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

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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

be unimportant and hence could reasonably be neglected. The naturalist Hamilton, however, saw social interaction between relatives everywhere in nature, and understood the potential for an evolutionary theory of altruism. He set about re-examining the fundamental theory of natural selection in the light of relatedness and the possibility that an individual's fitness is determined, in part, by the behaviors of its neighbors.

1.2.2 Classification of Social Behaviors

The first step was to provide a formal classification of social behaviors, and Hamilton's (1964) scheme does this on the basis of the fitness consequences of the behavior for the actor and for the recipient (Table 1.1). Mutually beneficial (+/+) behaviors increase the fitness of the actor and the recipient; selfish (+/−) behaviors increase the fitness of the actor and decrease the fitness of the recipient; altruistic (−/+) behaviors decrease the fitness of the actor and increase the fitness of the recipient; and spiteful (−/−) behaviors decrease the fitness of the actor and recipient (Hamilton 1964, 1970; West et al. 2007a). Typically, cooperation is used to refer to any behavior that increases the fitness of the recipient, i.e., either mutual-benefit (+/+) or altruism (−/+), which have also been grouped together as 'helping' behaviors (West et al. 2007a). Of the two 'harming' behaviors, selfishness (+/−) poses no conceptual difficulties, as it directly beneficial for the actor. Spiteful (−/−) behavior (Hamilton 1970) is more mysterious and rather neglected by social evolution theory (reviewed by Foster et al. 2001; Gardner and West 2004a); though it has been implicated in microbial and animal conflicts (Hurst 1991; Foster et al. 2001; Gardner and West 2004a; Gardner et al. 2004, 2007a).

This classification has not always been followed, and misuse of the terminology has generated much semantic confusion (reviewed by Lehmann and Keller 2006; West et al. 2007a). In particular, it is important to emphasize that this conventional classification is based on total lifetime fitness effects, and not simply the immediate consequences for fecundity or survival. Depending on the ecological context in which the individuals find themselves, there may be a rather complicated link between social behavior and the total fitness effects. This means that it can be far from trivial to determine whether a behavior is beneficial or deleterious for the actor or for any recipients. Furthermore, these fitness effects are absolute (or relative to the population as a whole) and not measured, for example, relative to an individual's

Table 1.1 A classification of social behaviors, based upon Hamilton (1964, 1970) and West et al. (2007a)

		Fitness impact for recipient	
		+	−
Fitness impact	+	Mutual benefit	Selfishness
for actor	−	Altruism	Spite

immediate social partners. This is important because some researchers later defined altruism in terms of involving a within-group fitness disadvantage (e.g., Wilson 1990), and so including even those behaviors that increase the absolute fitness of the actor when its share of the group benefit outweighs the within-group disadvantage (reviewed by West et al. 2007a; Foster 2008).

1.2.3   Neighbor-Modulated Fitness

If an individual's behavior can impact the fitness of other individuals, then an individual's personal fitness can depend upon the behaviors of others. Hamilton (1963, 1964) made explicit the possibilities for an individual's fitness to be a function of not only its own behavior (and hence the genes underlying this) but also the behaviors of its social partners (and hence the genes present in its social environment), and he termed this 'neighbor-modulated' fitness. This neatly partitions the individual's personal fitness into two components: (1) direct fitness, due to the behavior of the individual itself; and (2) indirect fitness, due to the behavior of social partners (Hamilton 1964; Brown and Brown 1981; West et al. 2007a, 2007b; Fig. 1.1a). Hamilton (1963, 1964) then took a 'gene's-eye' view, and showed that a gene for cooperation (or indeed any behavior) can be favored by natural selection if it
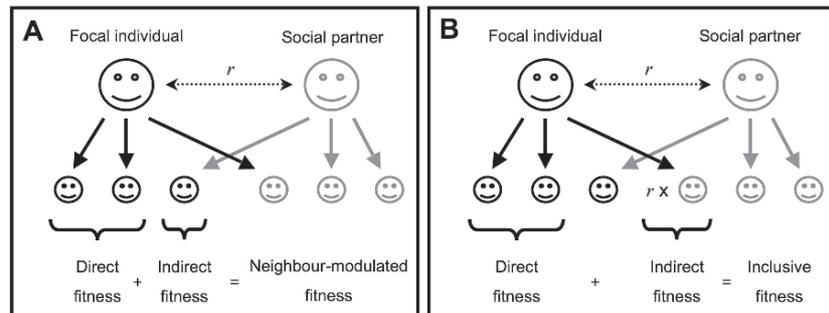
Fig. 1.1   Alternative approaches to fitness. a Neighbor-modulated fitness is the total reproductive success of a focal individual, and is the impact of its own behavior (*solid black arrows*) on its personal reproductive success (direct fitness) plus the impact of the behaviors of its social partners (*solid grey arrows*) on its personal reproductive success (indirect fitness). b Inclusive fitness describes the impact of the focal individual's behavior (*solid black arrows*) on its own reproductive success (direct fitness) and also the impact of its behavior (*solid black arrows*) on the reproductive success of its social partners (indirect fitness), the latter being weighted according to the relatedness (*broken arrow*) of the recipient to the focal individual. This describes how well the individual transmits copies of its genes to future generations, both directly and also via the reproduction of relatives. Because the focal individual is in control of its inclusive fitness, this provides the proper definition of Darwinian fitness in a social context: individuals should behave as if trying to maximize their inclusive fitness

provides a sufficient direct or indirect fitness benefit for its bearers. This provided a general explanation for the evolution of cooperative behaviors. For example, altruists can be favored by selection provided that they socialize with other altruists. The loss of personal fitness through the direct effect of their genes (manifesting in their own altruism) can be compensated by an indirect effect of copies of those same genes (manifesting in the altruistic behavior of neighbors).

By highlighting the importance of indirect fitness effects, Hamilton had effectively rendered Fisher's fundamental theorem (which neglected these) obsolete. Furthermore, he had shown that the Darwinian notion of individual organisms as agents striving to maximize their personal fitness was naïve. While many of today's researchers would relish the opportunity to topple such intellectual giants as Fisher and Darwin, Hamilton preferred synthesis over sensationalism, and was deeply concerned by these far-reaching consequences of his theory. Individual organisms do appear to behave as if they have an agenda, and Hamilton was motivated to find out if his formalism could explain precisely what the agenda is (Hamilton 1996). Certainly organisms do not act to maximize their direct fitness, as the evolution of altruism demonstrates. Nor can they be maximizing their neighbor-modulated fitness, because the indirect component of fitness is not under their command but is instead controlled by their social partners.

1.2.4 Inclusive Fitness

Hamilton's (1963, 1964, 1970) conceptual breakthrough was to break the link between parents and their offspring, and to reassign increments of reproductive success to individuals on the basis of behavior (Fig. 1.1b). This puts the focal individual (the actor) and its behavior firmly in the center of a new fitness accounting scheme (Grafen 1984, 2006). The actor's direct fitness, being the component of its personal fitness that it can ascribe to its own behavior, remains the same as in the neighbor-modulated fitness view. However, its indirect fitness is now made up of all the offspring of neighbors that can be attributed to its own behavior. A complication is that all non-descendant offspring are not valued equally, and in particular will not usually be as valuable as the actor's own progeny. For this fitness-accounting scheme to work, and be equivalent to neighbor-modulated fitness, the correct measure of value is provided by the coefficient of relatedness. The actor accrues more indirect fitness from helping a genetically similar relative than it does by providing the same benefit for a less-related neighbor. With relatedness providing an exchange rate (Frank 1998) that allows non-descendant offspring to be translated into effective numbers of descendant offspring, an individual's direct and indirect components of fitness can be added together to give a total which Hamilton termed 'inclusive fitness' (Hamilton 1963, 1964, Brown and Brown 1981). An important point to emphasize, which has resulted in some confusion, is that this logic rests on the *change* in inclusive fitness affected by the individual's behavior: the decrease in their own offspring weighted against the increase in relatives' offspring caused

by helping. Attempts to evaluate inclusive fitness by counting all the offspring produced in a population that have some positive relatedness to an actor can quickly lead to absurdities (reviewed by Grafen 1982).

