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An Intellectual History of Multilevel Selection: Reformulation and Resuscitation

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1 The Resurgence of Group Selection

The previous chapter depicted a rising chorus of consensus starting in the 1970s. Sober and Wilson describe how group selection was buried in the 1960s and 1970s and treated with utter contempt. It was so reviled that it was not forgotten, but recalled as an example of how *not* to think. Even in the 1980s, as Sober and Wilson recount, an unidentified, distinguished biologist once advised a younger colleague that there are three things that one does not defend in biology: *group selection*, *phlogiston theory*, and *Lamarckian evolution*. Indeed, discussion of group selection, at certain points in the history of evolutionary biology, evoked criticism and even ostracism, as illustrated by the following reflection shared by the still skeptical professor Detlef Fetschenhauer (2009):

Arguing with group-selection ideas in biology was for a long time like arguing with psychoanalytic ideas in psychology, namely an embarrassing signal of being old-fashioned and outdated. When some years ago I was giving a course on the evolution of human altruism at the department of biology at the University of Groningen I was told that I should not even mention group selection. The idea was regarded as so absurd it was not even worth[y] of being refuted. (p. 283)

David Sloan Wilson defended group selection unremittingly through these decades of withering criticism. Honing his reasoning on the whetstone of contrarian opinion, Wilson produced convincing arguments applicable to humans and human societies. Together, Sober and Wilson offer unique perspectives on group selection using comparative religion, field data, reviews of experimental work, and descriptions of parasitism and sex ratio. Comprehensive and various, their writings invariably wend their way back to human group selection, which they understand to be established and evident. “We claim,” Sober and Wilson write, “that human social groups are so well designed at the group level that they must have evolved by group selection.” Sober and Wilson, in short, see the stamp of evolutionary design on human groups, just as Darwin saw the stamp of evolutionary design on individual organisms. Within human populations, religion, language, and ideology are layered onto ecological and biological determinants, which jointly contribute to the formation of cooperating and competing groups. D. S. Wilson’s *Darwin’s Cathedral* and Sober and Wilson’s *Unto Others* are among a short list of works establishing the theoretical probability of human multilevel selection.

Sober and Wilson (1998, p. 51) invoke Kuhn (1962) to explain the contrast between group selection’s real explanatory power and its attenuated impact. In the rejection of group selection, Sober and Wilson see science not progressing in a straight line toward truth, as Kuhn warned that it would not. William’s work on sex ratio and Lewontin’s work on virulence are cited by Sober and Wilson as empirical examples of group selection functioning as a “significant evolutionary force.” Nevertheless, these and other avenues of extant evidence have remained relatively unasimilated. “Normal science,” Sober and Wilson write, “did its job, but somehow it failed to have the right impact.” These and other supportive

empirical studies have not “forced a general reassessment of group selection theory.” Accordingly:

Many evolutionary biologists continue to play the ‘group selection is dead’ song ... Little wonder, then, that scholars from other disciplines who are interested in evolution have heard almost nothing about these scientific developments. (p. 51)

Modern formulations of group selection as one among other levels of selection within multilevel selection theory remain conflated with what has been called *naïve group selection*, perhaps equally so within the minds of those opposing and those neglecting group selection. Extending back to the aforementioned work of Wynne-Edwards (1962), naïve group selection posited Panglossian circumstances, whereby species husbanded resources by limiting population growth for the good of the whole population. The *naïve* aspect of naïve group selection derives from its failure to incorporate plausible opposing forces to those of individual selection. Naïve group selection might then be compared to idealized conceptions of communism in its theoretically final utopian state. Both theories promote the good of the whole, but both lack any viable controls on individual group members that might undermine the collective good to benefit their selfish ends. This is why one is actually absent in nature and the other is impracticable in human sociopolitical affairs. By way of contrast, modern formulations of group selection within multilevel selection theory are akin to governmental forms employing checks and balances, keeping opposing forces in dynamic tension. Illustrating the point, Wilson (2016) speaks thus of the opposing forces between individual and group selection:

Cooperators might be at a selective disadvantage compared to free riders and exploiters within the same group, but groups composed primarily of cooperators are at a selective advantage compared to groups crippled by free riders and exploiters. Natural selection takes place both within and between groups. Group-beneficial adaptations can evolve if between-group selection is strong enough to oppose disruptive within-group selection. (pp. 33–34)

Competition from rival groups is the implicitly stated counterweight to selfishness within the group. In addition to external competition from rival groups, selfishness is societally controlled by a system of reward and punishment meted out within societies to coerce noncooperators, as will be discussed in Sects. 5 and 6 of this chapter as well as in Part II of this book.

