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— GAIL R. POOL

## GROUP LIVING

Chances are that you see groups of animals every day. A flock of birds surrounding a rubbish bin, mosquitoes buzzing in a mating swarm, a pack of dogs running down the street, and worker ants marching along a pheromonal trail are all examples of animal groups. Groups are aggregations of individuals that range in size from a few to thousands, and include both relatively stable and ephemeral aggregations. This diversity in size and permanence makes the study of the evolution of grouping behavior a challenge, but several themes emerge from the contemporary literature. All involve quantifying the costs and benefits of aggregation as well as identifying constraints that may prevent individuals from living alone.

Aggregation often involves active decisions made by animals, but it also may occur passively. Consider the case of planktonic larvae, which are distributed by oceanic or tidal currents. Although such aggregations require no additional explanation, they offer the opportunity for more complex social relationships within them. The benefits for acquiring food and reducing the risk of predation are the most common explanations for group living, whereas increased competition, reproductive suppression, and the increased risk of parasite or disease transmission are commonly cited costs.

Animals may aggregate around important resources. For example, patches of food may attract individuals of one or more species and create ephemeral foraging aggregations. Group members need not be related, nor even of the same species, to forage together on an important resource. Group size will be limited by the amount and defensibility of the food and by the presence of other known patches of food: larger groups will be seen around larger patches, and less defensible food (such as widely scattered seeds) will support larger groups than the same amount of food distributed in a defensible patch. In some cases, animals may distribute themselves according to the ideal free distribution, where food intake (and presumably fitness) is equivalent among all patches. [*See* Ideal Free Distribution.]

Competition and dominance relationships may make it less profitable for some individual to remain in a group. Dominant or "despotic" individuals—those that restrict free access to resources—increase the cost of remaining in a group for subordinates and, if dominants successfully defend resources, illustrate one reason why observed group sizes may not fit an ideal free distribution. In more permanent social groups, kinship may have an important effect on the relationship between despotism, which leads to biased fitness, and the benefits of sociality. Relatives, who can potentially gain indirect reproductive success by helping raise kin, should be more likely to reside in despotic groups than nonrelatives, who can gain direct fitness only by rearing their own offspring.

The payoffs of being in a group of a particular size vary depending on whether an individual is in the group or trying to join the group. If being in a group is beneficial, nongroup members will gain fitness by joining, even if the fitness of already-present members is reduced by the addition of another individual. Such "insider–outsider" conflicts remain to be better understood, but they may explain why group sizes are often larger than what is seemingly optimal.

There are other benefits from foraging in groups. Specifically, groups of insectivorous or carnivorous animals may flush more prey and have greater foraging success compared to solitary individuals. Such activity need not be highly coordinated, but group hunting, as reported in some social carnivores, involves the coordinated movement and behavior of several individuals (see Vignette). Additionally, group living may facilitate food finding for group members either through information centers (aggregations where information about the location of food is exchanged) or through more simple direct observations of the foraging success of others.

Conspecifics may form ephemeral aggregations around no identifiable resource. For example, males of lekking species (e.g., mosquitoes) aggregate and await visits by females, whereupon males will display and attempt to mate. [*See* Leks.]

Individuals may aggregate to reduce the risk of predation. Such antipredator benefits of aggregation may be obtained several ways.

Predation risk is "diluted" in larger groups because there are alternative prey. Assuming a predator will kill only one individual, the risk of predation declines with the addition of each individual and quickly asymptotes. Other functional relationships are possible, and the benefit may remain if predators take more than one individual. Marlin attacking tightly clumped schools of small fish kill many fish, but a solitary fish would make an easy target and the prey would continue to group despite ongoing attacks.

Animals in groups should have a greater ability to detect predators. Detecting predators with sufficient time to escape is a challenge many species face, and the presence of more eyes (and ears) to detect predators may be directly translated into survival.

Both detection and dilution models predict that individuals will allocate less time to antipredator vigilance and more time to foraging, as group size increases. These changes in time allocation are widely reported in birds and mammals. Scramble competition for a finite resource in which individuals forage more because competition increases with group size could produce a similar group size effect.

Assuming the case of antipredator vigilance, a question arises about whether animals modify their vigilance simply because other individuals are present or in response to the vigilance patterns of others. The original models assumed that there was perfect information transfer from the individual first detecting a predator and the rest of the group. Without perfect information, animals detecting predators may be safer than those relying on the information from others. Recent studies have questioned this assumption of perfect information transfer on both theoretical and empirical grounds and suggest that antipredator benefits are not likely to rely on "collective detection," and that the conceptually simple distinction between detection and dilution may be more complex and interrelated than originally envisioned.

Within a group, an individual's position with respect to others and the edge may affect predation risk. Centrally located animals are generally considered to be relatively safer, but this need not always be so. Predators can be viewed as being surrounded by a "zone of danger"—individuals within this zone of danger are likely to be killed. Fast-moving, agile predators (e.g., some raptors) may have a relatively large zone of danger, and centrally located individuals may be no safer than peripheral ones.