Natural selection can be viewed as maximizing neighbor-modulated fitness. Equivalently, it can be viewed as maximizing inclusive fitness. These two quantities are simply the fitness measures that emerge from alternative but equivalent accounting schemes for reproductive success (Frank 1998). Both correctly describe the individual's success in transmitting copies of its genes into future generations, whether this be done directly through its own personal reproductive success irrespective of whose behavior was involved (neighbor-modulated fitness) or else through that reproductive success of its genetic relatives (including itself) which can be attributed to the focal individual's behavior (inclusive fitness). The benefit of the inclusive fitness view is that it is directly and causally tied to the focal individual's behavior, and thus better captures the apparent agenda underlying organismal behaviors (Grafen 1984, 2006; Hamilton 1996). Organisms are expected to behave as if they value the reproductive success of their neighbors (devalued according to their genetic relatedness) as well as their own reproductive success. In short, they behave as if they are trying to maximize their inclusive fitness (Grafen 2006).

Thus, with inclusive fitness, Hamilton rescued the Darwinian view of natural selection leading to the appearance of agency at the organismal level and showed that Darwinian agents need not be altogether selfish. However, inclusive fitness has often been regarded incorrectly as an altogether separate force in evolutionary biology, which can work against traditional natural selection. Maynard Smith (1964) coined the phrase "kin selection" to describe this apparently new process. This term has stuck despite also giving the impression of a narrowed application of the theory to interactions between kin only. Although close kinship is a robust mechanism for generating genetical relatedness between social partners, inclusive-fitness theory applies more generally to any interactions between genetically similar individuals, irrespective of whether they have a close genealogical relationship (Hamilton 1964a).

1.2.5 Hamilton's Rule

Hamilton's theory of indirect fitness effects is encapsulated in the pleasingly simple 'Hamilton's rule', (Hamilton 1963, 1964, 1970), which simply states that a behavior is favored when it leads to a net increase in the inclusive fitness of the actor.

$$-c + br > 0 \qquad (2.5.1)$$

The components of the rule are: (1) the direct fitness cost of the behavior for the actor, c: (2) the fitness benefit for the recipient, b; (3) the genetic relatedness of the recipient to the actor, r. Thus, $-c$ represents the impact of the behavior on the direct fitness of the actor, and br represents the impact of the behavior on the indirect

fitness of the actor. The rule makes explicit the possibilities for even costly behaviors to be favored, provided they lead to sufficiently large benefits for the actor's relatives. A derivation of Hamilton's rule from both neighbor-modulated-fitness and inclusive-fitness perspectives is given in Box 1.

Although Hamilton's rule provides a powerful conceptual aid for reasoning about social evolution, theoretical analyses do not typically use the rule as a starting point. Rather, various different methodologies can be applied to obtain a result that can then be interpreted as a form of Hamilton's rule, to gain insight into what it means (Taylor and Frank 1996; Frank 1998; Gardner et al. 2007b). One particular methodology that has revolutionized the way in which social evolutionary models are made and analyzed in recent years is the 'direct' (neighbor-modulated) fitness approach (Taylor and Frank 1996; Frank 1997, 1998). A sketch of this method is given in Box 2.

Box 1 Derivation of Hamilton's rule

Although Hamilton derived his rule from an inclusive fitness perspective (the effect of the actor on others), it can also be derived from a neighbor-modulated fitness perspective (the effect of others on the actor). The following derivation is due to Queller (1992; see also Frank 1998). We begin by fitting a model of an individual's fitness (w), as a linear function of that individual's genetic breeding value (g; Falconer 1981) for a trait of interest and the average genetic breeding value exhibited by its neighbors (g'), to a population of interacting individuals:

$$w = \overline{w} + \beta_{w,g \cdot g'}(g - \overline{g}) + \beta_{w,g' \cdot g}(g' - \overline{g}) + \varepsilon, \qquad (B1.1)$$

where: $\overline{w}$ is the average fitness of the individuals in the population; $\overline{g}$ is the average genetic breeding value of the individuals in the population; $\beta_{w,g \cdot g'}$ is the least-squares partial regression of the individual's fitness on its own genetic breeding value; $\beta_{w,g' \cdot g}$ is the least-squares partial regression of the individual's fitness on it's partners' average genetic breeding value; and ε is the uncorrelated error. From Price's (1970) theorem, the change in the average genetic breeding value due to the action of natural selection ($\Delta \overline{g}$) is given by:

$$\overline{w}\Delta \overline{g} = \text{Cov}(w, g), \qquad (B1.2)$$

where 'Cov' denotes a covariance. Substituting our model into this, we have:

$$\overline{w}\Delta \overline{g} = \beta_{w,g \cdot g'}\text{Cov}(g, g) + \beta_{w,g' \cdot g}\text{Cov}(g', g), \qquad (B1.3)$$

(continued)

Box 1 (continued)

so a condition for the average breeding value of the trait to increase ($\Delta \overline{g} > 0$) is:

$$\beta_{w,g \bullet g'} + \beta_{w,g' \bullet g} \frac{\mathrm{Cov}(g',g)}{\mathrm{Cov}(g,g)} > 0. \qquad \text{(B1.4)}$$

Note that this is based on the assumption that $\mathrm{Cov}(g,g)$, which is the additive genetic variance, is nonzero, and hence is necessarily a positive quantity. This condition for increase is Hamilton's rule, in its neighbor-modulated fitness guise. The additive effect of the individual's own genetic breeding value for the trait of interest, holding fixed the effect of its neighbors' genes, is $\beta_{w,g \bullet g'} = -c$, i.e., it describes the direct cost of the social behavior. Similarly, the effect of the neighbors' average breeding value on the focal individual's fitness is the indirect fitness (in the neighbor-modulated sense) benefit $\beta_{w,g' \bullet g} = b$. Finally, the ratio of the two covariances can be rewritten as the least-squares regression of an individual's social partners' breeding values on its own breeding value ($\beta_{g',g}$), and is equal to the coefficient of relatedness (r; Queller 1992; Frank 1998). Substituting these terms in gives the more familiar Hamilton's rule: $-c + br > 0$.

We have assumed a population in which all individuals are equivalent. The derivation of Hamilton's rule in class-structured populations has been given by Taylor (1990). Using this assumption of equivalence, we can readily derive the inclusive fitness version of Hamilton's rule. Simply, if the effect of genes in one's social environment (g') on one's fitness (w) is $\beta_{w,g' \bullet g}$, then by symmetry this is also equal to the impact of one's genes (g) on the fitness of neighbors (w'), which can be written as $\beta_{w',g \bullet g'}$ (Queller 1992). Substituting into inequality (5), we have:

$$\beta_{w,g \bullet g'} + \beta_{w',g \bullet g'} \frac{\mathrm{Cov}(g',g)}{\mathrm{Cov}(g,g)} > 0, \qquad \text{(B1.5)}$$

which makes explicit the partitioning of the inclusive fitness effect (left hand side of inequality (B1.5)) into direct and indirect fitness components. Moreover, this emphasizes that the behavioral effects of genes carried in neighbors do not count towards inclusive fitness (the regressions are partial, with respect to g, and holding g' fixed; Hamilton 1964; Grafen 1984).

1.2.6 *Levels of Selection*

Although Hamilton's genetical theory of social evolution was in part developed as an antidote to careless appeals to group or species-level benefits for cooperation (Allee 1951; Wynne-Edwards 1962), recent years have seen renewed interest in the

Box 2 'Direct' (neighbor-modulated) fitness approach

Although inclusive fitness is a conceptually easier way of understanding social behavior (Taylor et al. 2007), and indeed is the proper way of thinking about social adaptations in a Darwinian sense (Grafen 2006), it is often technically simpler to analyze models of social evolution using a neighbor-modulated fitness approach. Here, we outline one popular approach that has been very successful in recent years (Taylor and Frank 1996; Frank 1997, 1998; Taylor et al. 2007; see also Rousset 2004). Confusingly, it has often been termed a 'direct fitness' approach, though 'neighbor-modulated fitness' is a preferable alternative that does not conflict with prior usage of the terms 'direct' and 'indirect'.

