

REVIEW

The group selection controversy

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Abstract

Many thought Darwinian natural selection could not explain altruism. This error led Wynne-Edwards to explain sustainable exploitation in animals by selection against overexploiting groups. Williams riposted that selection among groups rarely overrides within-group selection. Hamilton showed that altruism can evolve through kin selection. How strongly does group selection influence evolution? Following Price, Hamilton showed how levels of selection interact: group selection prevails if Hamilton's rule applies. Several showed that group selection drove some major evolutionary transitions. Following Hamilton's lead, Queller extended Hamilton's rule, replacing genealogical relatedness by the regression on an actor's genotypic altruism of interacting neighbours' phenotypic altruism. Price's theorem shows the generality of Hamilton's rule. All instances of group selection can be viewed as increasing inclusive fitness of autosomal genomes. Nonetheless, to grasp fully how cooperation and altruism evolve, most biologists need more concrete concepts like kin selection, group selection and selection among individuals for their common good.

Introduction

Darwin's theory of evolution by natural selection was often deemed incompatible with the evolution of cooperation. Here, if an agent reduces its own reproduction to help others, this cooperation is called altruism (West *et al.*, 2007a). However, even if a behaviour favoured through its helpfulness to others enhances the expected lifetime reproduction of all involved, it may reduce the reproduction of some agents when partners cheat. In fact, natural selection often favours costly or risky cooperation (Darwin, 1859:236–243). Nonetheless, selection's supposed incompatibility with cooperation sparked a series of disputes between attackers and would-be defenders of Darwin.

Some invoked selection among groups or populations to explain cooperation. Even now, when nearly all agree that cooperation and altruism are fully compatible with Darwinism, bitter disputes continue over what language is appropriate for the processes involved. This paper

reviews major features of the group selection controversy, focusing on the dispute between Wynne-Edwards, who promoted group selection, and Maynard Smith and George Williams, who opposed it, and the beginnings of its resolution. Finally, I criticize the attempt to dismiss group selection by simply subsuming it under inclusive fitness.

Group selection grabbed biologists' attention when Wynne-Edwards (1962, 1963, 1965) invoked it to explain why animals exploit resources sustainably. Citing Wright's (1929, 1945) view on how group selection could influence evolution, he proposed that most animal populations do not overexploit their resources as people so often do because those groups in a species that do not overexploit their resources survive to multiply. He assumed that this group selection could overcome over-exploiters' within-group advantage of more rapid reproduction. His work crystallized a latent fashion for group selection as a way relationships of interdependence can evolve even if a participant can gain at least temporary advantage by failing to contribute to a relationship it benefits from. Maynard Smith (1964), however, revealed this fashion's insecure foundations. First, Wynne-Edwards's major examples of behaviour promoting

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population regulation – territoriality, and social hierarchy that denies a group's lower-ranking members access to food when it is scarce – can result from competition among individuals. Second, selection among groups easily overrides selection within groups only if each group is founded by members from one parent group and groups exclude all immigrants. Group selection remained popular, however, until Williams (1966) expanded Maynard Smith's approach into a book. Williams argued that adaptations ascribed to group selection could be explained in other ways. Like Maynard Smith, Williams also believed that group could override within-group selection only if groups multiplied and died as groups. In other words, group selection must reflect differential survival and reproduction of whole groups, yielding group-level adaptations, a process Williams considered most unlikely. Most biologists accepted these conclusions. Nonetheless, Williams' aggressive hostility to group selection, his failure to show just what conditions allow group selection to override selection within groups and his brusque dismissal of some well-respected naturalists' observations kept the controversy alive. Understanding this controversy and its ramifications sheds light on the interplay of competition and cooperation in evolution.

I will discuss the group selection controversy and the interplay between competition and cooperation in terms of the following questions:

- 1 What was the 'prehistory' of this controversy?
- 2 After the controversy exploded, what processes were shown to influence evolution? How can kin selection, individual selection, the genome's common interest and selection among groups affect evolution?
- 3 Once group selection was demonstrated, D. S. Wilson tried to widen its domain. How should group selection be defined and circumscribed?
- 4 Is group selection just a form of 'generalized kin selection'? If so, how should this affect the way we think about evolution?

Prehistory

What developments made biologists so receptive to the ideas of Wynne-Edwards? To begin with, Darwinian evolutionary theory has long been blamed for its emphasis on competition, supposedly to the exclusion of cooperation and mutual aid (Kropotkin, 1902; Margulis, 1998). After all, cooperation is a fact of life. To compete more effectively with others, many animals live in cooperative groups. Mutualisms such as those between eukaryotes and their mitochondria, corals and their zooxanthellae, and plants and their pollinators, have transformed whole ecosystems. Ecosystems themselves are not only arenas of competition but webs of interdependence, commonwealths on whose integrity all members depend (Leigh & Vermeij, 2002).

In response, some tried to 'tweak' Darwinism to bring out features favouring the good of group or ecosystem. Thus, Dunbar (1960) proposed that selection among ecosystems discriminated against those where competition within or among populations favoured rapid exploitation of resources that generated potentially ecosystem-destroying population oscillations. Natural selection at any level, however, presupposes differential replication of discrete entities, a condition Dunbar's ecosystems do not satisfy.

Group selection is not invoked only for the evolution of cooperation. Wright (1929) invoked—but did not model—group selection as part of his shifting balance of evolution, remarking that 'Finally, in a large but subdivided population, there is a continually shifting differentiation among the local races, even under uniform static conditions, which, through intergroup selection, brings about indefinitely continuing, irreversible, adaptive and much more rapid evolution of the species as a whole'. Here, Wright invoked group selection because he thought that in large panmictic populations, selection on an allele is driven by its average contribution to fitness even if effects of substitutions at different loci are so nonlinear that a genotype's fitness bears little relation to the sum of its genes' average fitnesses (Wright, 1978). Group selection, on the other hand, would spread throughout the species those good genotypes which were fixed by chance in small groups. Wright (1932) viewed this 'shifting balance' as a process that tested genotypes, not the average merits of individual genes.

Sturtevant (1938) recognized that selection among groups might 'bring about characteristics favourable to the group but unfavourable to the individual'. He viewed insect societies as groups with just such characteristics. He knew, however, that in many social insect species, workers reproduce and inferred that selection within a colony could undermine the colony's good. He accordingly wondered how selection within colonies, among colonies and among populations of colonies jointly shaped the evolution of colony characteristics.