As implausibly posited in the case of naïve group selection, groups never compass whole species. Instead, groups can range from immediate families to extended kinship bands and to nation-states but ineluctably fracture before progressing toward the whole of a species. Wilson (2016) recently made this point: “Social interactions almost always take place in groups that are small, compared to the total population” (pp. 33–44).

Writing a subsequent chapter in Wilson’s edited volume, *Complexity and Evolution: Toward a New Synthesis for Economics*, Gowdy, Mazzucato, van den Bergh, van der Leeuw, and Wilson (2016) follow the theme, providing the following maxim: “Adaptation at any level of a multitier hierarchy requires a process of selection at that level and tends to be undermined by selection at lower levels” (p. 336). Envisioning a hierarchical view of society with ascendant levels of aggregation, Gowdy and colleagues understand the tendency for *disruptive self-serving behaviors* to serve as a brake in the progression from one rung to the next on the ladder of aggregation. In doing so, Gowdy et al. (2016) plainly illustrate the nature of the conflict: “What’s good for me can be bad for my family. What’s good for my family can be bad for my clan. All the way up to what’s good for my nation can be bad for the global village” (p. 336). Gowdy and colleagues’ rendering recalls a well-known Arabian proverb: “It was me against my brother; me and my brother against our father; my family against my cousins and the clan; the clan against the tribe; and the tribe against the world” (Uris, 1984, p. 14).

This heady realism, grounded in an evolutionary truism, is precisely what Enlightenment philosophers attempted to work against as they promoted cosmopolitanism, as seen through the writings of Montesquieu (1964): “If I knew something useful to me, but prejudicial to my family, I would reject it from my mind. If I knew something useful to my family, but not to my country, I would try to forget it” (p. xviii; in the introduction by Healy). Following the chain of reasoning to its logical conclusion,

Montesquieu (1964) concludes: “If I knew something useful to my country, but prejudicial to Europe, or useful to Europe and prejudicial to the human race, I would regard it as criminal” (p. xviii; in the introduction by Healy).

Even as the opposing forces of selfish individualism are obviously operative, it does not follow that the processes of social selection are invariably pulled all the way down the ladder of aggregation such that evolution never takes place at the group level. Unfortunately, something of an ideological consensus emerged wherein individual selection was thought to be *invariably* stronger than group selection. Instead of imagining a dynamic interplay of vying forces, sometimes stronger, sometimes weaker, and sometimes equal in either synergy or opposition, critics of group selection admitted the theoretical possibility of an interplay so weak as to nearly never be able to overbalance individual selection’s countervailing forces. Nevertheless, opponents of group selection saw the stable formation of aggregations in families, clans, tribes, states, and nations and, perforce, had to explain their existence in alternative ways. Pinioned between the necessity to explain reality and the unwillingness to consider group selection as a factor came *inclusive fitness theory*, *evolutionary game theory*, *selfish gene theory*, and indeed “most of the theories of social evolution that emerged during the second half of the twentieth century,” which were nothing other than efforts to “explain apparent group-advantageous behaviors without invoking group selection” (Wilson, 2016, p. 34). According to Wilson’s (2016) and later Okasha’s (2006) reading of the history of the controversy surrounding group selection, the emerging synthesis cannibalizes rather than discounts alternative theories, such that they become incorporated into multilevel selection theory:

In retrospect, the theories developed to explain apparent group-advantageous behaviors without invoking group selection can be seen to have the logic of multilevel selection embedded within their own structures. They offer different perspectives on a single causal process rather than invoke a separate causal process, a topic discussed under such terms as pluralism and equivalence. (p. 34)

Notwithstanding opposition, and bolstered by decades of thought, theory, and comparative analysis, Wilson has moved on, understanding selective pressures to impart directional selection in response to group competition over and above the drag of individual selection. More than this, Wilson extends his claims to insist, not only on the possibility that group selection can be strong enough to exist but that it can sometimes come to dominate individual selection, especially in instances of evolutionary transition.

2 Neo-group Selectionism

The idea of multilevel selection, as outlined above, changed incrementally so as to have become a very different concept when compared to its original formulation; yet, this distinction is not always evident to critics of group selection. Even Borrello does not pointedly differentiate group selection as understood by Wynne-Edwards from group selection as understood within modern multilevel selection theory. He comes closest to doing this toward the end of his book; and it is certain that the author himself understands this distinction. Still, there is no real discussion of how group selection operates in conjunction with individual selection or, for example, how groups are simultaneously challenged with free-riding exploiters from within and cohesive rival groups from without. From that time till this, group selection has been supported by the research underpinning all the bulleted points below, in addition to becoming embedded in a matrix of multilevel selection theory wherein individual and group selection are known to simultaneously operate and dynamically interact.