The approach is based on the reasonable assumption of vanishing genetic variation in the social evolutionary traits of interest (Taylor and Frank 1996; Frank 1998). We may write fitness (w) as a function of the individual's genetic breeding value (g), that of its neighbors (g'), and the population average ($\bar{g}$); i.e., $w(g,g',\bar{g})$. We assume that fitness is a differentiable function of each of these genetic arguments and, using the chain rule of differential calculus, we can write:

$$\frac{\mathrm{d}w}{\mathrm{d}g} = \frac{\partial w}{\partial g} + \frac{\partial w}{\partial g} \times \frac{\mathrm{d}g'}{\mathrm{d}g}. \tag{B2.1}$$

Evaluating at $g = g' = \bar{g}$, due to the assumption of vanishing genetic variation, the partial derivatives can be reinterpreted as the cost and benefit components of Hamilton's rule, i.e., $\partial w/\partial g = \beta_{w,g \cdot g'} = -c$ and $\partial w/\partial g' = \beta_{w,g' \cdot g} = b$, and the derivative of neighbor breeding value by one's own breeding value is the coefficient of relatedness $\mathrm{d}g'/\mathrm{d}g = r$ (Taylor and Frank 1996; Frank 1998). Setting Eq. (B2.1) to zero, and solving for $\bar{g} = g^*$, we obtain an equilibrium point that can then be assessed for evolutionary and convergence stability (Maynard Smith and Price 1973; Eshel and Motro 1981; Taylor 1996). Again, we have assumed for simplicity that all individuals can be treated as if they are equivalent, though class-structure is readily implemented, as described by (Taylor and Frank 1996; Frank 1998; Taylor et al. 2007).

theory of levels of selection (e.g., Keller 1999; Okasha 2006). After the development of the inclusive fitness theory, Hamilton and Wilson pointed out the usefulness of an alternative approach that phrases social evolution in terms of selection between and within groups, rather than separating individual fitness into direct and indirect components (Hamilton 1975; Wilson 1975). However, the theory of group selection has historically been plagued by unfortunate confusion and controversy (above) that has somewhat left it in the wings, as compared to inclusive-fitness theory, which has matured as a field of study, boasting formal though conceptually simple foundations,

and enjoying very good empirical support. At present, group-selection theory comprises a large amount of verbal discussion and a collection of mathematical models that appear to provide helpful insights but are lacking in conceptual unity (see Okasha 2006 for a recent review).

A formal basis for the theory of group selection has been suggested by Hamilton (1975), building upon the work of the tragic genius George Price. Price's (1970) theorem, which underpins the canonical derivation of Hamilton's rule (Hamilton 1970), has also been applied to levels of selection in evolution (Price 1972; Hamilton 1975). This approach partitions the total evolutionary response to selection into distinct between-group and within-group components. Importantly, it does this in a completely general and formal way, and so can be applied to any model, providing a common foundation upon which to rest any group-selection analysis. This partition can be very useful for conceptualizing the potential tension between the interests of individuals and the needs of the group (Hamilton 1975). When these interests come into conflict, Price's approach allows their relative strengths to be compared and the balance between these two evolutionary pressures to be determined in a precise, quantitative way.

However, there are some important caveats. It can often be difficult to decide which particular collections of individuals constitute groups, and yet this decision has important consequences for how we ascribe evolutionary change to group selection. Also, the approach can lead to apparent absurdities, such as diagnosing the operation of group selection even when considering non-social traits (Heisler and Damuth 1987). For example, if physical strength enhances individual fitness in a straightforward way, then some groups will be fitter than others simply because they contain, by chance, stronger individuals. The consensus in the group-selection literature seems to be that identifying this as 'group selection' is incorrect. An alternative approach, termed 'contextual analysis' (Heisler and Damuth 1987), mirrors the neighbor-modulated fitness approach discussed above, and describes individual fitness as a function of its own behavior and also the behavior or other characteristics of its group. A least-squares regression analysis identifies the impact of the group character on individual fitness as a description of 'group selection'. This procedure avoids the incorrect diagnosis of group selection in the hypothetical example of individual strength. However, it has its own difficulties (Heisler and Damuth 1987; Goodnight et al. 1992). If we consider again the selection for individual strength, but now assume soft selection (Wallace 1968) is in operation so that every group is constrained to have the same total fitness, then an individual with particularly strong group mates will tend to have lower fitness than it would in another group. Contextual-analysis diagnoses group selection in this scenario, because individual fitness depends on the group environment. However, group selection is typically phrased in terms of fitness differences between groups, so there appears to be a mismatch between the formalism and the fundamental process that it was intended to capture. Thus, while a levels-of-selection (or contextual-analysis) perspective can be very useful for describing and conceptualizing social evolution, a fully satisfying formal theory of group selection (defined as the differential success of groups) remains to be developed.

It is important to emphasize that the levels-of-selection approach does not suppose that a different type of natural selection is in operation, but rather it provides an alternative way of conceptualizing the same process of natural selection that is described by inclusive fitness theory (Hamilton 1975; Grafen 1984). Indeed, both derive from the same fundamental evolutionary theorem (Price 1970, 1972), and it is usually straightforward to switch between these different views when considering a particular model. The contentious 'levels-of-selection' debate has long been solved, or rather it has been shown to be empirically vacuous, turning, as it does, upon an issue of differences in approach rather than any real disagreement as to how natural selection operates (Reeve and Keller 1999).

1.3 Mechanisms for the Evolution of Cooperation

1.3.1 General Overview

Hamilton provided a general explanation for the evolution of cooperation, or indeed any social behavior; namely that the behavior is favored if it increases the actor's inclusive fitness. Thus, explanations for cooperation rely on either direct fitness benefits (i.e., mutual benefit) or else indirect fitness benefits (i.e., altruism) (Brown 1987). Although this says nothing about the actual mechanisms involved, it is helpful to distinguish mechanisms supporting the evolutionary maintenance of cooperation on the basis of direct versus indirect fitness benefits (Fig. 1.2). We emphasize that mechanisms need not be mutually exclusive, and cooperation will often be dependent on a mixture of direct and indirect fitness benefits. The following tour of mechanisms is based upon the recent reviews of Sachs et al. (2004), Lehmann and Keller (2006) and West et al. (2007a, 2007b).
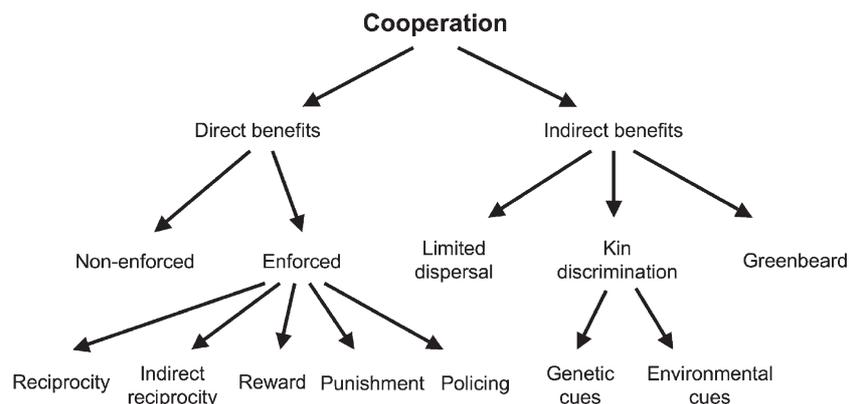
Fig. 1.2 A classification of mechanisms favoring the evolution of cooperation, based upon West et al. (2007a, 2007b)

1.3.2   Direct Fitness Benefits

1.3.2.1   Non-Enforced

By-product benefits – The simplest explanations for cooperation involve direct-fitness benefits that arise naturally from the behavior, and where the benefit to other parties can be regarded as a fortunate side effect (Sachs et al. 2004). Such by-product benefits are exemplified in Hamilton's model of the 'selfish herd' (Hamilton 1971). In the simplest form of herding behavior, an individual that joins a herding group will gain a personal benefit from protection against predators. At the same time, however, group fitness is also increased, so there is no individual and group conflict. An interesting possibility is that species-level selection favors cooperative systems with cooperation based upon by-product benefits, or equivalently, species where a group member has intrinsic constraints on the evolution of cheating. For example, it has been suggested that social species that arise with pleiotropic constraints between potential cheating strategies and a personal cost will persist better than those where cheating can readily arise. This predicts that the genome to phenome mapping in extant social species will tend to constrain cheating (Foster et al. 2004, 2007; Rankin et al. 2007).