Later, Wright (1945) took the first step toward a quantitative theory of group selection. He realized that, just as genetic variance within a group governs the effectiveness of selection among its individuals (Fisher, 1930), so genetic variance among groups governs the effectiveness of selection among groups. Wright accordingly calculated how group size and exchange of migrants among groups influenced genetic variance among groups. He considered a locus with two alleles of equal fitness, A and a , in an array of identical groups. For simplicity, let each group have N haploid adults, let successive generations be distinct, and in each generation let a proportion m of these adults be exchanged at random among groups as migrants. If Q is A 's frequency in this array of groups, then the among-group variance in A 's frequency is $Q(1 - Q)/(2mN + 1)$ (Wright, 1931:128,

1945:417). Knowing the group lifetime L in individual generations, among-group genetic variance and average within-group genetic variance, one can tell whether group selection overrides equally strong selection within groups (Lewontin, 1970). Wright, however, did not do this. Instead, he wrote an equation for change in gene frequency, which was useless because there was no way to predict the behaviour of its most crucial variable, A 's frequency among migrants.

Finally, Lewontin (1962) provided a generally accepted example of group selection. He was concerned with the factors controlling the spread of t -alleles in a colony of 70 house mice. In Lewontin's case, 85% of the sperm in males heterozygous for the t -allele carry t , but males homozygous for t are sterile. In a large, panmictic population, this t -allele's frequency would be 0.7. In his colony of 70 mice, however, the frequency was 0.37. If the colony divides into breeding groups of two males and six females apiece—the normal size of natural breeding groups, the extinction of breeding units where both males become homozygous for t depresses t 's frequency to this level. Lewontin (1962) concluded that selection among breeding groups played a major role in arresting the t allele's spread in this laboratory colony. Lewontin (1965) concluded that selection among breeding groups played the same role in nature. Indeed, Lewontin's example reflects an interaction of selection among alleles within individuals, selection among individuals, genetic drift and selection among populations. Williams (1966) accepted this as the only convincing example he knew of group selection.

Lewontin's study helped to concentrate minds on the conditions required for group selection to work. In his system of mouse groups, a damaging distorter spreads in chain reaction from group to group as long as a group infected by the distorter infects more than one other group before dying out. Group selection arrests the distorter's spread only if, during an infected group's lifetime, less than one distorter-carrier, on the average, infects another group (Leigh, 1971:247; Maynard Smith, 1976). The more the individuals per group and the less a distorter diminishes its bearers' fitness, the more individuals will be infected before a distorter that successfully infects a group eliminates it. Successful emigration must be rare, groups small and the distorter quick to kill infected groups, for group selection to arrest the distorter's spread.

In sum, selection among groups was invoked for two purposes. Most invoked it to explain the evolution of cooperation among individuals, whether of the same or different species. Wright invoked it to explain the evolution of advantageous genotypes when the effects of different gene substitutions interact nonlinearly. Although Wright realized that genetic drift could create the variation among groups needed for group selection, and simulations of Lewontin (1962) demonstrated its role in controlling the spread of segregation distorters in

house mice, no one developed the mathematical theory needed to compare the effectiveness of within- versus among-group selection. This failure may explain the extraordinarily rapid shifts of opinion in the 1960s concerning the role of group selection in evolution.

Kin selection serves the common interest of the genome

In 1964 a new explanation was proposed for the evolution of altruism among animals. Hamilton (1964a,b) developed the theory of kin selection to show how social behaviour could evolve among animals. In essence, an animal's genes spread faster if their carriers help relatives when they can do so without excessive risk to their own reproductive prospects. The decisive criterion for when to help is Hamilton's rule. Following Hamilton (1964a), let r_i be the genealogical relatedness of an agent to individual i , the expected proportion of the agent's genes at an autosomal locus identical by descent from a recent common ancestor to genes at this locus in individual i . Nowadays this relatedness is defined as the regression of an autosomal allele A 's frequency in individual i on its frequency in the agent (Hamilton, 1970, 1972; Bourke & Franks, 1995:12–18); Hamilton (1963) foresaw this development.

To formulate Hamilton's rule, let c be the cost to the agent's reproduction from some altruistic act and b_i the prospective increase from it of individual i 's reproductive output. Then this act benefits the agent's genes if

$$\sum_{i=1} b_i r_i > c$$

To incorporate kin selection in population genetics, Hamilton (1964a) introduced the concept of an individual's 'inclusive fitness'. He originally calculated relative inclusive fitness as the individual's own reproduction, less that due to help from others, plus the spread of its genes from assisting relatives. Following another road that Hamilton (1964a:5) noticed but did not take, Queller (1985), Taylor & Frank (1996) and Taylor *et al.* (2007) partitioned an individual's fitness into the part of its reproduction secured by its own behaviour, plus that enabled by help from others. Hamilton's formulation gives a more immediate sense of how insect societies can evolve. Queller's shows the distinction between an individual's advantage and the genome's common interest more clearly. Although ant workers are sterile, selection favoured the evolution of ant societies because the genes involved gained more from the queen's hyper-reproductivity than they lost from worker sterility.

Anticipating the 'green-beard' alleles of Dawkins (1976), Hamilton (1964b; 24–25) imagined an allele whose bearers recognized and helped other bearers. Such an allele spreads if the cost to a bearer's fitness of helping other bearers is exceeded by the increased spread of this allele resulting from this help. Hamilton considered this circumstance a logical extension of his inclusive fitness

concept, even though his original vision of inclusive fitness focused on individuals, whereas this extension focused on an allele's fitness (Gardner *et al.*, 2007:215). Except, perhaps, for an ambiguous reference in Hamilton (1971), Hamilton never revisited 'green-beards'. Later, I will show that the spread of green-beard alleles does not necessarily serve the common interest of autosomal genes. Henceforth, following Hamilton (1975), I refer to kin selection as a process driven by genealogical relationships.

Kin selection is more likely to be effective when donor and beneficiary are more closely related, and when the ratio of relative i 's benefit to actor's cost, b_i/c , is high (West Eberhard, 1975). Kin selection is invoked to explain phenomena as varied as parental care (Lewontin, 1970), offspring from previous clutches helping their parents rear younger siblings (Emlen & Wrege, 1988) and the evolution of social behaviour in insects (Hamilton, 1964b; West Eberhard, 1975; Ratnieks *et al.*, 2006; Boomsma, 2007; Hughes *et al.*, 2008). This theory assumes weak selection when the coefficient of relatedness is calculated assuming neutrality, as is often the case (Hamilton, 1964a, 1987a; Michod & Hamilton, 1980). Genealogical relatedness of two individuals is the same for all autosomal loci; so, kin selection serves the common interest of autosomal genes.