Groups of animals may be more effective at deterring predators or of warning conspecifics about predation risk. Nesting colonial birds mob both aerial and terrestrial predators in or around the colony. Such communal defense, whether coordinated or not, may reduce the likelihood of predation or nest predation for all group members. Animals in groups may emit special signals designed to warn conspecifics about the risk of predation. [*See* Alarm Calls.]

### COOPERATIVE HUNTING IN SOCIAL CARNIVORES

There has been some controversy over the reasons large social carnivores form groups. Early analyses focused on the conspicuous and coordinated communal hunting seen in lions and wild dogs. Subsequent detailed analyses of the benefits of group hunting success in lions found that the per capita food intake was the lowest at the most common group size, seemingly refuting this obvious hypothesis. However, per capita intake ignores the costs of pursuing and capturing prey, which may be substantial in species that chase their prey over long distances. More recently, detailed studies of both the costs and the benefits of group hunting in wild dogs suggested that group members increased the amount of food acquired each day *per* kilometer they chased prey, and that viewed this way, wild dogs live in nearly optimally sized groups.

—Daniel T. Blumstein

Animals may aggregate for energetic benefits not directly related to food. Breeding male emperor penguins huddle together through the long Antarctic winter and move, in a more or less continuous trudge, from the colder periphery to the center of the group, and out again. Solitary penguins would freeze to death. Studies of alpine marmots have demonstrated that these hibernating rodents increase their chance of overwinter survival by hibernating socially in groups.

Perhaps the most interesting groups are those with more stable aggregations, for it is in these groups that animals often engage in apparently altruistic behavior, and some significant costs of sociality emerge. [*See* Social Evolution.] Stable groups include a remarkable variety of mating and spacing systems, which range from colonies of more or less solitary ground squirrels living in patchy habitat, to nesting birds that may engage in communal nest defense, to complex communal societies characterized by individuals' delaying dispersal from their natal group, having specific behavioral roles, and illustrating reproductive skew (i.e., not all individuals within the group breed), and to the truly eusocial Hymenoptera and thrips, with their fixed social castes. [*See* Eusociality, *article on* Eusociality in Mammals.]

Understanding the occurrence and dynamics of these more permanent and complex groups also generates the new problem of disentangling evolutionary origin from maintenance. [*See* Adaptation.] When the net benefit of remaining in more ephemeral groups changes, we expect individuals to behave in dynamic ways so as to maximize their fitness. However, some constraints may both foster the formation of more permanent societies and reduce or eliminate options for their residents. For example, sociality in ground-dwelling sciurid rodents (squirrels, prairie dogs, and marmots) is largely explained by their inability to reach adult body size in their first year of life. Females of relatively small species that mature quickly can disperse and reproduce independently. Some of these species live in colonies containing many breeding females. In contrast, the larger-bodied marmots are unable to mature in their first year of life and social groups (groups of animals that interact with each other and share a home range and burrows) contain litters from one or more years. Despotic breeders may suppress reproduction of their offspring, but related nonbreeders help thermoregulate their nondescendant kin and obtain an indirect fitness payoff for doing so.

Colonial life has other costs. Pathogens and parasites are likely to pass easily between individuals living in large colonies as seen in both black-tailed prairie dogs and bank swallows, where individuals in larger groups have more ectoparasites. Studies of the highly colonial bank swallow also illustrate the competitive costs associated with sociality: competition for nesting material and sites is greater in larger colonies, and animals interfere with each other more than is seen in less social species. And, even though animals may aggregate to reduce predation risk, studies of colonially nesting birds demonstrate that predator attack rates increase in highly conspicuous nesting colonies. Interestingly, this greater attack rate is offset by the collective defense and predator mobbing often seen in colonially nesting birds.

[*See also* Cooperation; Optimality Theory, *article on* Optimal Foraging; Reciprocal Altruism.]

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## GROUP SELECTION

Throughout the history of biology, higher-level units such as social groups, species, and ecosystems have been described as well adapted to their environments in the same sense that individual organisms are well adapted. However, the process of natural selection does not automatically evolve adaptations at all levels of the biological hierarchy. Consider an individual-level adaptation such as cryptic coloration in birds. Individual birds vary in the degree to which they can be seen against their background, and in every generation the most conspicuous individuals are removed by predators. If phenotypic variation is heritable, individuals will evolve to be more cryptic over time. Now consider a social adaptation such as members of a bird flock warning each other about approaching predators. It is not obvious that callers will survive and reproduce better than noncallers. If uttering a cry attracts the attention of the predator, then callers place themselves at risk by warning others. In general, groups function best when members provide benefits to one another, but it is difficult to translate this kind of social organization into the currency of relative fitness upon which natural selection is based.

Darwin (1871) was aware of this problem and proposed a solution. Suppose there is not just one flock of birds but many flocks. Furthermore, suppose that the flocks vary in their proportion of callers. Even if a caller does not have a fitness advantage within its own flock, groups of callers will be more successful than groups of noncallers. In short, Darwin imagined a process of natural selection among groups in addition to a process of natural selection among individuals within groups. Groups can evolve into adaptive units, but only if there is a process of group-level selection that is stronger than the often opposing process of individual-level selection. This was the origin of an approach to evolutionary biology called multilevel selection theory (reviewed by Sober and Wilson, 1998). The general rule that emerges