Feedback benefits – A related form of direct fitness benefit comes when an individual's direct fitness is dependent on the success of other members of its group, or a shared group trait. When this occurs, an actor can be selected to cooperatively invest in the group in order to ensure their own personal prosperity. What makes this arguably distinct from by-product benefits is that, while both increase group fitness, with feedback benefits the action will tend to decrease the relative fitness of the individual in the group. An example of this, which has been termed 'weak altruism' in the group-selection literature, is cooperative nest founding by multiple ant queens where all queens will work to ensure the colony's success because this later feeds back on their reproductive success (Wilson 1990). These feedbacks (along with kinship) are also probably important in vampire bats that share blood with others in their roosting group. By sharing, they ensure the survival of the group and the later receipt of blood when they themselves fail to forage (below, Foster 2004). More generally, such feedback effects are central to the evolution of between-species cooperation (Sachs et al. 2004), where one species invests in another species because its own success is dependent on the success of its mutualist ('partner-fidelity' feedback). For example, ants that live symbiotically in a plant will be often selected to invest in the survival, if not always the reproduction, of their host (Yu and Pierce 1998; Foster and Wenseleers 2006).

1.3.2.2   Enforced

Cooperation can also be enforced. That is, cooperation by an actor is often encouraged by specific adaptations in its social environment that function to make

defection costly. It is important in discussing enforcement to recognize that there are two levels. There is what might be called 'primary enforcement', where cooperation is promoted in an actor with the facultative return of cooperation by the recipient and then there is 'secondary enforcement', which involves a separate currency or currencies of punishment or reward, such as actively harming a defecting individual. Secondary mechanisms, however, carry additional costs to the enforcer, and only seem likely when first-order enforcement is not possible. That is, secondary enforcement is only expected if a potential enforcer is either noncooperative, or their cooperation is not directed specifically at the defecting individual. For example, most cooperation by social insect workers is directed at the colony as a whole, through behaviors like guarding, brood rearing, and nest building (Wilson 1971), which limits their ability to engage in primary enforcement by redirecting their cooperation away from a particularly rebellious worker.

Primary enforcement – Primary enforcement can be viewed from two equivalent perspectives: as rewarding cooperation with cooperation, or punishing defection with defection. Trivers (1971) showed that such conditional behavior will readily promote cooperation in a world where individuals can recognize and remember others. He termed this 'reciprocal altruism', but it is better described as 'reciprocal cooperation' because it derives a direct fitness benefit and is thus mutually beneficial rather than altruistic (West et al. 2007a). This idea was later developed in the ingenious computational tournaments of Axelrod and Hamilton (1981) who presented programmers with a challenge: in a game of repeated interactions where cooperation leads to mutual gain, but exploitation of other cooperators leads to even greater gain (the 'Prisoner's dilemma'), design a winning behavioral strategy. Despite the submission of some complex programs, the winning strategy was very simple: "Tit for Tat" (TFT). This strategy would cooperate in the first round, and subsequently mirror the play of its partner from the previous round. It is reciprocal cooperation, as when TFT encounters a cooperator they enjoy a cooperative interaction, but TFT will not allow its cooperation to be exploited by a defecting partner. Following Axelrod and Hamilton (1981), many theorists picked up on the Prisoner's dilemma game, often more as a mathematical problem than a biological one, and now there are a myriad of variants on both the scenario and its solution (reviewed by Doebeli and Hauert 2005; Lehmann and Keller 2006). A closely related idea is that of indirect reciprocity, whereby helping others improves one's reputation, which then increases the chances of being helped (Nowak and Sigmund 1998; Mohtashemi and Mui 2003; Panchanathan and Boyd 2004; Semmann et al. 2004). Along with reciprocal cooperation, indirect reciprocity appears to be very important in human cooperation, but the requirement for recognition and memory of others means they probably occur in relatively few other species (Hammerstein 2003).

More generally there are many active behavioral mechanisms that reward cooperative behavior in social interactions, but do not require the recognition and memory of reciprocal cooperation. Central to this is the idea of partner choice, where individuals either preferentially interact and/or cooperate with the more cooperative individuals in a population (Bull and Rice 1991; Noe and Hammerstein

1994; Ferriere et al. 2002; Johnstone and Bshary 2002; West et al. 2002a; Sachs et al. 2004; Foster and Wenseleers 2006). Theory suggests that partner choice is central to the evolution of between-species cooperation because, being behavioral, it is both local and rapid in effect (West et al. 2002b; Foster and Kokko 2006; Foster and Wenseleers 2006). In support of this, a large body of empirical data is emerging that suggests that partner-choice mechanisms are widespread and common in many mutualisms (Sachs et al. 2004; Foster and Wenseleers 2006). A familiar example of this is the ability of pollinators to rapidly leave plants that do not provide them with enough nectar, which means that pollinators tend to carry the pollen of cooperative plants rather than those that cheat the mutualism (Darwin 1859; Smithson and Gigord 2003). Another example, which is often discussed in terms of punishing sanctions, is legumous plants that appear to shut off the oxygen supply to root nodules inhabited by rhizobial bacteria that have not contributed enough fixed nitrogen to their host (West et al. 2002a, 2002b; Kiers et al. 2003; Simms et al. 2006).

Secondary enforcement – In many social species, including humans, systems of enforcement occur that are separate from primary cooperation (Oliver 1980). This raises the problem of why reward or punish cooperation, given that it can be costly to do so (Sober and Wilson 1998; Fehr and Gachter 2000; Sigmund et al. 2001; Boyd et al. 2003)? Like primary cooperation, this can again be answered by direct or indirect fitness benefits (Gardner and West 2004b). An important corollary is that although rewarding behaviors can favor cooperation, by doing so they automatically generate the need for continued rewards. In contrast, punishment can favor cooperation, and once it is established, there is no further need to punish. Thus, systems of rewards are inherently costly and systems of punishment, cheap (Gardner and West 2004b), which may explain the apparent prevalence of punishment and the rarity of rewarding in the natural world (Clutton-Brock and Parker 1995).

Another type of negative secondary enforcement, which may be termed policing (Starr 1984; Ratnieks 1988; Frank 1995), operates when the system is organized so that the individual simply cannot gain through uncooperative behavior. When there is no avenue for cheaters to gain an advantage within their group, individuals can only enhance their own fitness by cooperatively improving the fitness of the group as a whole (Frank 2003; Wenseleers et al. 2004a; Ratnieks et al. 2006; Wenseleers and Ratnieks 2006a, 2006b). For example, within honeybee colonies, unmated workers can lay unfertilized eggs that would develop into males that compete with the queen's sons if left to develop. But workers are selected to destroy each other's eggs (worker policing), because they are more related to the sons of the queen (their brothers) than they are to the sons of other workers (their nephews; Starr 1984; Ratnieks 1988). Although worker egg laying does occur, it is much rarer than is predicted by theory in the absence of policing (Wenseleers et al. 2004a; Ratnieks et al. 2006; Wenseleers and Ratnieks 2006b). Striking empirical support for this comes from a comparison with colonies in which the queen has died, where policing breaks down. Under these conditions, many workers develop their ovaries and compete over reproduction (Wenseleers and Ratnieks 2006b).

As with the origin of primary cooperation (by-product benefits, above), any enforcement system will only be evolutionarily stable if they evolve in a way that cannot be evaded. This again, therefore, predicts that trade-offs or pleiotropic relationships will be important, and that the enforcer will exploit them to prevent evasion by an enforcee. A nice example of this is the cooperative bioluminescence caused by the bacterium *Vibrio fischeri* bacterial symbionts that live in the light-emitting organ of the bobtail squid *Euprymna scolopes*. The symbiotic relationship is based upon the bacteria providing bioluminescence that might aid the squid in darkness or camouflage it from below against the bright ocean surface. Amazingly, the squid appears able to enforce light production in the bacteria by creating an environment in which the gene for light production is also pleiotropically required for bacterial growth (Visick et al. 2000; Sachs et al. 2004; Foster et al. 2007).

