

Preface

The apparently harmonious functioning of insect societies, the well-ordered coordination of packs of cooperatively hunting carnivores, and the seemingly selfless efforts of helpers in some species of communally breeding birds have long fascinated and puzzled naturalists. How, in a world of Darwinian struggle for life and survival of the fittest, can a behavior persist that obviously does not maximize the direct fitness of the actor but instead benefits others at considerable costs to the actor itself? Since early explanations of cooperation and altruism among animals as “good for the species” have been rejected, a number of attempts have been made to reconcile the existence of such behaviors with evolutionary theory. Among these, W.D. Hamilton’s concept of inclusive fitness (also known as kin selection) is most widely applicable. Hamilton (1964) showed that altruistic behavior that benefits other individuals can be stable in evolution if it is directed towards kin. According to Hamilton’s rule, altruism can spread in a population if the fitness benefits of the altruistic act (b) multiplied by the genetic relatedness (r) of the actor to the recipient are higher than the cost (c) in direct reproduction for the altruist:

$$b \times r > c$$

Genetic relatedness is therefore of fundamental importance for the evolution of helper systems and animal societies, such as those of social insects in which individuals forgo their own reproduction to help other individuals reproduce. The peculiar sex determination system of Hymenoptera, haplodiploidy, results in an unusually high relatedness among full-sisters, which on a superficial view seems to explain the widespread occurrence of altruistic worker castes in this taxon (ants, bees, and wasps) on relatedness grounds alone. Relatedness has therefore become one main focus of studies on social evolution in insects. The advent of molecular genetic techniques, allowing an easy estimation of nestmate relatedness, further contributed to the focus on relatedness in explaining social behavior. But Hamilton’s rule consists of two additional parameters, the costs (c) and benefits (b) of the altruistic acts, both hidden in the individuals’ ecology and demography and therefore more difficult to quantify. Although their importance was clearly pointed out already in Hamilton’s original work, social insect studies on such factors have long been overshadowed by studies on the genetic composition of their societies.

In contrast, investigations on cooperatively breeding birds and mammals traditionally focused more on ecological factors, which delay offspring dispersal and favor philopatry. The importance of ecological factors is probably more apparent in these animals, as they are generally investigated in the field, while many results on social insects come from laboratory studies. Three hypotheses for the evolution of cooperatively breeding in social mammals or birds have been proposed: (a) the ecological constraints hypothesis, according to which independent breeding is difficult because of the limitation of nesting sites or high dispersal mortality; (b) the life-history hypothesis, which states that a species' life-history characteristics limit opportunities for independent breeding; (c) the benefits of philopatry hypothesis, which stresses the long-term direct benefits of staying at the natal nest, such as inheritance of the natal territory. These hypotheses are not mutually exclusive: while ecological constraints (representing the costs of independent breeding) and philopatric benefits (representing the benefits of staying at home) appear to dictate variation in the behavior among individuals of the same species, interspecific differences in life histories can profoundly influence these costs and benefits between species.

During recent years, a large amount of data both on genetic and ecological factors influencing social behavior has accumulated, which provides the opportunity for a comparative analysis of social evolution. In this book, we intended to use information from a large range of social taxa, including vertebrates and invertebrates, (i) to investigate the importance of ecological factors and genetic relatedness for the occurrence of social behavior and (ii) to determine whether there are common patterns that favor social life. It appears the time is particularly ripe for such a synthesis because it has repeatedly been argued that relatedness as a driving factor in social evolution has received undue attention and that kin selection is less important than traditionally assumed. We believe that many of these claims are based on misunderstandings about the term "kin selection," which is too often equated with relatedness. Showing that variation in relatedness does not have the expected outcome on the degree of social behavior, for example, when individuals do not nepotistically feed those to which they are most closely related, does not mean that kin selection does not apply. If feeding more closely related individuals was more costly than indiscriminately feeding all relatives, kin discrimination would not be selected.

Approaches like the 'new group selection' (multilevel selection, trait-group selection) theory may make it easier to quantify the importance of those factors, which are currently hidden in the costs-and-benefits terms of Hamilton's rule. However, in contrast to what is occasionally assumed they do not provide real alternatives to kin selection but instead present a different perspective. Kin selection and new group selection are interconvertible. According to new group selection, the evolution of altruism is not favored if the covariance of traits among individuals within a group is not larger than that between groups. Kinship is the most prominent mechanism to create such a covariance.

This book attempts to provide a broad overview of the ecology of social evolution across large parts of the animal kingdom. Chapter 1 provides a theoretical background of social evolution and thus prepares the ground for the investigations of

sociality in various model systems, starting with the ‘non-classical’ social insects, social aphids (Chap. 2) and thrips (Chap. 3), and the classical societies of social Hymenoptera (wasps, Chap. 4; bees, Chap. 5; ants, Chap. 6) and termites (Chap. 7). Chapters 8–11 cover social vertebrates: birds (Chap. 8), horses (Chap. 9), African mole-rats (Chap. 10), and primates (Chap. 11). In the final chapter (Chap. 12) we try to provide a synopsis on emerging patterns of factors favoring cooperation and altruism among individuals and we outline future perspectives. Taxa that are not covered in special chapters are included in the final chapter, if possible.

Ecology of Social Evolution

Korb, J.; Heinze, J. (Eds.)

2008, XII, 266 p., Hardcover

ISBN: 978-3-540-75956-0