Slowly, as if by erosion, consensus was selectively undermined in the decades thereafter, with fewer and fewer evolutionists stalwartly denying the possibility of group selection in the present (Okasha, 2006). Critics have historically harbored notions of group selection that are antiqued or otherwise inadequately operationalized, rendering the derived critiques irrelevant. Common to the intellectual history of group selection, skeptics have based their deconstructions from false premises, starting from an understanding of group selection that no longer is, or never was. Now accepted among most evolutionists, the modern formulation of

group selection within the broader framework of multilevel selection is becoming better known.¹ Group selection, as the most controversial level of selection within multilevel selection theory, has been established on new grounds, having been clarified in the following ways (Grueter, Chapais, & Zinner, 2012; Mayr, 1970; Richerson et al., 2016; Wilson & Sober, 1989, 1994):

- Groups were operationally defined
- Groups were understood as fluctuating between different levels of aggregation and kin relatedness²
- Group selection does not always end in the extinction between one of the two groups. Instead, there can be *character displacement* wherein one group is marginalized or enters a different ecological zone at the point at which it comes into contact with the other group
- Group selection can still occur even while migration and gene flow take place; this happens when migration and gene flow are strategic or directional, such that gene flow drives, rather than undermines, between-group differences
- Group selection does not start where individual selection stops; rather, both processes can occur simultaneously³
- Group selection provides an emergent group-level advantage even if the trait in question was neither self-sacrificial (it was actually under positive individual-level selection) nor social in any sense initially
- Traits that are selected for at the group level may well have been initially generated via individual level selection

Even when properly differentiated from naïve group selection, group selection has remained controversial mostly because it has been theorized to require certain preconditions, such as the punishment of cheaters, free riders, social loafers, and related individually selected opportunists. Take the example of *altruism*: Altruism might be selected for, with the effect that the altruistic group becomes a superior competitive unit relative to less altruistic groups. The population of the altruistic group may therefore expand to the detriment of competitor populations. Staying with the example, that altruistic group, however, is prone to exploitation from population members who do not add to aggregate altruism or who

actively undermine it. Within the altruistic group, if free riders and cheaters then reproduce to the detriment of their altruistic neighbors, mean altruism will be brought down to the level found among other populations, eliminating the group's prior advantage. Consequently, to maintain high mean altruism, the proliferation of free riders and cheaters must be counteracted. This is a fair criticism, but one that has been duly answered. For instance, in eusocial insect colonies, group-selected colony cohesion is enforced by selectively consuming any eggs laid by workers, attacking ovulating workers,⁴ and policing by other means. In historical and contemporary human populations, we find analogous mechanisms that thwart free riders, for instance, shaming, incarceration, ostracism, sanctions, fines, and related mechanisms, reviewed in Chap. 5's fourth section. Selfish individuals do indeed attempt to undermine groups and group selection, but these selfish individuals may suffer depressed fitness in consequence of group punishment. In the context of such group punishment, altruism can become individually adaptive, leading to the evolution of an altruistic group. Humans are especially capable of this form of self-domestication wrought by imposing socially selective pressures on one another. An additional point made by Wilson and Sober (1998) is that cheater detection and punishment may be more common mechanisms among highly intelligent humans, making human group selection more plausible.

One can then see how multilevel selection recovered theoretical respectability as it differentiated itself from naïve group selection, after which multilevel selection demanded thoroughgoing consideration for having undergone successful operationalization and theoretical defense. The work of Okasha (2006) furthered multilevel selection's renaissance. As seen in reading Okasha, social groups have emergent properties, meaning that the *within-group* component of selection is not necessarily a simple additive function of the within-group fitness of constituent individuals, because the interactions among individuals produce a nonadditive component to the mix. There are thus two types of multilevel selection characteristics hypothesized by Okasha (2006): Type 1 (*MLS1*) multilevel selection characteristics are individual difference traits, and their corresponding aggregates, that affect both the individual's relative fitness and the aggregate fitness of individuals within the group, and Type

2 (*MLS2*) multilevel selection characteristics are traits of the collectives that are irreducible to the phenotypes of the constituent individuals, wherein the collectives' fitness is defined as that of parent groups multiplying into offspring groups. The Type 2 group selection characteristics can at times become so pronounced, presumably as reflected by the between-group component of selection in the Price equation, that some have characterized the entire insect societies as *superorganisms*, with constituent individuals assuming the role of specialized parts selected to function as integral components of a discrete, collective entity (e.g., Korb & Heinze, 2004; Leigh, 2010; Reeve & Hölldobler, 2007; Wheeler, 1910, 1911; Wilson & Sober, 1989; Wilson & Wilson, 2008; Wilson & Hölldobler, 2005).