1.3.3 Indirect Fitness Benefits

1.3.3.1 Limited Dispersal

Probably the most widely applicable mechanism for generating indirect fitness benefits for cooperation is population viscosity, or limited dispersal, leading to genetic structuring of populations (Wright 1945; Hamilton 1964, 1971). This means that even indiscriminate altruistic behavior incurring a personal cost and providing a benefit to neighboring individuals could enhance the actor's inclusive fitness because those neighbors are on average closely related kin (Hamilton 1964, 1971). This promises to be a very general explanation, because it requires no complicated cognitive faculty that allows the discrimination of kin and ensuing nepotism, and thus applies to simple organisms such as bacteria. For example, siderophores are compounds exuded by bacteria to promote iron-uptake (Guerinot 1994; Ratledge and Dover 2000). These compounds are costly for the individual to produce but can be used by any cell in the vicinity, and so may represent an altruistic public good (West and Buckling 2003). Selection experiments that impose a low-dispersal, viscous population structure can result in an evolutionary response for the bacteria to increase their average production of siderophores, due to the increased indirect fitness benefits accrued through the neighboring cells being closely related kin (Griffin et al. 2004). However, things are not so straightforward. As well as generating high relatedness between neighboring individuals, population viscosity can also lead to intensified competition between relatives, which can inhibit the evolution of cooperation (see section 1.4.1).

1.3.3.2 Kin Discrimination

Increased relatedness to the recipients of one's cooperation (and hence an increased indirect fitness benefit) can be achieved if individuals have the ability to recognize their kin and to bias their cooperative behavior towards them. Kinship can be inferred on the basis of 'environmental' cues (Grafen 1990), such as close proximity

in the natal nest, and the retention of this memory and its influence on social behavior later in life. For example, environmental cues are central to the evolution of the impressive cooperation in social insects, where kinship is typically indirectly inferred from cuticular chemicals that are acquired through presence in the nest (Singer 1998). In addition, kinship is inferred by song similarity in some cooperatively breeding birds (Hatchwell et al. 2001) Alternatively, kinship could be inferred on the basis of genetically determined phenotype and hence shared genes (Grafen 1990). If the main cause of genetic similarity is genealogical closeness, then a social partner who shares one or several 'marker' genes in common with the actor will likely share many genes in common, including those encoding cooperation, through recent co-ancestry. For example, sterile 'soldier' larvae among the polyembryonic parasitoid wasp *Copidosoma floridanum* discriminate and protect their closest kin on the basis of the composition of their extraembryonic membrane yet aggressively attack other individuals sharing the same internal environment of the host (Giron and Strand 2004). However, genetic kin recognition is relatively rare, perhaps due to the difficulty of maintaining genetic variability at the marker loci (Crozier 1986; Rousset and Roze 2007).

1.3.3.3   Greenbeards

To demonstrate that it is genetical relatedness rather than genealogical relationship that forms the fundamental basis of indirect fitness benefits, Hamilton (1964) outlined an interesting thought experiment. Supposing that the bearer of a cooperative gene could directly recognize and preferentially aid other carriers of that gene, then cooperation would be favored by natural selection even if these individuals were not genetically similar at any other loci. This could happen if the gene for cooperation also had a pleiotropic effect, which advertised that its bearer was a carrier of the gene. Alternatively, the cooperation, advertisement and recognition functions could be encoded by separate but closely linked genes that would segregate as a single Mendelian unit, i.e., a supergene. Dawkins elaborated on this idea in his book *The Selfish Gene* (Dawkins 1976), in a memorable illustration in which the advertisement for possession of the gene was the growth of a conspicuous green beard. Such 'greenbeard' altruism has been implicated in the stalk-forming behavior of social amoebae. Here, a cell-adhesion protein encoded by the *csaA* gene is responsible for both the commitment to altruistic stalk-formation and also for gaining access to the social group in the first place (Queller et al. 2003). Interestingly, Hamilton's thought experiment also permitted a darker interpretation in which a greenbeard gene that caused harm towards neighbors not bearing the conspicuous marker could also be favored (Hamilton 1964), and this could explain even downright spiteful behaviors (Gardner and West 2004a). Such a mechanism has been discovered in the fire ant *Solenopsis invicta*, where workers carrying a variant of the *gp9* gene kill non-carrier queens in multiple-queen colonies (Keller and Ross 1998, Foster et al. 2001; Krieger and Ross 2002).

Although greenbeard genes are superficially similar to kin discrimination, and both are based upon genetic relatedness, the details of the inference of genetic

similarity are quite different. Kin discrimination relies on the inference of genealogical closeness and hence a high expected genetic similarity over all loci, including the cooperation loci, whereas the greenbeard mechanism relies on the inference of genetic similarity at the cooperation loci due to pleiotropy or physical linkage. However, in practice, elements of both kinship and greenbeard recognition will usually be involved when genetic markers are used to infer relatedness as cooperation loci (West et al. 2007b)

It is important to emphasize that the greenbeard theory was not intended to represent a plausible mechanism for the evolution of cooperation, but rather it provided an illustration that highlighted that genetic similarity and not genealogical closeness per se is the basis of genetic relatedness. In principle, the greenbeard mechanism does provide an explanation for cooperation, but in practice there are several reasons for suspecting it to have only a minor role to play. In particular, if a new allele were to arise by mutation at the greenbeard locus that could encode the beard (and thus enjoy receiving cooperation) without committing itself to cooperation, then this would be strongly favored by selection (Roberts and Sherratt 2002). Also, a greenbeard gene that produces relatedness only at a single locus will generate conflicts with the rest of the genome that does not share the same relatedness patterns across individuals. As a result, there is expected to be strong selection for modifier genes elsewhere in the genome that disrupt the expression of this costly cooperation (Okasha 2002; Grafen 2006; Lehmann and Keller 2006; Helantera and Bargum 2007). Thus, greenbeards that arise in the absence of associated whole-genome relatedness are expected to typically have a transient existence over evolutionary timescales.

1.4 Making the Ecology Explicit

The general overview of the previous section has focused on the act of cooperation, and has provided a sketch of physical and behavioral mechanisms that can make cooperation mutually beneficial, as well as behavioral and genetic mechanisms that ensure sufficient relatedness between actor and recipient for even altruistic cooperation to be favored. The ecology of social organisms has been largely implicit. However, an understanding of the population and its environment is critical as ecology impacts on every component of inclusive fitness. Within Hamilton's rule, the direct cost (c) and benefit (b) of a social behavior are meaningless except within the context of a population of individuals competing for genetic representation among future generations, and the genetic structure of social groups, which determines the coefficient of relatedness (r), is crucially dependent upon population processes. Furthermore, in recent years, some areas of theoretical sociobiology have started to more explicitly consider ecology and its effects of social evolution. Here we briefly review three such areas: (1) the theory of reproductive skew, (2) cooperation in viscous populations, and (3) the tragedy of the commons.

1.4.1 Ecological Constraints and Skew Theory

One of the most fundamental behavioral decisions that social organisms make is whether to remain in their group or, conversely, to leave the group and go it alone (Stacey and Ligon 1991). Not all social organisms have this option (workers in many social insects are unable to mate or found a new colony) but there are many where dispersal decisions shape the social group. This includes many of the less-derived social insects (Bourke and Franks 1995; Queller and Strassmann 1998; Ratnieks et al. 2006) but also many groups of charismatic social vertebrates (Emlen 1991; Hatchwell and Komdeur 2000; Clutton-Brock 2002; Griffin and West 2003), which have helper individuals that remain in the social group and aid in the care of their relatives' offspring. The study of these groups has consequently focused on the costs and benefits of dispersal, and understandably central to this is the notion of ecological constraints (Keller and Reeve 1994; Emlen 1995; Pen and Weissing 2000; Kokko et al. 2001; Lehmann et al. 2006). If dispersal and group founding is costly and risky, it will often pay, in a fitness sense, to stay and help in an established group, even if the individuals that you raise are less related to you than your own offspring. This logic has been much discussed in the vertebrate literature where, in addition to ecological constraints from dispersal, there may also be explicit benefits for remaining in the group, such as when this group occupies a particularly good territory (Stacey and Ligon 1991) or when large groups have higher fitness than small ones (Kokko et al. 2001). Similar ideas underlie the theories of "reproductive-head start" (Queller 1989) and "assured-fitness returns" (Gadagkar 1990) for the evolution of sociality in insects, which both emphasize that nests take time and are risky to found, so staying with an established nest can have strong fitness advantages.

