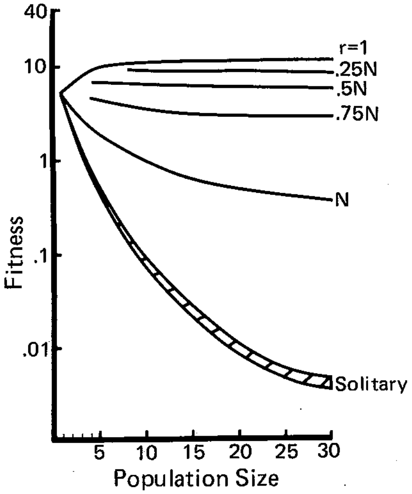

Fig. 2

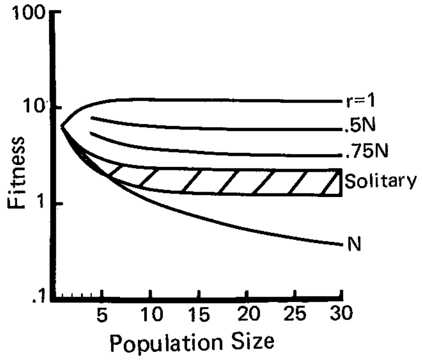

Fig. 3

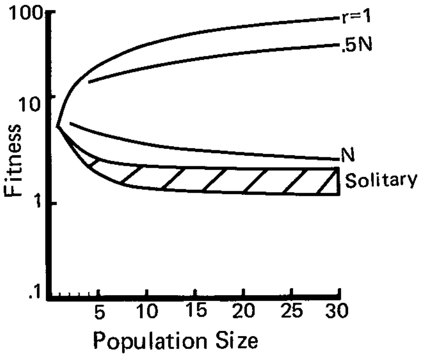

Fig. 4

An interesting phenomenon occurs as the quality of the habitat increases and it is able to support more animals. For example, when the habitat can support 20 individuals, only the 5 lowest-ranking individuals would be induced to leave the group (Fig. 1). Thus, when food abundance increases in a habitat, a smaller percentage of the group will leave. Even though animals of equal percentile ranks get proportionately less of γ_x as the size of the group increases, the benefits of collective predator defense increase disproportionately as group size increases. Therefore, as the size of a group increases, its members find remaining in the group more profitable than living alone.

←

Fig. 1. Relationship between the expected fitness of an individual and the size of the population, given that the visibility of the habitat is low ($C_i = D_i = 0.1$; $C_G = 0.8$), that the level of competitive inequality among members in a group is much more severe ($a = 0.1$) than among randomly dispersed individuals ($a = 2$), that the beneficial effects of neighbors are small ($b = c = 0.1$), and that $\alpha_x = 1$, $\beta_x = 0.1$, and $\gamma_x = 100$. The hatched area depicts the expected fitness of an animal aged x living alone as one of the N randomly dispersed individuals in the population; the bottom line reveals the expected fitness of the "average" solitary individual, whereas the top line reveals the expected fitness of the solitary individual that is the best competitor. The solid isoclines depict the expected fitness of an animal aged x living in a group. Each isocline connects the expected fitness of an animal of a given rank but living in groups of different sizes. The most dominant animal's fitness isocline is labeled $r = 1$, whereas the most subordinate is labeled N. The other isoclines correspond to animals in the 90th percentile ($0.9N$), the 80th percentile ($0.8N$), and so on. If we assume that the habitat can only support 10 individuals and all are originally arranged in a group, the open circles show that the expected fitness of the sixth ranking individual would be higher if it remained as the sixth ranked individual in a group of six than if it left the group and lived as one of five randomly dispersed individuals. See the text for a more complete description, but for this case, six individuals will live in a group and four will live randomly dispersed about the habitat.

Fig. 2. Relationship between the expected fitness of an individual and the size of the population, given that the visibility of the habitat is low ($C_i = D_i = 0.1$; $C_G = 0.8$), that the level of competitive inequality among members of a group is only slightly more severe ($a = 1$) than among solitary individuals ($a = 2$), that the beneficial effects of neighbors are small ($b = c = 0.1$), and that $\alpha_x = 1$, $\beta_x = 0.1$, and $\gamma_x = 100$. The hatched area depicts the expected fitness of animals living alone, and the solid isoclines depict the expected fitness of animals by rank living in a group.

Fig. 3. Relationship between the expected fitness of an individual and the size of the population, given that the visibility of the habitat is high ($C_i = D_i = 0.4$; $C_G = 0.8$), that animals living alone or in a group experience the same level of competitive inequality ($a = 1$), that the beneficial effects of neighbors are low ($b = c = 0.1$) and that $\alpha_x = 1$, $\beta_x = 0.1$, and $\gamma_x = 100$. The hatched area depicts the expected fitness of animals living alone, and the solid isoclines depict the expected fitness of animals by rank living in a group.