Another way that modern multilevel selection theory has distinguished itself from naïve group selection theory is in gaining greater clarity regarding the level of biological organization of the objects at which altruistic behavior is directed. Many otherwise respectable theorists previously made what would now be considered somewhat extravagant claims regarding the motivating principles behind much observed animal behavior. Dawkins (1976), for example, points out that

Konrad Lorenz, in *On Aggression*, speaks of the 'species preserving' functions of aggressive behaviour, one of these functions being to make sure that only the fittest individuals are allowed to breed. (p. 8)

Thus, the dominant wolf is depicted as not pursuing dominance for his own selfish reproductive benefit, but instead, for the higher purpose of this principle of racial hygiene; with equal implausability, the subordinate wolf is ostensibly accepting of his nonreproductive status as consistent with this self-effacing eugenic strategy for the good of the species. Although an argument might be made from modern multilevel selection theory that acceptance of dominance hierarchies might have evolved for the "good of the group," the idea that these behaviors evolved for the benefit of the *entire species* now sounds to us as highly improbable. Unlike the artificially created groups of captive wolves that Lorenz (1966) studied, we now know that naturally formed wolf packs in the wild are extended families that accrete around a core group of parents and their

adult offspring. The mechanism that ensures the generally amicable relations among dominants and subordinates is not loyalty to some eugenicist ideals for their species, but the fact that the individuals are genetically related and thus subject to the conflict-moderating forces of kin selection.

Such ideas from naïve group selection theory nonetheless disseminated widely into the popular culture and found their way into the narratives of many nature documentaries and educational resources. To this day, the website of the *International Wolf Center* (2019) makes the following rather extravagant claim with equally cavalier disregard for any conceptual plausibility or support from evolutionary theory:

All of these ungulates have adaptations for defense against wolves, including a great sense of smell, good hearing, agility, speed, and sharp hooves. As these prey are so well adapted to protecting themselves, wolves feed upon vulnerable individuals, such as weak, sick, old, or young animals, or healthy animals hindered by deep snow. By killing the inferior animals, wolves help increase the health of their prey population a tiny bit at a time. When inferior animals are removed, the prey population is kept at a lower level and there is more food for the healthy animals to eat. Such “culling” also ensures that the animals which reproduce most often are healthy and well suited for their environment. Over many generations, this selection helps the prey become better adapted for survival.⁵

The evident implication here is that wolves do not prey upon the weak and the sick merely because they are much easier to capture and subdue, but instead out of eugenical regard for the genetic health of the prey species and the provision of sufficient resources and *lebensraum* for the fittest among them to survive. One might reasonably wonder why wolves would have evolved any desire to improve the antipredator adaptations of their prey populations, making them more difficult to hunt in the future. Given our current understanding of the principle of natural selection, this narrative appears implausible to the point of absurdity.

In contrast to the gist of these narratives, modern multilevel selection theory requires one to specify exactly at what level(s) of biological organization any adaptation is selected and by what mechanism. Furthermore, all this theoretical debate regarding the sometimes conflicting interests of

“individuals” and “groups” does little to clarify precisely what one means by a “group.” Does one mean a bounded and kin-structured social group, a local population, an entire species? These questions must be answered for the theory to have any coherence whatsoever. For example, some group selection theories use smaller units than the deme to model “trait-groups,” which is a collection of individuals defined on the basis of common properties, or heritable traits. Wilson (1975) explains this usage as follows:

Evolution’s most easily conceived population unit is the deme, and it is determined by the movement occurring during the dispersal phase. Yet most ecological interactions, in terms of competition, mating, feeding and predation are carried out during the nondispersal stages in the smaller subdivisions, which I term “trait-groups.” In some cases the trait-groups are discrete and easily recognized, such as for vessel-inhabiting mosquitoes and dung insects. In other cases they are continuous and each individual forms the center of its own trait group, interacting only with its immediate neighbors, which comprise a small proportion of the deme. (p. 143)