The most theoretical attention to these ecological costs and benefits, however, came through the rapid but ephemeral rise of skew theory in the 1990s, which sought to explain patterns of reproductive sharing among individuals in animal societies. That is, why is it that in some social species many individuals reproduce (low skew) while in others it is restricted to one or a few individuals (high skew)? Skew theory started with a simple expansion of Hamilton's rule by Vehrencamp (1983a, 1983b), who modeled a social group containing two individuals: a subordinate, who can choose to stay or leave; and a controlling all-powerful dominant, who can choose to cede some reproductive rights to the subordinate. After Vehrencamp, things went quiet for a decade or so, but they were resurrected and extended by Reeve and Ratnieks (1993) and Keller and Reeve (1994).

Predictions from skew theories rest upon two key ecological factors: (1) the expected personal success of an individual who leaves the colony and attempts to found a new group on their own (x, dependent upon ecological constraints); and (2) the benefit to the original colony if the individual stays and helps ($k - 1$, where k is the group productivity with the subordinate, and 1 is without). From Hamilton's rule, this predicts that a subordinate will be favored to disperse from the social group when:

$$x > r(k-1), \tag{4.1.1}$$

where r is genetic relatedness between subordinate and dominant. However, when the subordinate can be very helpful to the dominant, it will pay the dominant to give some reproduction to the subordinate and attempt to make them stay. This staying incentive (s), representing the proportion of group reproduction given over to the subordinate) will select for the subordinate to stay when:

$$x < sk + r[k(1-s)-1], \tag{4.1.2}$$

and one can calculate a similar equation for peace incentives that reduce fighting in the social group (Reeve and Ratnieks 1993; Keller and Reeve 1994). From this simple beginning, skew theory rapidly diversified into a comedy of additional models, each differing in their specific assumptions on the relative power of the individuals, the information available, and whether and how the individuals negotiate their reproductive share (e.g., Reeve et al. 1998; Robertson et al. 1998; Cant and Johnstone 1999; Johnstone and Cant 1999a, 1999b; Johnstone et al. 1999; Kokko and Johnstone 1999; Ragsdale 1999; Cant and Johnstone 2000; Crespi and Ragsdale 2000; Hamilton 2000; Johnstone 2000; Reeve 2000; Reeve and Emlen 2000; Nonacs 2001, 2002; Jeon and Choe 2003; Reeve and Jeanne 2003). What became rapidly evident is that the relationship between the key variables like skew, group productivity, relatedness, and ecological constraints are extremely labile and differ greatly depending on which assumptions are used. One could therefore always find some support for the theories no matter what was found empirically (Reeve and Keller 2001; Heg et al. 2006; Nonacs 2006; Nonacs et al. 2006).

While the emphasis on ecology seen in skew models is commendable, their inability to make clear predictions has been a big problem. A possible solution is to focus instead on testing the different models' assumptions. However, assessing key assumptions such as whether a dominant actually concedes power rather than has it taken from them is not trivial (Clutton-Brock 1998), and the number of assumptions required to make predictions rises rapidly when more than two individuals interact (Johnstone et al. 1999). Further troubles for skew models come from the fact that some easily lose evolutionary stability (Kokko 2003), and that the fitness advantages given by the common assumption of sophisticated decision-making behavior can be very small relative to much simpler behavioral strategies that seem much more realistic (Nonacs 2006). In summary, skew theory provides general support for the importance of ecology in social evolution but, arguably, has not succeeded in incorporating ecology into social evolution theory in a more meaningful way than is achieved by Hamilton's original work. This is made particularly evident by the rise of the simpler "tug-of-war" skew models (Reeve et al. 1998; Reeve 2000; Langer et al. 2004; Heg et al. 2006), which assume that no individual has complete control, and whose principle prediction mirrors that of Hamilton's rule : that decreased relatedness will decrease group performance.

1.4.2   Cooperation in Viscous Populations

One of the earliest attempts to give a quantitative account of the evolution of
cooperation was that of Wright (1945) who, in a book review article, outlined the
argument that altruism could be favored in the context of viscous population struc-
ture. Wright framed this argument in terms of group selection, and was able to
provide an approximation for the ratio of the variance between and within groups
under varying degrees of dispersal. He understood that individual dispersal would
diminish this genetic structuring of the population, and hence slow the action of
within-group selection against altruists, but also that some dispersal is required to
spread this altruism over the whole population. From this, Wright reasoned that
altruism would be most favored with a tiny but nonzero rate of dispersal. However,
a mathematical proof for this was lacking.

Hamilton (1964a, 1971) picked up the thread in his account of inclusive fitness,
and reframed Wright's scenario in terms of population viscosity leading to a high
coefficient of relatedness between actor and recipient. Setting the argument in more
explicitly ecological terms, Hamilton (1964, 1971, 1975) revealed the previously
hidden problem of kin competition, and drew attention to an earlier treatment by
Haldane (1923) who had shown that this could reduce the between-family differ-
ences in fitness that are crucial in this context. Limited dispersal not only brings
relatives together to socialize, but also to compete for resources, and this could
work to inhibit the evolution of cooperation. Having outlined this important caveat,
Hamilton nevertheless argued that viscous populations would be those in which we
would most expect to see altruism flourishing.

Much later, Wilson and colleagues (Wilson et al. 1992) performed simulations
of cooperation evolution in purely viscous populations of the sort discussed by
Wright to provide a more accurate quantification of the limited dispersal effect.
Surprisingly, they could find no appreciable impact of the rate of dispersal on the
evolution of cooperation. This puzzling simulation study was soon followed by an
analytical 'island' model by Taylor (1992a), who used an inclusive fitness approach
to recover the same result. Amazingly, whether asexual or sexual reproduction was
assumed, and whether the model involved haploid, diploid or haplo-diploid modes
of inheritance, the parameter controlling the rate of dispersal simply cancelled out
of the analysis: cooperation evolved just as readily in fully mixing populations as it
does in viscous populations (Box 3). Taylor (1992b) followed this analysis with a
model of cooperation in a viscous 'lattice' population, and again recovered the
same result. For reasons that remain somewhat obscure, in an apparently wide class
of models the relatedness-enhancing effect of limited dispersal is exactly balanced
by the competition -enhancing effect of limited dispersal.

The situation is not always so bleak for viscosity and cooperation, however.
Haldane (1932) had sketched a model similar to Wright's in which selection
between groups was mediated not by differential production of individual dis-
persers but by differential production of daughter groups, which compete for
living space with other groups. Haldane suggested that if groups are small, then

Box 3 Impact of rate and pattern of dispersal

Rate of dispersal

Consider, as Wright (1945) does, that groups are made up of N individuals, and for simplicity we will assume that individuals are haploid and that a single locus controls their cooperation strategy. We begin with a population that is genetically uniform at this locus, and consider the fate of a vanishingly rare mutant allele that subsequently appears and increases the cooperation of its bearers by a small amount. Cooperation incurs a relative fecundity cost C and gives a total benefit B that is shared equally among all members of an individual's social group (including itself). We assume $B, C \ll 1$. Hence, the relative fecundity of a cooperator in a group containing i cooperators is:

$$f_i = 1 + B\frac{i}{N} - C, \tag{B3.1}$$

the average fecundity of her group is:

$$\overline{f}_i = 1 + (B - C)\frac{i}{N}, \tag{B3.2}$$

and the fecundity of the average group is:

$$\overline{\overline{f}} \approx 1. \tag{B3.3}$$

We now assume that: the offspring disperse to a random group elsewhere in the population with probability d, or else remain on their natal group with probability $1-d$; all adults die; and density-dependent regulation returns each group to size N and the juveniles mature to adulthood to take us back to the beginning of the lifecycle. Then, the fitness of the cooperator in the group of i cooperators is:

$$w_i = d\,f_i\frac{1}{\overline{\overline{f}}} + (1-d)\frac{f_i}{d\overline{f}_i + (1-d)\overline{f}} \approx 1 + (B - (1-d)^2(B-C))\frac{i}{N} - C. \tag{B3.4}$$

Denote the expected proportion of cooperators in an individual's group, averaging over all cooperators rather than over all groups, as R. Hence, the average fitness of a cooperator in this population is:

$$w \approx 1 + (B - (1-d)^2(B-C))R - C. \tag{B3.5}$$

Note that R is the expected relatedness of an individual to a randomly drawn member of its own group, including itself. Thus, the relatedness between different group mates is r, which satisfies $R = (1/N) + ((N-1)/N)r$. Substituting into our expression for the average fitness of cooperators, obtains:

