Judith Korb
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Editors

Ecology of
Social Evolution

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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.

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Chapter 1
The Evolution and Ecology of Cooperation – History and Concepts

Andy Gardner(✉) and Kevin R. Foster

Abstract We review the historical development of theory on the evolution and ecology of cooperation. Darwin launched this topic of inquiry with a surprisingly modern discussion of how fitness could be derived from both personal reproduction (direct fitness) and the reproduction of family (indirect fitness), and the anarchist Petr Kropotkin forever wove ecology into sociobiology with his book on *Mutual Aid*. From there, an eccentric group of protagonists took the helm and developed theories of social evolution with clear (although sometimes implicit) links to ecology. Here we provide a summary of the foundational theory, including Hamilton's rule, neighbor-modulated fitness, inclusive fitness, and levels of selection; discuss the classification and semantics of social behaviors; and give a brief overview of the various mechanisms that have been invoked to explain cooperation. Recently, models have emerged that frame the evolution of cooperation in an explicitly ecological context, including the theories of reproductive skew, cooperation in viscous populations, and the tragedy of the commons. In particular, rates and patterns of dispersal strongly influence fitness, the costs and benefits of sociality, and genetic relatedness in social groups. This is an exciting time for ecological sociobiology and there is a great need for studies that combine careful natural history with social evolutionary theory.

1.1   Introduction: The Historical Puzzle of Cooperation

"If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection." Darwin (1859)

Charles Darwin clearly recognized the problem that cooperation poses for his theory of evolution by natural selection. Natural selection favors the individuals

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who have the greatest personal reproductive success, so it is unclear why an organism should be selected to enhance the fitness of another. How then can cooperation evolve? This question has been central to the development of social evolution theory. As we will see in this chapter, solid theoretical foundations have been laid, and the fundamental processes are now well understood. Indeed, Darwin himself seems to have understood the problem rather well. Later in the chapter of *The Origin of Species* from which the above quote was taken, Darwin discussed two archetypes of social cooperation: the mutualism between pollinators and his beloved orchids, and the death of the stinging honeybee worker. Plant-pollinator traits had, earlier in his book, been linked to individual benefits for each of the parties involved: "individual flowers which had the largest glands or nectaries, and which excreted most nectar, would oftenest be visited by insects, and would be oftenest crossed; and so in the long-run would gain the upper hand", and worker altruism was to be explained by benefits to the community, which he linked specifically to family relations: "with social insects, selection has been applied to the family, and not to the individual". Despite his ignorance of the mechanisms of heredity, Darwin had pre-empted the two major classes of modern explanation for social evolution: (1) direct fitness benefits, or an increase in the actor's personal reproductive success; and (2) indirect fitness benefits, or an increase in the reproductive success of relatives who share genes in common with the actor.

Darwin, then, held a fairly sophisticated understanding of social evolution. He also appreciated the importance of ecology as a central shaping force in natural selection. Darwin did not use the word ecology but frequently made reference to "conditions", which appears to be similar to modern notion of ecology – the relationship between an organism (or population) and its environment. However, he seems to have given less thought to the intersection of ecology and sociality. For this, one had to wait for the eccentric but rich writings of the anarchist prince Petr Kropotkin who launched the 20th century interest in social evolution with his book: *Mutual Aid: A Factor in Evolution* (Kropotkin 1902). Kropotkin took an unapologetically positivist and biased view of the natural world, providing a long list of examples of animal and human cooperation in an attempt to counter the prevailing Darwinian view of the "harsh, pitiless struggle for life". Notably, Kropotkin's musings were ecologically oriented from the very start. His ideas were inspired by how "the struggle against nature", for which he often cited the terrible Siberian snowstorms, can be a more powerful force than any struggle among members of the same species. On this basis, he argued that cooperation will often evolve rather than competition. From a theoretical standpoint, Kropotkin's work is a good deal less sophisticated than Darwin's, and he seems not to have understood the fundamental principles of natural selection as well as his intellectual predecessor. Nevertheless, Kropotkin's book was an important antithesis to the contemporary focus on competition, and formed a landmark work that introduced two central principles of social evolution: firstly, that cooperation is abundant in the natural world; and secondly, that ecological conditions are central to its evolutionary success.