Social insects include societies, such as honeybees and leaf-cutter ants, so wonderfully organized that some call them superorganisms (Wheeler, 1928:304; Hölldobler & Wilson, 2009). Indeed, the analogy between the development of division of labour within a wasp colony as it grows from a single fertilized female and the growth and differentiation of a metazoan from a fertilized egg was fruitful enough to provide the basis for a prize-winning book (West Eberhard, 2003). The evolution of insect societies is considered a major transition of evolution (Maynard Smith & Szathmáry, 1995).

Showing how social insects could evolve is perhaps the finest triumph of kin selection theory. One must interpret this remark with care. Relationship alone is a wretched predictor of when social behaviour evolves: other circumstances modulate the ability of kinship to favour social behaviour among insects (Hamilton, 1972:206; Hunt, 2007; Hölldobler & Wilson, 2009). Haplodiploidy, which creates a relatedness of three-fourths between monogamous mothers and their daughters, is neither necessary nor sufficient for the evolution of insect societies. Termites, which are diploid, all live in social colonies because their ancestors, like ancestral wasps and ants, lived as enduring family groups in valuable nests. These groups had long-lived, monogamous reproductives, extensive parental care and benefited greatly from collective defence against predators or competitors. Dispersal to found new nests was risky and uncertain. Dispersers' young survived only if their mother lived long enough for them to mature. In a larger, safer colony, however, a worker's help enhanced

its inclusive fitness even if it died early (Queller, 1989; Gadagkar, 1990). Indeed, many of these conditions must apply for haplodiploids to evolve true societies (Thorne, 1997). Nonetheless, kin selection allowed biologists to make sense of the evolution of insect societies where some members refrain from reproducing (Wilson, 1971:307–335; West Eberhard, 1975, 1981, 1987), as I will now outline.

In insects, the transition to complex social life begins when a daughter faces the choice between helping her dominant mother reproduce on an established nest and founding a new nest on her own (West Eberhard, 1975). If the mother mates only once, the daughter is more closely related to subsequent young, shifting the balance of advantage somewhat toward helping her mother. As kin selection theory predicts, the original social ancestors of the eight clades of social wasps, bees and ants considered by Hughes *et al.* (2008) were all monogamous. Even so, in insect societies with few workers, all resembling the queen, there is often overt reproductive conflict between queens and workers that would be queens (Heinze *et al.*, 1994; Ratnieks *et al.*, 2006).

In more complex hymenopteran societies, workers can distinguish fellow members from nonmembers (Hamilton, 1987b). Hamilton believed that this power to discern and reject unrelated strangers that might be cheaters was crucial to the evolution of complex societies. Members of social clones of aphids cannot distinguish members from nonmembers: despite far closer relatedness among members, aphid societies are never as complex as those of ants or honeybees (Hamilton, 1987b).

When workers cannot mate, social evolution passes a 'point of no return' (Boomsma, 2007). Division of labour becomes more definite. Specialized division of labour and, sometimes, morphology, and reduced reproductive capacity means that workers' inclusive fitness is often higher when they help their queen than when they produce male young, even if the queen mates multiply, reducing her workers' relatedness to her young (West Eberhard, 1975; Boomsma, 2007). Indeed, in large, complex ant colonies, workers treat their queen as a valued resource, rather than a rival (Hölldobler & Wilson, 1990:194). Leaf-cutter ants, *Atta* and *Acromyrmex*, and army ants, *Eciton*, have complex societies with elaborate division of labour that proceeds automatically, without enforcement by the queen (Hölldobler & Wilson, 1990). These societies have signalling systems that organize workers' activities in accord with their colony's needs (Hamilton, 1987b), like those coordinating the activities of a metazoan's cells (Bonner, 2000). In these societies, the queen mates many times (Villesen *et al.*, 2002; Denny *et al.*, 2004). Multiple mating increases a colony's genetic diversity. Genetic diversity enhances its resistance to pathogens (Hamilton, 1987b; Denny *et al.*, 2004; Hughes & Boomsma, 2004, 2006), allowing truly giant colonies to evolve. This genetic diversity may also be needed to partition workers effectively over tasks (Hughes *et al.*, 2003).

Honeybees, *Apis* spp., also have large, complex societies with elaborate but automatic division of labour and effective signalling systems for coordinating different activities (Seeley, 1995). Here, too, the queen mates many times, enhancing its colony's disease resistance (Seeley & Tarpy, 2007). The resulting genetic diversity plays an essential role in distributing workers appropriately over tasks (Mattila & Seeley, 2007). Among honeybees, however, unmated workers can lay male eggs. Such egg-layers do not work: after all, the work of others provides abundant resources for them to exploit. Here, multiple mating causes kin selection to shape the workers' common interest in helping their queen. Workers are less related to half-sisters' eggs than to their queen's eggs. As they benefit more from the rearing of their queen's eggs, they eat eggs laid by half-sisters (Ratnieks & Visscher, 1989; Visscher, 1996). Kin selection thus played a double role in shaping honeybee societies. As the effectiveness of policing increases in wasp and bee societies, the proportion of reproductives among workers in these societies decreases, whereas, among these same societies, this proportion of reproductives is higher where workers are more closely related (Wenseleers & Ratnieks, 2006). Either sterilization or policing of workers seems necessary for large, complex insect societies to function smoothly.

The genome's common interest, adaptation and fair meiosis

Kin selection, the name given by Maynard Smith (1964) to the process described by Hamilton (1964a), expresses the common interest of an organism's autosomal genes, for the criterion of when to help applies equally to every autosomal locus (Bourke & Franks, 1995). Indeed, adaptation serves the common interest of autosomal genes. Sex ratio and sex allocation normally express the common interest of autosomal genes, which usually override effects of sex-linked genes that challenge this common interest (MacArthur, 1961; Leigh *et al.*, 1985; Hamilton, 1987a; Grafen, 2006).