Box 3 (continued)

$$w \approx 1 - \left(C - \frac{B - (1-d)^2 (B-C)}{N} \right) + \frac{(N-1)(B - (1-d)^2 (B-C))}{N} r, \qquad \text{(B3.6)}$$

and since the condition for cooperators to invade is $w > 1$, this yields Hamilton's rule, $-c + br > 0$, where:

$$c = C - \frac{B - (1-d)^2 (B-C)}{N}, \qquad \text{(B3.7)}$$

$$b = \frac{(N-1)(B - (1-d)^2 (B-C))}{N}, \qquad \text{(B3.8)}$$

i.e., both the direct and indirect fitness effects of cooperation are modulated by the ecological parameter: the rate of dispersal, d. As Wright (1945) noted, dispersal also impacts on the genetic structure of populations, and this can be shown by calculating the coefficient of relatedness r in terms of model parameters. If we subscript the relatedness coefficient to denote the generation in which we take our measurement, then we can write the following recursion:

$$r_{t+1} = (1-d)^2 R_t = (1-d)^2 \left(\frac{1}{N} + \frac{N-1}{N} r_t \right), \qquad \text{(B3.9)}$$

because with probability $(1-d)^2$ neither of the two individuals dispersed from its natal group. Solving for equilibrium $r_t = r_{t+1} = r$, we have:

$$r = \frac{(1-d)^2}{N - (N-1)(1-d)^2}, \qquad \text{(B3.10)}$$

i.e., relatedness is indeed also dependent on the ecology of the population. Note that a very curious result is recovered when we substitute this relatedness expression into our Hamilton's rule, to derive a condition for increase in cooperation. We obtain:

$$-C + \frac{B}{N} > 0, \qquad \text{(B3.11)}$$

so that although ecology impacts individually upon the cost and benefit and coefficient of relatedness, it does not influence the overall condition for cooperation to be favored. Indeed, in this simple model, cooperation evolves just as readily (or unreadily) in a viscous population as it does in a fully mixing population (Taylor 1992a). It is important to note, however, that how we

Box 3 (continued)

classify this cooperation is dependent on the ecological details. Focusing on the region of parameter space over which cooperation is favored, depending on the rate of dispersal, the cooperation may be altruistic (c, $b > 0$) or mutually beneficial ($c < 0$, $b > 0$) (Rousset 2004).

Pattern of dispersal

Things are changed somewhat when we consider the effect of varying the pattern of dispersal. The following investigation of 'budding' dispersal is based upon the 'tribe splitting' model of Haldane (1932) and the analysis of Gardner and West (2006). We begin by making the same assumptions as in the previous individual dispersal model. However, we now assume that, after social interaction has determined individual fecundities: offspring randomly collect together with other juveniles on their patch to form a 'bud' of N individuals, which either disperses with probability d_B to a random patch, or else remains on the natal patch with probability $1-d_B$; then all adults die; then of all the buds finding themselves competing for space on a particular patch, one is chosen at random to escape being destroyed by density dependent regulation; and then finally we allow for random exchange of individuals at rate d_I between patches.

Implementing these assumptions gives a new expression for the expected fitness of a cooperator in a group of i cooperators:

$$w_i = d_B f_i \frac{1}{\overline{f}} + (1-d_B)\frac{f_i}{d_B \overline{f_i} + (1-d_B)\overline{\overline{f}}} \approx 1 + (B - (1-d_B)^2(B-C))\frac{i}{N} - C. \tag{B3.12}$$

The new assumptions also impact the recursion for relatedness, r:

$$r_{t+1} = (1-d_I)^2\left(\frac{1}{N} + \frac{N-1}{N}r_t\right). \tag{B3.13}$$

Following the same procedure as before, we derive a Hamilton's rule describing the condition for increase in cooperation, $-c + br > 0$, where:

$$c = C - \frac{B - (1-d_B)^2(B-C)}{N}, \tag{B3.14}$$

$$b = \frac{(N-1)(B - (1-d_B)^2(B-C))}{N}, \tag{B3.15}$$

$$r = \frac{(1-d_I)^2}{N - (N-1)(1-d_I)^2}. \tag{B3.16}$$

Box 3 (continued)

Thus, as before, ecology impacts all the components of Hamilton's rule: budding dispersal, by mediating the degree of kin competition, impacts on the fitness components; individual dispersal, by mediating the genetic structure of populations, impacts upon the coefficient of relatedness. This budding model has decoupled the competition and relatedness effects of dispersal that were bound together in the previous model. Indeed, the budding dispersal model becomes mathematically equivalent to the individual dispersal model when we impose the constraint $d_B = d_I = d$. However, in contrast to the individual dispersal model, the condition for increase in cooperation is not generally independent of the ecology, and is given by

$$\frac{1-(1-d_B)^2}{(N-1)(1-(1-d_I)^2)+1-(1-d_B)^2} B > C. \qquad \text{(B3.17)}$$

In the special case of zero exchange of individuals between groups ($d_I = 0$), equilibrium relatedness is 1 (clonal groups), and this condition for increase reduces to $(B-C)d_B > 0$. Here, so long as there is some relaxation of kin competition due to budding dispersal ($d_B > 0$), then any act that gives a net increase to group fecundity ($B-C>0$) is favored by selection.

by chance some daughter groups would be more altruistic than others, and this random replenishment of between-group variation would provide a possibility for sustained group selection for altruism. This stochastic 'tribe-splitting' model of group selection resisted quantitative exploration, though a simulation study by Goodnight (1992) produced results that seemed to confirm Haldane's argument, and showed that altruistic cooperation could readily evolve in this model. More recently, Gardner and West (2006) rephrased the model in terms of kin selection, and provided a straightforward analytical treatment of the model and conditions for when cooperation would be favored (Box 3). Thus, the pattern as well as the rate of dispersal has important implications for our understanding of social evolution. Various other ecological and demographic details examined in the context of cooperation in viscous populations include: population elasticity (Taylor 1992b; Mitteldorf and Wilson 2000; van Baalen and Rand 1998); overlapping generations (Taylor and Irwin 2000; Irwin and Taylor 2001); hard versus soft selection (Rousset 2004; Gardner and West 2006); transgenerational cooperation (Lehmann 2007); and catastrophic disturbances (Brockhurst 2007; Brockhurst et al. 2007).

An empirical verification of the importance of kin-competition came with the discovery that male fighting in fig wasps is just as brutal in species where the

competitors are highly related, i.e., full brothers, as in species where they are generally unrelated (West et al. 2001). Localized competition in the fig is of an intensity that overrides the relatedness incentive for self-restraint. Similarly, localized competition has been shown to reduce cooperative contribution to public goods in bacteria (Griffin et al. 2004) and humans (West et al. 2006). Such effects have led to the development of a concept of 'effective' relatedness. Relatedness is a relative measure of genetic similarity, taken with respect to the population average. However, defining the population is a somewhat arbitrary matter. Queller (1994; and see Kelly 1994) suggested that the effects of kin competition could be subsumed into the coefficient of relatedness by measuring genetic similarity with reference to the 'economic neighborhood', i.e., the scale at which competition occurs, rather than the population as a whole. This has proven to be a useful conceptual aid, and leads to the simple idea that as competition becomes more localized, and hence the genetic similarity to one's competitors increases, the effective relatedness towards one's social partners is decreased. Thus, as a general rule of thumb, local competition should inhibit the evolution of cooperation. Also, because the effective relatedness can be driven below zero and become negative, local competition should promote the evolution of harmful or even spiteful behaviors (Gardner and West 2004a; Gardner et al. 2004, 2007a). In all of these cases, ecology is the key to making predictions for social evolution.