The spirit of Kropotkin's book, which combined a distinctly ecological perspective with a somewhat naïve view of the underlying evolutionary processes,

was carried by Allee (1927, 1951) and Wynne-Edwards (1962) into the mid-20th century. Both authors were impressed by how often individuals appeared to cooperate but, like Kropotkin, were somewhat uncritical in their attempts to explain the evolutionary advantage of such behavior. In particular, they were often too ready to appeal to species or population-level benefits for social traits, in an attempt to give an evolutionary explanation for the phenomena that they described. The error in thinking that traits frequently arise through species-level selection is now one of the famous fallacies of evolutionary biology (Williams 1966; Trivers 1985), and we only provide a quick illustration here. Consider the common occurrence of infanticide in many mammals. One might be tempted to infer that individuals kill their own young in order to keep the population size down so as to prevent overexploitation of the available resources. However, it is also clear that, if this were the case, any individual not committing infanticide would enjoy a greater number of descendants than its peers, and therefore such fitness-promoting behavior would be rapidly selected. In other words, the selection of individuals within a sizeable population will usually be more powerful than any population-level selective effects. Unsurprisingly, it turns out that infanticide is frequently driven by one individual killing the offspring of its neighbors, for its own selfish advantage. As we will see below, the differential success of groups (Price 1970; 1972; Hamilton 1975; Wilson 1975) or species (Williams 1966; Nunney 1999; Rankin et al. 2007) can be important in social evolution. However, arguments based on the existence of these processes must be applied very carefully and without neglecting competition between individuals within each of these units (Williams 1966; Trivers 1985).

Not all authors were making this error in reasoning. Many contemporaries of Allee and Wynne-Edwards appear to have had a clearer and more modern view of how cooperation could evolve in a world dominated by individual or even gene-level selection. For example, the polymath H. G. Wells, who is better known for his science fiction than for his science fact, likened the beehive to a single organism, with the sterile workers as its somatic tissue. Together with Julian Huxley, and his son G.P. Wells, he reasoned that:

"*The instincts of the workers can be kept up to the mark by natural selection. Those fertile females whose genes under worker diet do not develop into workers with proper instincts, will produce inefficient hives; such communities will go under in the struggle for existence, and so the defective genes will be eliminated from the bee germ-plasm.*" (Wells et al. 1929)

An appreciation of how sophisticated sociality could evolve was also apparent in the writings of a number of other authors during this period. This includes R. A. Fisher who, in the following year (Fisher 1930), appealed to benefits for family members in order to explain why it should benefit a caterpillar that has already been eaten to be both colorful and distasteful. Following Wells et al. (1929), further lucid explanations for the evolution of social insect workers were provided by Sturtevant (1938) and Emerson (1939). Notably, although these authors embraced the group-level arguments used by Allee and Wynne-Edwards, they were careful to restrict attention to family groups. Like Darwin, therefore, they avoided the species or group-selection fallacy by correctly combining group and kin

thinking. Haldane (1932, 1955) similarly explained worker altruism and is more famously remembered for his colorful quip on how many brothers or cousins he would have to trade his own life for in order to, genetically speaking, break even. Haldane (1932) is also notable for sketching a model of 'tribe-splitting' that might account for the evolution of altruism, though no concrete results were derived. A comparable group-selection model was later provided by Wright (1945), who pursued the algebra a little further though without producing any concrete results. It is clear, therefore, that several authors understood that social traits can be favoured by natural selection even when they come at a cost to the individual. However, a formal understanding of the underlying processes did not arrive until the 1960s, with Hamilton and the theory of inclusive fitness.

1.2 Hamilton and the Foundations of Social Evolution Theory

1.2.1 The Genetical Theory of Social Behavior

Hamilton's (1963, 1964, 1970) theory of inclusive fitness was arguably the greatest of the contributions to Darwinism made in the 20th century. It not only provided a lucid and quantitative general account of the evolution of social behaviors but it also led to a deeper understanding of natural selection and the elusive concept of Darwinian fitness. It is remarkable that such work emerged at a time when the genetics of behavior was still a highly controversial topic, strongly tied to the recent memory of the eugenics movement. Even more remarkable is that this great contribution to evolutionary theory was the work of a solitary postgraduate student.

The young Hamilton's clear intellectual predecessor was R. A. Fisher, whose masterpiece *The Genetical Theory of Natural Selection* (Fisher 1930) had placed Darwinism on the firm theoretical foundations of Mendelian genetics. Fisher recast Darwinian fitness as an individual's genetic contribution to future generation, and described natural selection in terms of changes in gene frequencies. His central result, the fundamental theorem of natural selection, is a mathematical proof of Darwin's verbal argument that those adaptive traits that are retained by the sieve of natural selection are those that operate to enhance the fitness of the individual (Grafen 2003). A gene causing a behavior that increases the fitness of its bearer will, by definition, be favored by natural selection, and hence those behaviors that accumulate in natural populations will be those that best serve the selfish interests of the individual.

Fisher's proof came with a tantalizing caveat. He explicitly neglected the possibility of interactions between genetic relatives, which he understood could lead to indirect fitness consequences of carrying genes. This means that carrying a particular gene could be associated with having higher fitness, even if the direct effect of the gene was to reduce the fitness of its bearer. This was a nuisance for Fisher, but he did not linger on the problem for too long, suggesting that these would generally