The common interest of autosomal genes has nearly eliminated conflict between the good of individual genes and the good of their carriers, as measured by their autosomal genomes' inclusive fitness (Hamilton, 1964a). Selection among genes conflicts with selection among individuals if a segregation-distorter allele that biases meiosis in its own favour imposes a phenotypic defect on its bearers. Selection at loci unlinked to the distorter, however, favours mutants that restore the fairness of meiosis, suppressing the distortion and sparing some of their descendants the phenotypic defect segregation distortion would have inflicted on them. As selection at every unlinked locus favours restoring the fairness of meiosis, fair meiosis reflects the common interest of the genome (Leigh, 1971, 1991). The common interest of the genome has enforced an

astonishing degree of fairness in meiosis among autosomal loci: segregation distortion is a very rare phenomenon (Crow, 1979, 1991). In many lineages, simple ways to bias meiosis seem to have been eliminated (Crow, 1979:146). For example, inactivating the Y chromosome is a common way of preventing the biasing of sex ratios through Y chromosome distortion (Hamilton, 1967). Duplicating the chromosomes just before the 'reduction divisions' that produce haploid gametes prevents the spread of 'sister-killer' chromosomes (Maynard Smith & Szathmary, 1995:157). The common interest of the genome has not brought transposable elements to order (Hurst & Werren, 2001), and fair meiosis does not control cytoplasmic genes (Maynard Smith & Szathmary, 1995). Nonetheless, fair meiosis is widespread enough to ensure that alleles at chromosomal loci almost never spread unless they benefit their carriers (Leigh, 1991; Leigh & Rowell, 1995). Fair meiosis eliminates nearly all conflict between selection on chromosomal genes and selection among individuals. Contrary to Wilson & Sober (1989), it is entirely logical to treat genes-in-individuals differently from individuals-in-groups: few groups have mechanisms suppressing selection among their individuals as effective as fair meiosis and the lock-step simultaneity in reproduction of all chromosomal genes.

Hamilton (1964b) imagined an allele, called a green-beard by Dawkins (1976), which spreads because its helpers help other bearers, or injure nonbearers. Is this a useful extension of the inclusive-fitness concept? Both Hamilton (1964b) and Dawkins (1982) considered the simultaneous appearance of an ability to recognize fellow 'green beard' bearers *and* a propensity to help them too unlikely for serious attention. Haig (1996), however, showed that an allele affecting the adhesiveness of cells in its bearers could act as green-beards. And indeed, in social amoebae, a green-beard allele causes amoebae bearing it to stick together, excluding other bearers, when the time comes to form a spore-dispersing fruiting body (Queller *et al.*, 2003).

Alexander & Borgia (1978) and Dawkins (1982) saw that a green-beard allele's spread can impair the autosomal genome's common interest, just a secret mutual-aid association like the mafia can impair the common good of society. Haig (1996) showed how differential attraction between the placentae of green-beard embryos and the surrounding cells of green-beard mothers, which prejudices the prospects of non-green-beard embryos, could spread the green-beard allele at the expense of its bearers' inclusive fitness. In red fire ants, *Solenopsis invicta*, workers bearing the b-allele at the Gp-9 locus kill queens lacking b. This green-beard behaviour maintains b in the population, even though b is lethal when homozygous (Keller & Ross, 1998). This is an exact parallel to segregation-distorters such as t-alleles (Lewontin, 1962). Helantera & Bargum (2007) remark, moreover, that, although a green-beard allele

benefits when its bearer offers costly help to an unrelated bearer, alleles at unlinked loci in this bearer do not: green-beards necessarily give rise to genetic conflict. As these considerations suggest, there is no evidence that green-beards played any role in the evolution of division of labour between reproductives and workers in metazoan societies (Helanterä & Bargum, 2007).

Representing group selection as kin selection

G. R. Price and W. D. Hamilton opened a way to understand the interplay of selection among individuals within a group and selection among groups. Price (1972a) and Hamilton (1975) derived equations for this interplay satisfying most of the desiderata of Lewontin (1970). I will simplify their models to bring out the essential features of this interplay. I first derive Price's (1970) theorem for a population of haploids. Let z be a quantitative characteristic, let Z_i be its value in individual i , and let W_i be i 's fitness, the expected number of offspring in the next generation of an individual with value Z_i of z . Finally, let Z'_i be the average value of z in i 's offspring. Thus, the change in this characteristic's average value Z from generation t to generation $t + 1$ is

$$\begin{aligned} Z(t+1) - Z(t) &= \Delta Z(t) = \sum_i (W_i Z'_i - Z_i) / W \\ &= \sum_i [(W_i - 1)Z_i + W_i(Z'_i - Z_i)] / W, \end{aligned}$$

where W is the population's mean fitness. This equation can be rewritten as

$$\begin{aligned} \Delta Z &= \{\text{cov}(W_i, Z_i) + E[W_i(Z'_i - Z)]\} / W \\ &\equiv \{\text{cov}(W_i, Z_i) + E[W_i \Delta Z_i]\} / W. \end{aligned}$$

The second term includes both changes from recombination among epistatic loci and the effects of environmental change. $\text{Cov}(W_i, Z_i) = \beta_{WZ} V_Z$, the regression β_{WZ} of fitness on Z_i , times the population's variance V_Z in Z_i . Thus, we obtain Price's theorem,

$$\Delta Z = [\beta_{WZ} V_Z + E(W_i \Delta Z_i)] / W.$$

If $\ln W$ depends linearly on Z_i , and if $|W_i - W| \ll W$, then $\beta_{WZ} / W \approx d \ln W / dZ_i$. More generally, β_{WZ} / W represents the intensity of selection on Z .

Now let each individual i be a distinct group of individuals, let each group have N individuals apiece, and let $\Delta Z_i = Z'_i - Z_i$ be the change from within-group selection of group i 's average value Z_i of z . This is $\text{cov}(w_{ij}, z_{ij})$, where z_{ij} is z 's value in individual j of group i and w_{ij} individual ij 's within-group fitness. Let $\Delta Z_i = \text{cov}(w_{ij}, z_{ij}) / W_i = \beta_{wz} V_z(i)$, where $V_z(i)$ is the variance of z within group i , β_{wz} is the regression of within-group fitness w_{ij} on z_{ij} , which is assumed the same for all groups, and β_{wz} / W_i is the intensity of within-group selection on z_i . Thus,

$$\Delta Z = \{\beta_{WZ} V_Z + \beta_{WZ} E[V_z(i)] + E_{ij}(w_{ij} \Delta Z_{ij})\} / W,$$

where the first term represents the effect of group selection, and the second that of selection within groups (Price, 1972a; Hamilton, 1975, eqn 3). The first two terms represent the partial effect of selection on Z in precisely the same sense that Fisher's fundamental theorem represents the partial effect of selection on mean fitness (Price, 1972b; Ewens, 1989; Frank, 1997:1718).

