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Animal Society

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Synonyms

Complex group

Definition

Cooperative group living.

What Is an Animal Society?

Many animals form groups, either ephemerally or permanently, including schools of fish, colonies of seabirds, or herds of ungulates. However, many fewer species form more complex social groups that are often referred to as societies (Fig. 1). Defining a "society" is a difficult task because the term has different meanings to researchers in different fields. For example, the most advanced animal societies – eusocial insect societies – are defined by three criteria: (1) overlapping generations, (2) cooperative care of young, and (3) reproductive division of labor (i.e., many individuals in a group are temporarily or permanently sterile) (Wilson 1971). Yet, many cooperatively breeding vertebrate societies are also described by the same three criteria (Sherman et al. 1995). Despite many structural similarities, there are key differences between insect and vertebrate societies, the most important being that vertebrate societies lack permanently sterile individuals that aid in cooperative care of young and other tasks. Instead, nonbreeding "helpers" in most vertebrate species maintain the ability to reproduce, and often do so, later in life. In contrast, nonbreeding "workers" in most eusocial insects are not only sterile, but often morphologically and behaviorally distinct as well. Perhaps, then, the simplest definition of society, and one that encompasses vertebrates, insects, and other invertebrate species that form complex groups, is: cooperative group living (Rubenstein and Abbot 2017).

The Evolution of Animal Society

Whether in insects or vertebrates, animal societies are quite rare; less than 10% of birds, roughly 5% of mammals, and less than 2% of insects form societies. Most of these animal societies consist of kin (in other words, they are family groups), though this is not a prerequisite for complex groups characterized by cooperation. However, interacting repeatedly with kin is important because it makes cooperation and altruism more likely to evolve. Indeed, William D. Hamilton's classic work on inclusive fitness (both the direct

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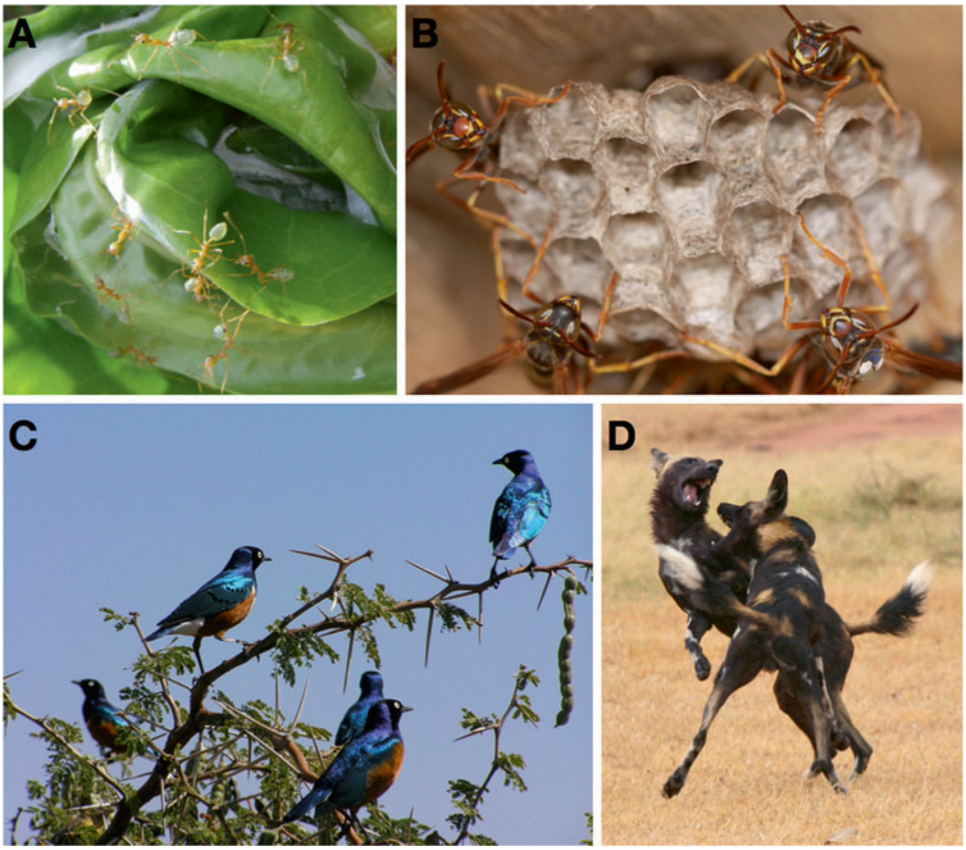