Fig. 4. Relationship between the expected fitness of an individual and the size of the population, given that the visibility of the habitat is high ($C_i = D_i = 0.4$; $C_G = 0.8$), that animals living alone or in a group experience the same level of competitive inequality ($a = 1$), that the beneficial effects of neighbors are high ($b = c = 0.7$) and that $\alpha_x = 1$, $\beta_x = 0.1$, and $\gamma_x = 100$. The hatched area depicts the expected fitness of animals living alone, and the solid isoclines depict the expected fitness of animals by ranking living in a group.

As the level of competitive inequality is reduced (Fig. 2), regardless of the carrying capacity of the habitat, a greater percentage of individuals will live in groups. For example, if the habitat can support 10 individuals, only the bottom 2 will be induced to leave the group. The 8th-ranking individual should not leave the group because it could raise its fitness by living alone only if it could be 1 of 2 randomly dispersed individuals. But if it leaves the group, it will be 1 of 3 randomly dispersed individuals. Thus, it appears that as differences in ability among individuals decrease or as evenness of the resource distribution increases, larger groups will form.

It is interesting to note that as the parameter *a* increases in value, the fitness of all percentile levels increases. In part, this increase results from the fact that the percentage of effective watches increases (a' increases as well), but because the percentage of changes in fitness is inversely correlated with rank, the effects of competition should not be ignored.

In more open habitats, where both the predator and the prey are more likely to detect each other (see Figs. 3 and 4), some interesting changes in behavior occur.

If an open habitat can support only 5 or fewer individuals and the level of competitive inequality among individuals is the same for individuals living either alone or in a group, then each individual will do better living in a group as opposed to living as 1 of 5 or fewer solitary animals (Fig. 3). As before, however, this comparison is somewhat misleading. For example, if a habitat can support 10 individuals (Fig. 3), only the bottom 3 individuals will be induced to leave the group. By comparison, in the previous example (Fig. 2), in which parameter *a* also equaled 1, only 2 members of a group of 10 were induced to leave the group. Thus, it appears that as habitat visibility improves, the size of the groups residing there will be smaller because in open habitats, the advantages of many eyes' assisting in detecting a predator is diminished. Thus, as long as competition among individuals in a group is at least as severe as that among solitary individuals, the relative risks of living alone decrease in more open habitats.

When the presence of neighbors greatly enhances an individual's feeding success, then there are habitat carrying capacities at which it always pays for all animals, regardless of rank, to live in a group. For example, under the conditions of the simulation depicted in Fig. 4, if the habitat can support only 2 individuals (actually almost 3 individuals), each individual will derive its highest fitness by living in a group. For a habitat capable of supporting 10 individuals, only the most subordinate individual will derive a higher fitness by living alone. Thus, it appears that habitats in which the beneficial affects of neighbors are large, even if the benefits associated with collective predator detection are small, will be populated by large groups. (This effect would be attenuated somewhat if the level of competitive inequality were increased.)

Thus, for any given set of conditions, either Strategy 1 (both dominant and subordinate live in a group) or Strategy 2 (the dominant lives in a group and the subordinate lives alone) will be evolutionarily stable. But which of these two strategies an animal chooses will depend on its rank in the group. As external conditions change, or as the animal's competitive ability changes, it is likely that its choice of an evolutionary stable strategy will also change. The more dominant an individual, the more likely it is to live in a group, regardless of environmental conditions. The more subordinate an individual, however, the more likely it is to remain in a group when the visibility of the habitat is low, when the level of competitive inequality among group members is low, when the carrying capacity of the habitat is high, and when the presence of neighbors greatly enhances its feeding success.

VI. DISCUSSION AND CONCLUSIONS

We have seen that ethologists have made great strides toward formulating a predictive theory of social organization. Speculative explanations as to how the forces of predation and foraging considerations operate to influence the formation of a social system have been replaced by mathematical formulations. These formulations, which are based on biological principles, have generated many insights into why and under what environmental conditions groups could form. These formulations have also provided insights into what attributes best adapt individuals for particular types of social systems.

Whereas mathematical models were originally used to investigate the effects of predation or the effects of foraging demands, they are now beginning to be used to study the combined action of predation and foraging. In the social game model, general fitness functions, based on aspects of predatory and competitive behavior, are used to predict when and under what circumstances an animal should either live alone or live in a group. The importance of rank (competitive ability) is clearly demonstrated: under certain conditions subordinate individuals could acquire a higher fitness by leaving the group. Because many factors—such as age, size, sex, and past experience—influence competitive ability, this model provides a means of examining many dynamics of social behavior. For example, because competitive ability changes with age, the model predicts that animals of certain ages should temporarily abandon living in groups. In fact, additional insights into the importance of age effects can be derived if one simply allows the age-specific parameters, α_x, β_x, and γ_x, to vary.