3 Pressing the Offensive

Only more recently have Wilson, Sober, and other *neo-group selectionists* (Okasha, 2006) have gotten beyond arguing for group selection’s existence and have gone on to insist on its theoretical superiority. Co-opting kin selection, casting it as a form of group selection, is only one of several tenets undergirding Wilson and Sober’s conclusion that group selection is not only plausible but also powerful (Okasha 2006, p. 177 et seq.). Staying with the example of kin selection, we find that Nowak, Tarnita, and Wilson (2010) insist that it is kin selection, more than group selection, that “requires stringent assumptions, which are unlikely to be fulfilled by any given empirical system.” These include the assumption that interactions between organisms are additive and pairwise, thus excluding any situation with synergistic effects or where more than two organisms interact. Moreover, inclusive fitness is relevant only to a limited set of population structures (Bahar, 2017, p. 277). Along with Tarnita and Wilson,

Nowak finds inclusive fitness to provide no special biological insight that could not be otherwise better accounted for using the more generalized theory of group selection. Again, this is just one example of how neo-group selectionists have taken the offensive, which can be seen as a qualitatively different level of defense, one that looks a lot more like offense.

In the view of neo-group selectionists, ecological factors (such as the distribution of food) are thought more relevant than genetic relatedness to group formation and cooperation. This conclusion is evidently based on observations of eusocial insects. For example, observation and experimentation witnessed unrelated termite colonies merge into super colonies, both from naturally occurring and artificially imposed ecological pressures (Howard, Johns, Breisch, & Thorne, 2013). Indeed, when the comparative literature is systematically searched, eusociality and genetic relatedness are demonstrably uncoupled, thus breaking the association between one and the other, resulting in the following claim (Nowak, Tarnita, & Wilson, 2010):

Relatedness is better explained as the consequence rather than the cause of eusociality. Grouping by family can hasten the spread of eusocial alleles, but it is not a causative agent. The causative agent is the advantage of a defensible nest, especially one both expensive to make and within reach of adequate food.

Nowak and colleagues presume that the causal arrow assumed in inclusive fitness theory should be reversed. In other words, ecological conditions pressing toward eusociality sometimes allow high levels of relatedness, rather than high levels of relatedness allowing eusociality (Bahar, 2017).

In attempting this coup, D. S. Wilson, E. O. Wilson, Martin Nowak, and others have placed the pole more fully outside the bounds of what Jerry Coyne, Richard Dawkins,⁶ and other detractors find acceptable. The *Overton window* has historically been bounded on one side by positing that relatedness was the sole requirement for eusociality and on the other by positing that relatedness was necessary but not sufficient for the evolution of eusociality. By replacing relatedness with ecology as the prime determinant of eusociality, and then further relegating relatedness

to the role of a by-product rather than a driver of eusociality, Wilson, Wilson, and Nowak have fully inverted the relationship as it has been understood by many evolutionists. Attempting a dispassionate analysis of this partisan strife, H. Gintis, an economist and evolutionist, insists on the *analytical validity* and *ultimate importance* of kin selection. At the same time, Gintis does not understand kin selection to be a driving force in the “formation and evolution” of sociality. Nowak and Wilson, Gintis writes, were warranted in exposing kin selection’s limitations and thereby circumscribing its scope and influence, even as they went a step too far by “questioning its validity and in understating its [kin selection’s] contribution to sociobiology.” In turn those kin selectionists on the other side of the divide “err in claiming that organisms in a social species maximize their inclusive fitness and that inclusive fitness theory explains social structure” (Gintis, 2017, p. 184).

The preceding sections document a range of views on genes and relatedness as they are applicable to multilevel selection theory and group formation. Hamilton, following Price, came to see the debate as semantic, some product of perception that disappears with perspective. Others, like Nowak, have relegated relatedness to a product of cooperation, thereby inverting the traditionally assumed directionality of the causal arrow, as has been seen. However, most see genetic relatedness as a driver of cooperation, even as the ultimate importance of relatedness varies proportionally. Both Hamilton and Wilson consider relatedness necessary, though the Wilsonian model more readily recognizes extra-genetic, ecological variables, thereby assigning proportionally less influence to relatedness. Relatedness then finds its place as a necessary variable in sociality, though it is a precondition, rather than a lone cause. With relatedness effectively circumscribed came clearer and more comprehensive descriptions of the ways in which relatedness may weigh in favor of cooperation amid a broader multiplicity of causes, such as nest defense, territoriality, ecology, and life history traits. This is illustrated by those species with high relatedness that are not at all social, such as certain species of armadillo birthing septuplets, which, though genetically identical, go on to live more or less solitary lives (Greulich, 1938). In sum, with the possible exception of Nowak and some few other theorists, the spectrum of

opinion centers on how heavily weighted is relatedness, compared to other factors, with some degree of relatedness being necessary.