Animal Society, Fig. 1 A variety of insects (including the (**a**) ant *Oecophylla smaragdina* [© C. Moreau] and (**b**) wasp *Polistes fuscatus* [© E. Tibbetts]) and vertebrates (including the (**c**) superb starling *Lamprotornis superbus* [© D. Rubenstein] and (**d**) African wild dog *Lycaon pictus* [© D. Rubenstein]) form societies characterized by cooperative group living. In these and many other species, groups are comprised of primarily related individuals.

fitness benefits of reproducing and the indirect fitness benefits of cooperating to raise relatives) and the evolution of altruism set the stage for studies of animal societies (Hamilton 1964). Inclusive fitness theory is an explicit framework that governs the evolution of social traits, irrespective of taxonomy (Bourke 2011). According to Hamilton's Rule, a social action will be favored when its positive effect on indirect fitness is greater than its direct fitness cost: $rb > c$, or the product of the relatedness (r) between two individuals and the fitness benefit (b) an individual receives from the action valued against the fitness cost (c) to the individual expressing the action.

Hamilton's Rule has long formed the basis of how researchers approach studying animal societies and social evolution more broadly. Recognizing the importance of relatedness (r) in Hamilton's Rule, John Maynard Smith called the idea kin selection theory (Maynard Smith 1964). The central role of kin selection in promoting the evolution and maintenance of animal societies and cooperation more broadly has subsequently been demonstrated experimentally in numerous species of organisms ranging from wasps, to birds, to slime molds. Indeed, animal societies are most likely to form in species where the relatedness between parents and offspring is high because this ensures that the indirect genetic benefits gained by cooperating to raise kin are greater (Boomsma 2007). In other words, relatedness among group members (termed kin structure) is central to the formation of animal societies.

Although kin structure is important in the evolution of animal societies, relatedness is just one term in Hamilton's rule. The ratio of the costs and benefits of cooperating to raise others' young also influences whether altruism and animal societies will evolve. In most animal systems, the primary factor that influences the fitness costs and benefits of cooperative care of young is ecology. Ecology can constrain the ability of young to disperse and attempt to breed independently, thus promoting the formation of family groups and the adoption of cooperative rearing of kin (Emlen 1982). Additionally, the costs of rearing young in harsh and unpredictable environments can favor the formation of animal societies because additional caregivers may be needed to successfully rear young when conditions are bad (Shen et al. 2017).

Thus, just as Hamilton pointed out (Hamilton 1964), to understand the evolution of animal societies, one must jointly consider the interaction between relatedness and the factors (typically ecological) that shape reproductive decisions and fitness outcomes. From an individual perspective, young must decide whether to disperse and attempt to breed independently, or remain at home and help raise others' (typically kin) offspring. In vertebrates, these young individuals maintain the ability to reproduce no matter which decision they make. Even in some insect species like wasps (Fig. 1), individuals must make the decision to try and breed independently, or to remain at home and cooperate with relatives while sharing reproductive duties.

Conclusion

Although species that form cooperative groups are quite rare, societies in a range of animal taxa share many characteristics, including overlapping generations, cooperative care of young, and reproductive division of labor, where many individuals in a group are temporarily or permanently sterile. Indeed, societies in vertebrates and invertebrates are not only structurally similar, but they are also shaped by the same forces. Hamilton's Rule ($rb > c$) describes how altruism, such as cooperative care of young and reproductive division of labor, could evolve within a society. Indeed, kin structure and relatedness between group mates, as well the role that ecology and the environment plays in shaping the reproductive costs and benefits associated with altruism, influence the formation of societies in insects and vertebrates alike.

References

Boomsma, J. J. (2007). Kin selection vs. sexual selection: Why the ends do not meet. *Current Biology, 17*, R673–R683.

Bourke, A. F. G. (2011). *Principles of social evolution*. Oxford: Oxford University Press.

Emlen, S. T. (1982). The evolution of helping. 1. An ecological constraints model. *The American Naturalist, 119*, 29–39.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I and II. *Journal of Theoretical Biology, 7*, 1–52.

Maynard Smith, J. (1964). Group selection and kin selection. *Nature, 201*(4924), 1145–1147.

Rubenstein, D. R., & Abbot, P. (Eds.). (2017). *Comparative social evolution*. Cambridge: Cambridge University Press.

Shen, S.-F., Emlen, S. T., Koenig, W. D., & Rubenstein, D. R. (2017). The ecology of cooperative breeding behaviour. *Ecology Letters, 20*, 708–720.

Sherman, P. W., Lacey, E. A., Reeve, H. K., & Keller, L. (1995). The eusociality continuum. *Behavioral Ecology, 6*, 102–108.

Wilson, E. O. (1971). *The insect societies*. Cambridge: The Belknap Press of Harvard University Press.