Now let

$$z_{ij} = \begin{cases} 1, & \text{if individual } j \text{ in group } i \text{ cooperates,} \\ 0, & \text{otherwise.} \end{cases}$$

Let Z be the average value of z_{ij} in the whole system and Z_i be its average value in group i , as before. Let $w_{ij} = 1 + b(Z_i - z_{ij}/N) - cz_{ij}$. Here, c is the cost of providing a benefit that improves the fitness of every other member of group i by an amount b/N . If $|b - c| \ll 1$, $W \approx W_i \approx 1$, and $d \ln w_{ij} / dz_{ij} \approx \beta_{wz} / W_i = -c$, $d \ln W_i / dZ_i \approx \beta_{WZ} / W = b - c$, the partial effect of selection on Z is

$$(b - c)V_Z - cV_z = bV_z - c(V_Z + V_z).$$

$V_Z + V_z$ is the total variance V_T in z_{ij} . The intragroup correlation among members of group i in z_{ij} , which in the simplest case, is the average relatedness r of fellow group members, is $V_Z / (V_Z + V_z)$. Therefore, $\Delta Z > 0$ if $br > c$. This is Hamilton's rule that governs when kin selection favours helping relatives (Hamilton, 1975; Crow & Aoki, 1982). Here, group selection, like kin selection, expresses the common interest of autosomal genes.

Hamilton's rule for individuals divided into groups can be derived in another way (Queller, 1992). Let group i have N_i individuals and let individual j in group i have fitness $w_{ij} = 1 + b(Z_i - z_{ij}) - cz_{ij}$ as before. Now apply Price's theorem directly to the set of all individuals ij (Queller, 1992). We find that the partial effect of selection on Z is

$$[\text{cov}(z_{ij}, w_{ij})] / W = \{\text{cov}[z_{ij}, -cz_{ij}] + \text{cov}[z_{ij}, b(Z_i - z_{ij}/N_i)]\} / W.$$

Here, $\text{cov}[z_{ij}, -cz_{ij}] = -cV_T$, where V_T is the total variance in z among all individuals z_{ij} . $\text{cov}[z_{ij}, b(Z_i - z_{ij}/N_i)]$ is the covariance in z between the agent ij and its fellow group members. The agent ij 's average relatedness r to its fellow group members is given by the formula $\text{cov}(z_{ij}, Z_i - z_{ij}/N_i) / V_T$. Thus, selection favours increased Z if $(V_T/W)(rb - c) > 0$, i.e. to say, if Hamilton's rule applies (Queller, 1992; Gardner *et al.*, 2007). This derivation poses no restriction on the strength of selection.

Hamilton's rule applies even if a positive regression r of the helpfulness of neighbours interacting with an agent on the helpfulness of that agent's genotype arises from causes unconnected with genealogical relatedness (Hamilton, 1975; Queller, 1985; Fletcher & Doebeli, 2006, 2009). For example, playing a strategy related to tit for tat in an interaction resembling iterated prisoner's dilemma causes cooperators to associate with other

cooperators (Queller, 1985; Fischer, 1988; Fletcher & Zwick, 2006). Thus, the domain of Hamilton's rule and inclusive fitness far transcends that of kin selection (Hamilton, 1975; Grafen, 1985; Frank, 1997, 1998; Gardner *et al.*, 2007). It seems safe to say that the driving principle of adaptation is that, over the long term, selection favours those alleles that increase the inclusive fitness of their bearers' autosomal genome.

Can group selection override selection within groups?

In 1980, the central question about group selection was: what conditions allowed selection among groups to override within-group selection (Slatkin & Wade, 1978; Aoki, 1982; Crow & Aoki, 1982, 1984; Kimura, 1983)? To evaluate the relative strength of selection within and among groups requires calculating V_z/V_Z , the ratio of within- to among-group genetic variance. As the correlation in z_{ij} among a group's members is $r = V_z/(V_z + V_Z)$, $V_z/V_Z = (1 - r)/r$. Calculating V_z/V_Z is the easiest to do when genetic drift is the only source of among-group variance and among- and within-group variance influence each other only through the exchange of migrants among populations. Let each population have N individuals, and let a proportion m of the adults of this species be exchanged among these populations at random each generation. The exchange of migrants reduces the variance among populations by a factor $(1 - m)^2 \approx 1 - 2m$ each generation (Slatkin & Wade, 1978, eqn 5). On the other hand, in each generation genetic drift increases among-group genetic variance in Z_i by V_z/N , the variance among means of independent samples of size N from the normal distribution of values of z , with variance V_z , among the gametes produced by this group's parental generation (Slatkin & Wade, 1978). At steady state, $V_z/N = 2mV_z$, $V_z/V_Z = 2mN$. This conclusion could have been derived from the mathematics of Wright (1931). Like Wright's mathematics, this derivation assumes near-neutrality.

When can group selection override equally intense within-group selection? Let each group live L generations, and let a group whose average value of z is Z_i leave $1 + e(Z_i - Z)$ offspring groups. Here, $e/L = b - c$, for $b - c$ is measured per individual generation. Within and among-group selection are equally intense if a unit increase in Z_i has the same proportionate impact on the number of group i 's offspring groups as a unit decrease in z_{ij} has on ij 's within-group fitness. Thus, set $c = e$, $\Delta Z = e(V_z/V_Z)$. Group selection then overcomes an equally intense within-group selection if $2mNL = LV_z/V_Z < 1$. For group selection to overcome selection within groups, less than one successfully reproducing migrant may be exchanged per two populations per population lifetime. Aoki (1982), Crow & Aoki (1982) and Kimura (1983) derived equivalent conclusions by various methods. Indeed, if groups are

long lived, successful migrants must be very rare, and within-group inbreeding intense, for group selection to prevail over equally intense within-group selection.

Other factors may also influence V_z/V_Z . If each new group is founded by equal numbers of immigrants from M parent groups, among-group variance V_z is reduced by a factor $1 - [(1 - 1/M)/L]$ per individual generation, for a fraction $1/L$ of the populations are replaced by groups with among-group variance V_z/M . Similarly, if the species has only n groups, the chances of which group dies and which reproduces reduce V_z by a factor $2/nL$ per individual generation (Moran, 1962:79). V_z is in balance when

$$V_z/N = 2mV_z + V_z(M - 1)/ML + 2V_z/nL,$$

$$LV_z/V_Z = 2mNL + N(1 - 1/M) + 2N/n,$$

(Leigh, 1983, 1986). Group selection can override equally strong individual selection only if $V_zL/V_Z < 1$. For this to be, groups must exchange migrants very rarely, less than 1 of every N groups may be jointly founded by migrants from several parent groups, and there must be many more groups than individuals per group.