The purely theoretical literature on relative degrees of relatedness within and between social groups is mixed. Some mathematical simulations predict that high population *viscosity*, generated by the slow movement of individuals from their places of birth (also known as *philopatry*), tends to promote more local *cooperative* interactions among genetic relatives due to proximity but simultaneously tends to promote more local *competitive* interactions among genetic relatives for the same reason, with these two effects purportedly cancelling each other out (Mitteldorf & Wilson, 2000; Taylor, 1992; Wilson, Pollock, & Dugatkin, 1992). Other purely mathematical models have instead predicted the opposite (Schonmann, Vicente, & Caticha, 2013):

We conclude that contingent forms of strong altruism that benefits equally all group members, regardless of kinship and without greenbeard effects, can spread when rare under realistic group sizes and levels of migration, due to the assortment of genes resulting only from population viscosity. (p. 1)

The data from social insects on local genetic relatedness, however, is generally less equivocal than this body of theory. For example, much of the research on the evolution of sociality in primitive wasps has abandoned the strict kin selection model of Hamilton (1964), where shared genes must be identical by recent common descent, and their proportions inflated to elevated levels by the mechanism of *haplodiploidy*. This is largely because the most primitively social wasp colonies are not typically created by mother-daughter bonds, as envisioned by Hamilton's simplified model, but instead by *foundress associations* among fully fertile female wasps of the same generation coalescing to construct communal nests (e.g., West-Eberhard, 1967, 1969, 1975). Although their genealogies of origin are typically unknown to researchers, these foundresses have not been generally found by molecular genetic methods to conform to the levels of relatedness seemingly required by Hamilton's original model for kin-selected altruism to evolve. Nevertheless, they have often been found to be more closely related to each other within local groups than to the

general surrounding population outside of these groups (e.g., Blüher, 2018; Wehren Gaspar, López-Urbe, & Del Lama, 2007). This is not a purely accidental outcome of population viscosity, but is behaviorally mediated, at least in part, as foundresses have been observed to migrate among nests to maximize inclusive fitness: “A clear motivation for moving to new nests was high genetic relatedness; by the end of the foundress period all females were on nests with full sisters” (Seppa, Queller, & Strassmann, 2012, p. 1). Genetic relatedness among foundresses has also been proposed to play a contributory role in the degree of reproductive skew, or differential dominance, emerging among nestmates (e.g., Bolton, Sumner, Shreeves, Casiraghi, & Field, 2006; Sumner, Casiraghi, Foster, & Field, 2002). Such reproductive skew is believed to set the stage for more advanced stages of eusocial evolution, such as the evolution of the purportedly *sterile* worker caste.

With the understanding that genetic relatedness exists on a continuum and thus can proportionally influence cooperation, group selection becomes possible for distantly related human kin and even supranational human groupings that share genetic variance but also only for close hymenopteran or human kin. In consequence, we can see the logical extension of kin selection in *genetic similarity theory* (Rushton, 1998; Rushton & Nicholson, 1988; Rushton, Russell, & Wells, 1984), a theory which has been critiqued (Mealey, 1985) and thereafter successfully defended (Rushton, 2005). As with Hamilton’s (1975) updated inclusive fitness theory, genetic similarity theory subsumes relatedness among kin within a broader view of relatedness wherein trait similarities can foster cooperation and favoritism even when the genes underlying those traits reside in more distantly related conspecifics. In Rushton’s theory, genetically based favoritism and cooperation can thus operate in the province of mate preference, friendship, and *ethnic nepotism*. One can then cooperate with a group in competition with another as a result of having more shared genetic variance with one group than another and not necessarily based on any strong relatedness as found among siblings.