1.4.3 The Tragedy of the Commons

Another approach that has emphasized ecological aspects of social evolution is theory based upon the analogy of the "tragedy of the commons" (Rankin et al. 2007a). This analogy has its roots firmly in ecology, with a now-famous paper by Garret Hardin in the 1960s, which argued that, without curbs on individual-oriented human behavior, society is heading for ecological disaster (Hardin 1968). The name comes from the analogy of a commons pasture open to many herdsmen, where the best strategy for each herdsman is to add as many cattle as possible, even though this eventually causes the demise of the pasture. The tragedy arises because the benefit of adding an extra cow to the commons accrues only to its owner, while the cost is shared equally amongst all the users of the commons. In evolutionary terms, this is another way of phrasing the problem presented by cooperation, which often involves a tension between the individual and the group (Leigh 1977; Frank 1994, 1995; Foster 2004; Wenseleers et al. 2004b). To a great extent, this is the same problem that Hamilton solved long ago, but the tragedy of the commons analogy has utility because it explicitly describes the performance of the social group (Foster 2006). This has led to a modeling approach based upon neighbor-modulated fitness, but which emphasizes the tension between levels of selection. Notably, Frank (1994, 1995, 1996, 2003) has elegantly modeled the evolution of parasite virulence and policing behaviors by taking a tragedy of the commons approach. In these models, the neighbor-modulated fitness (w) of the individual in a group is

written as a function of its own selfishness (z) and of the average selfishness exhibited among the members of its group (z'):

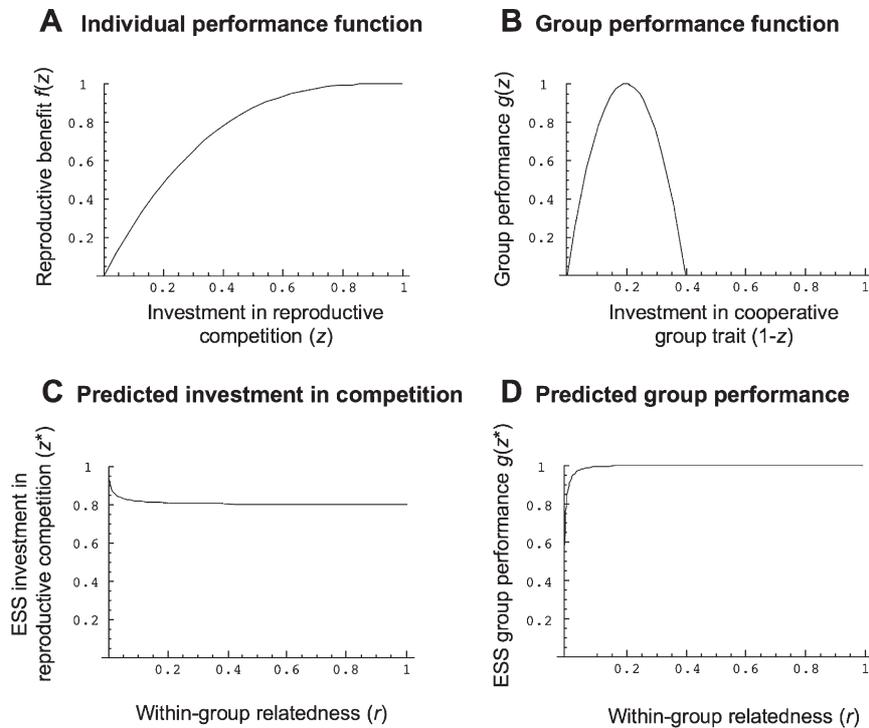$$w(z,z') = \frac{f(z)}{f(z')}\,g(z'),\qquad\qquad(4.3.1)$$

where the individual's relative share $f(z)/f(z')$ of the group's success increases with its own selfishness (z) and decreases with the average selfishness of the group (z'), and where the success of the group $g(z')$ decreases with the average selfishness of its constituent members (z'). Frank (1994, 1995) examined the simple form:

$$w(z,z') = \frac{z}{z'}(1-z').\qquad\qquad(4.3.2)$$

Using the standard neighbor modulated fitness approach outlined in Box 2, Frank found that the evolutionarily stable level of selfishness is $z^* = 1 - r$. If relatedness is absent ($r=0$) then full selfishness ($z^* = 1$) is predicted. However, a degree of relatedness ($r>0$) can avert the tragedy, and the group can be expected to enjoy some success ($g>0$).

The multi-level nature of such models lends them to ecological considerations. Most simply, one can ask how the shape of the within-group (f) and group-level (g) success functions affects the outcome of social evolution, and in particular, the extent of any social tragedy (Foster 2004). This reveals that the performance of social groups is enhanced whenever investment in either individual competition or, conversely, group-level cooperation provide diminishing returns (successive investments give smaller and smaller increments in reward). The ecology of many social species suggests that diminishing returns will be common, and therefore social tragedy may be typically less pronounced than simple linear models suggest. A nice example is blood sharing in vampire bats whereby the bats give blood to others in the group that did not manage to forage on a particular evening. Here the selfish benefits of holding onto blood diminish with the more blood that is retained as each bat can only use so much, which promotes sharing of at least some blood with the others (Fig. 1.3).

Further ecological realism has been built into this approach by models that express within-group and group-level performance as functions of group size, where, following the logic of the tragedy, group size decreases as more competition evolves (Rankin 2007; Rankin et al. 2007a; 2007b). A simple corollary of this is that species with intense competition will have small populations and may even drive themselves to extinction in a process termed 'evolutionary suicide' (Rankin and Lopez-Sepulcre 2005). This of course raises the question of why species do not frequently engage in so much competition that they drive themselves extinct. One solution is that the selective incentive for competition is density-dependent such that at low population density, competition is not selected and the species will not evolve the final *coup de grace* (Rankin 2007). However, it may also be the case that species have frequently driven themselves extinct through this process (Rankin and Lopez-Sepulcre 2005). This raises the interesting possibility for a species-level selection process to favor those species organized in such a way as to remove the selfish incentive that erodes

A **Individual performance function**

B **Group performance function**

C **Predicted investment in competition**

D **Predicted group performance**

Fig. 1.3 Blood sharing in vampire bats as an example of diminishing returns in a social trait (Foster 2004). Consideration of the ecological costs and benefits of blood sharing reveal that very low levels of relatedness are required for blood sharing to function extremely well. a Individual performance function $f(z) = 1 - (1 - z)^3$ based upon the empirically determined relationship between proportion of blood meal retained (investment in self) and time to starvation (Wilkinson 1984), which is used as a proxy for reproductive benefit. The curve closely approximates Fig. 2 in Wilkinson 1984 after the axes have been normalized to a 0 to1 range. b Relationship between investment in reproductive competition and group performance $g(z) = 1 - a(z - b)^2$ where $a = 25$, $b = 0.8$. This is based on the observation that around 20% of bats do not feed each night so that the remaining bats will have to donate on average 20% of their resources for all bats to have equal survival probability, which is assumed to maximize group survival. c Investment in reproductive competition at equilibrium ($z*$) as a function of within-group relatedness. d Group performance at equilibrium $g(z*)$ as a function of within-group relatedness. This predicts how close group performance matches that of a perfectly cooperative group and measures the tragedy of the commons. See Foster (2004) for more details

cooperation (Rankin et al. 2007b), which will moderate the degree of social conflict that we see in nature. Interestingly, this argument, which has its roots in an essay by J.B.S. Haldane (1939), is greatly strengthened when one considers ecological competition among species, because now competitive exclusion means that species even slightly weakened by internal competition can be driven extinct (Rankin et al. 2007b). This observation illustrates how explicit consideration of ecological processes can strongly affect the conclusions of a social evolution model.

1.5   Closing Remarks

Although it has played upon the minds of theoretical biologists ever since Darwin, the ecology of cooperation is far from being properly understood. On the one hand, we have seen that the formal foundations of social-evolutionary theory are well developed and that core results such as Hamilton's rule provide a conceptually simple but also a completely general framework in which to understand the evolution of cooperation in terms of direct and indirect fitness benefits. On the other hand, it is abundantly clear that the link between an individual's genes and its inclusive fitness is heavily mediated by ecology. We still have much to understand about these ecological effects, both theoretically and empirically. Like so many topics within evolutionary biology, there is a need for more work that combines theory with careful natural history, but as we proceed, we should remember the extraordinarily prescient work of Kropotkin, the father of ecological sociobiology, and his law of Mutual Aid :

"As soon as we study animals – not in laboratories and museums only, but in the forest and the prairie, in the steppe and the mountains – we at once perceive that though there is an immense amount of warfare and extermination…, there is, at the same time, as much, or perhaps even more, of mutual support, mutual aid, and mutual defence…" (Kropotkin 1902)

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