To be meaningful units of selection, groups must be very distinct entities with essentially 'uniparental' reproduction. Here, we are dealing with group selection as envisaged by Maynard Smith (1964) and Williams (1966, 1992), that is to say, group selection capable of producing group-level adaptation. These conditions seem so wonderfully improbable that, following Williams (1966), most biologists have focused almost exclusively on individual selection.

Improbability, however, does not mean impossibility. Group selection capable of overwhelming selection within groups, played a crucial role in some major transitions of evolution (Maynard Smith & Szathmary, 1995; Szathmary & Maynard Smith, 1995). The evolution of individuality in metazoans and metaphytes (Buss, 1987) hinged on the sexual production of zygotes that divided to produce clonal aggregates, a circumstance that nearly annihilated within- relative to among-aggregate genetic variance (Leigh, 1991). Similarly, the evolution of eukaryotes involved transforming the collective of a cell and certain of its intracellular parasites into an integrated individual, a unit of selection in its own right. After the bacterial ancestors of organelles, such as mitochondria and chloroplasts, colonized their hosts (Margulis, 1993), they excluded conspecific immigrants, and became capable of passing only from parent to daughter cell. These two circumstances locked the symbionts into a group selection (each group being a cell's symbionts) favouring their hosts' survival and reproduction (Eberhard, 1980; Cosmides & Tooby, 1981; Leigh, 1983). Selection favoured hosts who inherited organelles of a particular kind from only one parent because their zygotes were spared conflict between competing strains of organelles (Eberhard, 1980; Maynard Smith & Szathmary, 1995).

This circumstance further reinforced the group selection on intracellular organelles in their hosts' interest. Conflicts still occur: for example, where only the mother transmits organelles, mutants in organelle genomes favour all-female sex ratios (Maynard Smith & Szathmary, 1995). Nonetheless, group selection transformed symbionts into organelles which were such essential parts of their hosts that the idea they descended from independent organisms was originally greeted with crude ridicule (Margulis, 1998). Any symbiont with strictly uniparental transmission from hosts to their young is subject to a similar group selection in its host's interest, whose effects can be profound (Moran *et al.*, 2008).

Selection among groups also played a role in shaping insect societies (Sturtevant, 1938), and became supreme in those integrated enough to be called superorganisms (Holldobler & Wilson, 2009). Selection among groups is most effective in honeybees (Seeley, 1997), leaf-cutter ants (Holldobler & Wilson, 2009) and other insect societies organized as functional wholes to serve their queens' reproduction (Gardner & Grafen, 2009). These societies are justly called superorganisms because, as we have seen, their workers can almost never spread their genes except by helping their queen reproduce. Despite the diversity of genotypes within their societies, the suppression of reproductive competition among their workers makes them units of selection (Darwin, 1859:237–242), just as the mutual enforcement of fair meiosis makes eukaryotes units of selection. In neither case is the suppression of reproductive competition foolproof. At least one lineage of honeybee worker has evolved that, instead of helping their queens reproduce, reproduce apomictically through eggs fellow workers cannot detect and eat (Martin *et al.*, 2002). Like a vicious cancer, the multiplication of these parasitic workers kills their colony. Moreover, like cells of some infectious mammalian cancers (Murgia *et al.*, 2006; Pearse & Swift, 2006), these parasitic workers infect other colonies (Martin *et al.*, 2002). These parasitic workers discard the idea of honeybee superorganism no more than infectious cancers invalidate the concept of metazoan individuals. Although superorganisms are truly spectacular achievements of evolution, some of which have transformed ecosystems, they evolve rather rarely, and are far less diverse than, say, beetles or even bats. Most insect societies, like most other groups, experience selection within as well as among groups (Sturtevant, 1938).

Features favouring the survival and reproduction of groups evolve much more readily when there is no within-group counterselection. Fisher (1958:50) recognized that extinction and origin of species were far too rare to allow selection among species to overcome selection within species. Nevertheless, populations meet similar challenges, such as arranging genes in chromosomes or allocating effort to male and female functions, in different ways. Different solutions to these challenges

often have different impacts on the prospects of extinction or speciation. For example, some genetic systems may be far more vulnerable to segregation distortion, and some sex-allocation systems reduce the cost of sex. The very indeterminacy of selection within species offers a crucial opportunity for selection among species (Leigh, 1977; Rankin *et al.*, 2007).

Although this treatment of group selection, with its frequent assumptions of weak selection and additive gene action, sheds light on many phenomena, it ignores Sewall Wright's rationale for invoking group selection. If a genotype's inclusive fitness is poorly predicted from the sum of the average effects on inclusive fitness of its component alleles, can fit genotypes spread only in small subpopulations via chance crossings of 'adaptive valleys' (Wright, 1929, 1932, 1945)? When this is so, selection among groups may indeed play a crucial role in adaptive evolution. Experiments with group selection are most effective where genes contribute nonlinearly to group fitness (Goodnight & Stevens, 1997). Moreover, Gilpin's (1975) model of group selection on predator–prey communities hinges on progressive small increases in within-group predator advantage reaching a threshold where a further small increase precipitates a disproportionate increase in the group's prospects of extinction. It is urgent to understand how such experiments and theory relate to natural processes and what they tell us about the various ways natural selection can work.

Defining and circumscribing group selection

Disputes over how to define group selection began when Wilson (1975, 1977) introduced the concept of 'trait-group' or 'intrademic group' selection. Here, groups of N adults apiece are drawn at random from a pool of young. An individual's reproduction is governed by its success in competing with fellow group members for that group's supply of some limiting resource. Their young disperse to a common pool, from which the next generation's groups are drawn at random. If z is a quantitative characteristic, and V_T its total variance, then within-group variance is $(N - 1)/V_T N$ and among-group variance is V_T/N (Hamilton, 1975). Selection among trait-groups prevails if within-group selection is sufficiently slight relative to among-group selection. Trait-group selection sometimes has great biological importance (Wilson, 1980; Leigh, 1991, 1994), but it cannot drive integrated group-level adaptation. Superorganisms do not evolve by trait-group selection.