4 Commentary on the Controversy

We proceed to a summary statement of the levels of selection controversy; in doing so, we begin with an instructive quote from Gilpin (1975), orienting us in time and viewing this controversy as recapitulating that which surrounded evolution generally:

Group selection is thus an old concept that is believed in by many but has not been demonstrated to the satisfaction of anyone. The history of group selection perhaps resembles that of individual (Darwinian) selection up to about 1910. Both forms of selection were discovered by ‘economists’ working on human populations (Malthus and Carr-Saunders). For both, these economic ideas were shown to apply to animals (Darwin and Wynne-Edwards), which introduced a form of selection. But for both, the method of inheritance was not clearly defined. And for both, mathematical models of the evolutionary behavior had to await later development. (p. 8)

We select a second quote, like the one above, for its ability to stand aloof from the debate, giving perspective unavailable to partisans of either side (Hull, 1984):

One reason that the controversy over the levels at which selection takes place has remained so intractable is that some of the issues are basically metaphysical: what sorts of things are organisms in contrast to groups, what general characteristics must an entity have to be selected, can entities which have what it takes to be selected also evolve or are the requisite characteristics mutually exclusive, etc.? (p. 144)

In commenting on the levels of selection debate, Gintis (2017) notes that there is

a certain asymmetry in the mutual criticism of the two schools of thought. Few supporters of group selection deny the importance of inclusive fitness theory, while virtually all its opponents regularly deny the importance of group selection theory. (p. 192)

In contrast to these tendentious critics, Gintis (2017) accurately observes that “[t]he correct way of thinking is to embrace both atomistic [inclusive fitness] and structural [group selection] approaches and analyse the corresponding interplay of forces” (p. 192).

Evolution can operate on any entity whose heritable phenotypic variation results in differential fitness. Traditionally, that entity is understood to be the individual organism, and, of course, organisms evolve. Notwithstanding, groups also evolve, as they, too, are aggregates of heritable genetic material; they, too, display phenotypic variation; and they, too, evince differential fitness. In other words, *genes create phenotypes that exist at multiple levels of aggregation*: some at the level of cells, some at the level of individuals, and some at the level of groups of varying levels of complexity.⁷ Any of these levels can be the target of selection or, in other words, drive changes in gene frequencies. Thus situated as one level of selection by which gene frequencies within a species change, it should then be recognized that groups may be as small as an immediate family, or extend to larger aggregates, such as human tribes, states, nations, or continental populations. Accordingly, together with cells and organisms, these groups, both small and large, each comprise levels on which selection can operate; hence the term *multilevel selection*.

The various levels at which evolution operates within multilevel selection theory range from the obvious and long accepted to the contentious and vigorously debated. All understand that populations of organisms evolve over time. At the level of the family, selection can rest upon a basis of genetic relatedness as per *inclusive fitness theory*. However, beyond the confines of the family, or extended kinship networks, selection among larger aggregations of individuals, referred to as *group selection*, remains controversial in some quarters, as we have seen. Therefore, even as all see individuals as targets of selection, and most see families as targets of selection, there remains a fair degree of resistance to viewing populations, demes, tribes, nations, states, or continental populations as potential targets of selection. Group selection is part of multilevel selection. Multilevel selection theory, articulated later, did not replace as much as incorporate group selection. While always understanding evolutionary processes to proceed within the overarching framework of multilevel selection, we nonetheless focus on large, non-closely related groups and group

selection. *We attempt to level empirical data precisely at the group selection controversy, which remains the most contentious aspect of multilevel selection theory.* So yes, we are arguing for the validity of multilevel selection theory, but specifically doing so by attempting to buttress the “weakest” leg or level on which it partially stands, which is group selection.

Thus, with proper perspective, objections to naïve group selection have been co-opted as support for multilevel selection theory. Within this context, readers are brought to the understanding of the larger point, namely, that genes resident in groups of individuals can precipitate cooperation and cohesion such that lines of competition and conflict are often drawn along the fault line of genetic difference. At still a higher level of abstraction, we see colonial organisms, from siphonophores to slime molds, as cooperative, group-selected ventures. Moreover, eusocial insect colonies, with their high genetic relatedness, blur the boundary between individual and collective. Even multicellular life is in some ways a feat of group selection, in that it presupposes the cooperation of many genes to perpetuate the survival and reproduction of the entire organism via the suppression of selfish genetic elements.

5 Multiple Levels of Aggregation: A Brief Illustrative Survey

There is a growing body of literature on selfish genetic elements (Okasha, 2006, p. 145), of which cancer may be held out as the most well-known example (Fishman & Jainike, 2014).⁸ Looking to the case of cancer, we see that, if a cancerous uprising can beat the odds by mutating within a long-lived stem cell, and continue without repair in such a way that meaningfully and harmfully alters protein production, while also significantly boosting replication above and beyond the rate of other somatic cells, it can then metastasize (Greaves, 2000). Immunosurveillance (Schreiber, Old, & Smyth, 2011; Waldhauer & Steinle, 2008), inflammatory response (Grivennikov, Greten, & Karin, 2010), apoptosis (Kerr, Winterford, & Harmon, 1994), killer *T* cells (Krijgsman, Hokland, & Kuppen, 2018), natural killer cells (Morvan & Lanier, 2016; Wu &

Lanier, 2003), macrophages (Mills, Lenz, & Harris, 2016), and dendritic cells (Palucka & Banchereau, 2012) act to suppress mutinous cancer cells, just as federal, state, and local law enforcement work with prosecutors, judges, jailers, and executioners to suppress criminal, revolutionary, or treasonous citizens.