Although this model investigates some new facets of the social organization problem, it leaves many untouched. For example, it makes no provision for the possibility that subordinate animals that leave the group might derive a higher fitness by forming a new group rather than by remaining totally solitary. This omission could be rectified if one increases the number of strategies to account for a variety of dispersion patterns and incorporates the effects of intergroup competition into the general fitness functions.

More importantly, however, this model excludes considerations of inclusive fitness (Hamilton, 1964) from the general fitness functions. Certainly, groups consisting of closely related individuals display a much lower level of competitive inequality. As a result, subordinate individuals would be less likely to leave such a group. But other, more subtle complications of inclusive fitness could arise. Imagine two daughters' being induced by fitness considerations to leave the group. It is possible that the mother might follow them, and by joining them in a triad, she might lower their risk of predation and thus increase her inclusive fitness. And, in fact, group size and inclusive fitness could create even greater complications (cf. Charnov, 1977).

The model also ignores some potentially important ecological considerations. For example, the effects of interspecific competition are normally considered less intense than the effects of intraspecific competition and, as a result, have been ignored in investigations of patterns of social organization. The presence of a competitor species (Species B), however, could indirectly have two major effects on the species under consideration (Species A): (1) the presence of competitor species B could lower the effective resource level of the habitat, and (2) it could drastically alter the predation pressures on Species A.

The change in predation pressure that could result from the presence of a competitor Species B might occur in a complex fashion. If the competitor Species B is abundant and is being disproportionately consumed by the predator, then Species A would experience a low level of predation intensity. But the fitness payoffs to Species A associated with this level of predation could change dramatically; after reducing the abundance of the competitor Species B, the predator might disproportionately concentrate its attack on Species A. Then, in a while, after decimating Species A, it might again switch its feeding preference to competitor Species B, or it might even leave the habitat completely. In either event, the intensity of predation suffered by Species A would again be low. The importance of interspecific competition, therefore, depends on the frequency and the predictability of the predator's switching behavior. If many such oscillations in its behavior occur during the time interval during which the fitness of an individual of Species A is being estimated, then the model would be too simplistic and would make unrealistic predictions concerning an individual's decision to live alone or in a group. The extent to which this phenomenon is important in influencing patterns of social organization is yet to be determined.

I dwell on this particular consideration only to stress that although great strides have been made toward the formation of a predictive theory of social organization, much more work is needed. In the past, ethologists have ignored subtle ecological influences such as this one. But just as interest in sociality continues to grow, the scope of the investigation must also broaden.

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VIII. APPENDIX—GLOSSARY OF TERMS

A_i = area of an object

a = parameter reflecting level of competitive inequality

a' = parameter reflecting the proportion of competent predator lookouts

b = parameter reflecting the level of feeding enhancement

C_i = probability of a predator's detecting solitary prey

C_G = probability of a predator's detecting a group of prey

c = parameter reflecting the level of feeding enhancement

D_i = probability of solitary prey's detecting a predator

D_G = probability of a group of prey's detecting a predator

K_G = probability of predator's killing a prey living in a group

K_{NR} = probability of predator's killing at least 1 randomly scattered prey

K_R = per capita probability of a randomly scattered prey's being killed

min (x, y) = y or x, whichever is least

m_x = number of offspring produced during the time interval x to $x + 1$. (M_x = the fecundity of dominants; m_x = the fecundity of subordinates; M_{xG} or m_{xg} = the fecundity of dominant or subordinate in a group; M_{xR} or m_{xr} = the fecundity of solitary animals)

N = population size

P_f = probability of prey's mistakenly detecting a predator or of predator's mistakenly detecting a prey

P_x = probability of surviving from age x to age $x + 1$ (P_x = probability of dominant's surviving; p_x = probability of subordinate's surviving; P_{xG} or p_{xg} = probability of dominant or subordinate's surviving in a group; P_{xR} or p_{xr} = probability of dominant or subordinate's surviving as solitary animals)

r = competitive ability or rank

T = total amount of energy available in habitat

$V_{..}$ = fitness

V_x = fitness of an animal during interval x to $x + 1$

X_i = threshold past which increases in area no longer increase ability to detect an object

x = an animal's age

z = a coefficient

α_x = probability that an animal aged x will live to age $x + 1$ given that there are no predators in the habitat

β_x = conversion factor representing the ability of an animal aged x to convert calories into offspring

γ_x = maximum amount of calories that an animal aged x can acquire for reproduction, given that no competitors are present

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