Price's formalism is the best approach for handling problems involving trait-group selection, especially trait-group selection on the sex ratio (Frank, 1986). Imagine, for example, a haploid fly, a parasitoid, where successive generations are distinct. A trait-group is the set of fertilized females that lay eggs in one host: their young mate among themselves, and fertilized females fly off in

search of new hosts to lay eggs in. Let N flies lay eggs in each host. What sex ratio does selection favour? Hamilton (1967) first solved this problem by very different means, but Price's approach is easier to understand. Let V_T be the total genetic variance $V_z + V_Z$ in sex ratio of this population, where average within-group variance $V_z = (N - 1)V_T/N$, and among-group variance is $V_Z = V_T/N$. How does group size N affect optimum sex ratio? Let sex ratio be governed by two alleles, A and a, at a single locus. Let an animal's own allele determine its probability of being female: let an A-bearer have probability $r + dr$ of being female, whereas an a-bearer's probability of being female is r . In a group where A's frequency is q , A's effective frequency q' among this group's young is half of A's frequency among its female young, plus half of A's frequency among its male young. Thus,

$$q' = \frac{q(r + dr)}{2(r + q dr)} + \frac{q(1 - r - dr)}{2(1 - r - q dr)} \approx q + \frac{q(1 - q)(1 - 2r)dr}{2r(1 - r)}.$$

Here, the selective advantage of A over a is $(1 - 2r)dr/2r(1 - r)$; so,

$$d \ln w/dr = (1 - 2r)/2r(1 - r).$$

The group's total output of young is proportional to the number of females in the group, so $d \log W/dr = dr/r$. Balance is struck when

$$q(1 - q) \left[\frac{dr}{Nr} + \frac{(N - 1)(1 - 2r)dr}{2Nr(1 - r)} \right] = 0 \\ = \left[1 + \frac{(N - 1)(1 - 2r)}{2(1 - r)} \right] \frac{dr}{Nr}.$$

Therefore, $(N - 1)(2r - 1) = 2(1 - r)$, $2rN - 2r + 2r = 2 + N - 1$; $r = (N + 1)/2N$ (Hamilton, 1967). The smaller the group size N , the greater is the among-group variance relative to within-group variance and the more female biased the sex ratio. Hamilton (1967) first derived the optimum sex ratio by a very different method. Colwell (1981) rephrased Hamilton's derivation to show that sex ratio was female-biased because trait-groups with more female-biased sex ratios contributed more fertilized females to the next generation of trait-groups.

The predictions of such sex-ratio theory on how sex ratio varies with trait-group size have been confirmed repeatedly, especially for haplodiploids. Work has centred on minute wasps that grow up in fig seeds and pollinate fig trees (Corner, 1952, 1988; Herre *et al.*, 2008). Here, a trait-group is the set of fertilized female wasps that pollinate the flowers lining the inside of a single syconium (incipient fig fruit) and lay eggs in half of them. Each wasp larva matures within a single fig seed that its mother's sting transformed into a gall; the young wasps mate among themselves, and the fertilized females fly off to find other figs with flowers ready to lay eggs in. If the harmonic mean of the number of fertilized female egg-layers (foundress number) per syconium is N' , the optimum proportion of females among the young in a

syconium with N foundresses is $[2N'(N - 1)]/N'(4N' - 1)$ (Herre, 1985). As this formula predicts, the proportion of female offspring for a given foundress number N is higher in a species with lower harmonic mean foundress number N' (Herre, 1985). Moreover, this proportion most nearly matches prediction for the foundress numbers the species encounters most often, and those species of wasps that encounter the greatest variation in foundress number are best at adjusting sex ratio to foundress number (Herre, 1987; West & Herre, 1998; West *et al.*, 2000). All these suggest the importance of selection among as well as within trait-groups.

Indeed, 'trait-group' sex-ratio theory is one of a family of theories on how different behaviours or prospects of male and female young affect sex ratio (Trivers & Willard, 1973; Clark, 1978; West *et al.*, 2005). For example, if related males compete for mates while females disperse further (Hamilton, 1967) or if females are more likely to help their parents raise more young (Komdeur *et al.*, 1997), sex ratio should be female biased. Inclusive fitness predictions for sex ratio have been abundantly confirmed (West *et al.*, 2005). Many species with chromosomally determined sex ratios lack detectable variation in sex ratio (Williams, 1979), even though selection against slightly deviant sex ratio is very weak (Leigh, 1970). So far, endless labour has produced no cows or chickens with female-biased sex ratios. Nonetheless, a Seychelles warbler can adjust the sex of successive offspring in accord with its needs (Komdeur *et al.*, 1997), and many species show adaptive variation in chromosomally determined sex ratio (West *et al.*, 2005).

Predictions of how sex ratio varies with trait-group size accord with reality (West *et al.*, 2000), and the 'levels-of-selection' approach of Price (1972a) and Hamilton (1975) is the easiest way to derive them. Nonetheless, the question soon arose whether the process responsible is rightly called group selection (Colwell, 1981; Charlesworth & Toro, 1982). At first sight, one might think the dispute settled because Wilson's language seems well translated by the Price-Hamilton approach (even though Wilson himself never uses Price's theorem!). Several arguments, however, militate against Wilson. First, trait-group selection bears little relation to the selection among discrete groups envisaged by Lewontin (1962, 1970), Maynard Smith (1964, 1976) and Williams (1966, 1992), which was driven by the differential extinction and multiplication of whole groups. Second, in a criticism that anticipated developments in Sober & Wilson (1998), Charlesworth & Toro (1982) considered trait-groups too ephemeral to be the substrate for a genuine group selection. Finally, Wilson's trait-group approach applies equally to a continuously distributed population where individuals can mate only with a few near neighbors (Bulmer & Taylor, 1980), or a continuously distributed forest where trees compete with a few near neighbors for light, water and nutrients, but disperse seeds far beyond their immediate competitors (Leigh,

1991, 1994). Why speak of groups that lack natural boundaries?

Group selection, or the common interest among genes or individuals?

Later, new disputes arose over the meaning and scope of group selection. Two closely linked issues are involved. First, what sorts of groups are truly subject to group selection? Second, which instances of cooperation reflect the common interest of the individuals concerned, and which reflect group selection?

First, what groupings warrant invocation of group selection? Sober & Wilson (1998:79–86) viewed any pair as a group if the members interact repeatedly during some part of their lives in ways that influence their fitnesses. They called selection on this interaction group selection (Maynard Smith, 1998). For example, simultaneously hermaphroditic coral reef fish, *Hypoplectrus* spp., pair off every late afternoon, spawning repeatedly, exchanging sex roles in successive spawns. In effect, they trade eggs with each other, reducing the cost of sex by reducing their sperm production to the minimum needed to fertilize each other's eggs. More eggs are exchanged in each successive pair of spawns, as if the two fish were building up mutual confidence. If a fish that receives eggs at spawn n fails to reciprocate at spawn $n + 1$, its mate abandons it in accord with the canons of 'tit for tat', leaving the cheater to find, and build up confidence in, another mate (Fischer, 1980, 1981, 1988). This behaviour enforces their common interest in reducing expenditure on sperm. Sober and Wilson say that group selection on interacting pairs shaped these pairs' strategy of 'tit for tat'. These pairs, however, are not the discrete units presupposed by Lewontin's (1970) concept of group selection.

Indeed, many forms of cooperation reflect the common interest of the cooperators (Leigh, 1991, 2000). Among these hamlets, each fish serves its 'enlightened self-interest', and increases its prospective lifetime fitness, by a strategy that increases the prospective output of eggs and successful sperm of both partners (Leigh, 1991).

Sober & Wilson (1998:89–93) also argued that fair meiosis prevails because selection among individuals overcame selection among genes within individuals. I showed above that fair meiosis expresses the common interest of autosomal genes (see also Leigh, 1971, 1991): when a segregation distorter spreads a phenotypic defect, selection favours unlinked alleles that restore fair meiosis. Kin selection, which does not always favour an individual's good, also expresses this common interest, showing that the common interest of autosomal genes is not always identical to the individual's good.

Boehm (1997) and Sober & Wilson (1998:159–194) suggested that the egalitarianism prevalent within groups of hunter-gatherers abolishes within-group reproductive differentials, lending effectiveness to selection among groups, just as annihilating worker reproduction lends

effectiveness to selection among honeybee colonies (Seeley, 1997). Most groups of hunter-gatherers have moral codes promoting monogamy, and equal access to food, status and power among their adult males. These codes mandate group action to block any one individual or family from hoarding food, women or power, and punish 'free-loaders', who will not contribute their fair share towards their group's support (Boehm, 1993, 1999). Can this moral code really prevent the differential reproduction caused by covert adultery? More probably, its function is to give every group member adequate motive to cooperate with his fellows in preserving the welfare of the group on which they all depend. The emphasis on mutual enforcement suggests that the moral code serves the common interest of the group's members, as does that other 'moral code', the product of pure mechanism, that we call fair meiosis.

Indeed, cooperation among other long-lived groups of vertebrates also appears to reflect the common interest of their members. Group-living animals such as lionesses care for each other's young if each female benefits from keeping its group large enough to compete effectively with others (Packer *et al.*, 2001; Clutton-Brock, 2002; West *et al.*, 2007a:416). Male lions must join in a cooperative group to oust the resident group of males from a pride. Unrelated males will cooperate to take over a pride if they have equal reproductive access to females. However, if a group has more than three members, reproductive success is distributed less evenly among them. Thus, males in groups of four or more are all related: cooperation among nonrelatives occurs only when they share a common interest in the profits of cooperating (Packer & Pusey, 1982; Packer *et al.*, 1991). If a member of a monkey group lets a fellow member be killed or seriously injured through its own negligence, it endangers itself, for its own safety depends on its group's integrity (Leigh & Rowell, 1995). Cooperation among a group's members is particularly crucial when competition among groups is intense. Where monkey groups compete most intensely, dominants may be more accommodating to subordinates so that the group will make common cause in the day of battle (Sterck *et al.*, 1997). Where competition among groups favours cooperation within groups, Sober & Wilson (1998) quite naturally see group selection at work. Nonetheless, in groups whose members depend most on each other for their own welfare, and where cheaters are unlikely to be capable of joining other groups, cooperation reflects group members' common interest in their group's effectiveness. Cooperative group life does not always imply effective group selection.

Should group selection be eliminated by redefinition?

Perhaps in response to the extreme claims of D. S. Wilson, West *et al.* (2007a,b, 2008) denied the usefulness

of the concept of group selection. West *et al.* (2008:380) have a heading 'There is no formal theory of group selection', as if Price (1972a) and Hamilton (1975) had not deliberately developed just such theory. West *et al.* (2007a,b) claim that the rejection of the 'old group selection' remains fully justified. What this rejection must mean is the far more reasonable statement that 'There is no theoretical or empirical example of group selection that cannot be explained by kin selection' (West *et al.*, 2008:375). Even this statement appears outrageous until one remembers that for West *et al.* (2007a, 2008), 'kin selection' is shorthand for 'inclusive fitness'. Nonetheless, this language is meant to convey the generality of the inclusive fitness method. As we have seen, when applied to the autosomal genome rather than individual loci, the inclusive-fitness method is the most general we have for analysing the origin of adaptation (Grafen, 2006; Gardner *et al.*, 2007).

Is it useful, however, to suffocate the concept of group selection under the blanket of inclusive fitness? Some examples of 'trait-group selection' are clearly best handled by inclusive fitness methods. 'As against group selection, [inclusive fitness] provides a useful conceptual tool where no grouping is apparent' (Hamilton, 1975). Inclusive fitness is the appropriate formalism for asking whether effective seed dispersal promotes mutualism among neighbouring forest trees (Leigh, 1994).

Newtonian physics, however, has been formulated in various ways: Newton's three laws, least action principles and so forth. These formulations are equivalent, but different formalisms work better for different problems. As with physics, so with biology. A trivial example is that Price's theorem necessarily uses the same units for all levels of selection. Is it an accident that workers sharing the traditional concept of group selection all emphasized the centrality of group lifetime (Fisher, 1958:50; Lewontin, 1970; Leigh, 1983), whereas those working directly from Price's theorem did not (Hamilton, 1975; Crow & Aoki, 1982)? Similarly, a biologist seeking to understand the domestication of mitochondria would do better to recognize that the essential process in this domestication was that protomitochondria identified their future with their host cells' by locking themselves into a group selection in their hosts' interest. A theory such as that of Gardner *et al.* (2007) is too general to guide one's thinking about specific problems.

Fortunately, resolution of the group selection dispute may be approaching. Gardner & Grafen (2009) propose a formal theory of group adaptation in superorganisms. They define a superorganism as Hölldobler wished to define it (Hölldobler & Wilson, 2009:467), as a social group in which reproductive competition among members is almost entirely suppressed. This formalism analyses group adaptation using concepts entirely analogous to the fitness set (the array of possible group phenotypes) and adaptive function (the criterion for comparing these phenotypes' fitnesses) of Levins (1968).

They justly remark that although group selection maintains and modifies superorganisms, other processes helped drive their evolution. Indeed, social behaviour in hymenoptera must have started with daughters helping their mothers raise full siblings. Curiously, Gardner & Grafen (2009) only accept group selection if no within-group selection opposes it. Will this restraint eventually vanish before the formalism of Price (1972a) and Hamilton (1975)?

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