We learn more about multilevel selection when we observe obligate symbiotes intermediate a continuum of cooperation anchored on one extreme by complex multicellular bodies and on the other by solitary organisms. Lewontin (1970), Sober and Wilson assert, was the first to connect group selection to the evolution of virulence in parasites. Lewontin studiously differentiated group selection or *population selection* as he seems to have termed it in his 1970 publication *The Units of Selection*, from Wynne-Edwards's *species selection*. Though Lewontin believed the conditions were rare and the requirements strict, he countenanced group selection, providing two examples, one of which related to the virus *myxoma* and the evolution of its virulence. The myxoma virus was introduced purposefully to Australia to control the accidentally⁹ introduced rabbit population, the explosion of which was displacing native fauna and taxing native flora. The lethality of myxoma was legion. It killed almost 100% of infected rabbits, though the surviving few seemed to eventually have evolved resistance, which was confirmed via laboratory testing. Resistance within the rabbits is fully explicable and expected as an individually selected evolutionary outcome. Testing, however, was also performed upon free-ranging myxoma, which had evolved toward reduced virulence, a finding explicable through the lens of group selection. As Lewontin explained, myxoma was spread via mosquitoes into a single rabbit, and were thereafter trapped within that rabbit. The fate of host and parasite was one. As Lewontin states, a host rabbit then amounted to a deme from myxoma's perspective. Especially virulent groups or populations of myxoma extinguished themselves as they extinguished their hosts, making less virulent strains of myxoma comparatively more prevalent as they existed alongside the hosts they spared.

Sober and Wilson (1998, p. 50) then cite Nesse and Williams, who note that the evolution of virulence is now an obvious example wherein group selection and individual selection are opposing forces in selecting for altruism and selfishness. The contest will be decided based on the

“relative strengths of within-host and between-host competition in pathogen evolution.” Suggesting that between-host competition sometimes prevails, Miralles, Moya, and Elena (1997) found group selection sufficiently powerful to attenuate virulence, even as individual selection acted to augment virulence. In addition to group selection acting to decrease virulence in *horizontal transmission* of parasites to hosts, group selection can attenuate virulence in certain forms of *vertical transmission*, wherein parasites are transmitted from a host to that host’s offspring (Ferdy, 2009).

Mitochondria were free-living prokaryotes that merged with the ancestors of contemporary eukaryotes 1.45 billion years ago, giving rise to extant eukaryotic life (Gray, 2017; Sagan, 1967). Reflecting on these capabilities, Bahar (2017, p. 170) writes, “even for prokaryotes, then, the transition from individual to collective, with its delicately negotiated balance between competition and cooperation, occurs with comparative ease.”

In this vein, slime molds are of great interest. Illustrative of the miracle of slime mold formation, some amoebae form bricks in the stalk, which will never reproduce, allowing other amoebae to ably disperse from the heights gained by virtue of those below. Field studies of slime molds find aggregate slug formation from genetically distinct amoebae. Even as different amoebae species do not combine, slugs contain considerable intraspecific genetic diversity, which nevertheless does not preclude slug formation, even as some individual amoebae must come to comprise the stalk of the fruiting body, thus allowing others to persist at their expense (Bahar, 2017, p. 185).¹⁰

Coral is an association of animal-like polyps and photosynthetic algae that serves as a common example of obligate symbiosis among other species. Still further, siphonophores are of certain relevance. With more than one hundred species of these sea creatures being classed into three distinct suborders, one observes specialization in buoyancy, propulsion, and digestion (Kirkpatrick & Pugh, 1984). The Portuguese man o’ war, a famed representative of the order commonly mistaken for a jellyfish, displays remarkable division of labor and unitary integration. We learn still more about multilevel selection when we observe those organisms facultatively switching between solitary existence and colonial cooperation in

response to environmental demands. To this point are Bahar's extensive reviews of bacterial biofilms, secreted matrices within which individual bacteria become embedded so as to resist attack and transfer nutrients. Complex processes of chemical communication and genetic switching allow quorum sensing and coordinated responses to environmental changes of which the creation of biofilms is only one example.¹¹

Sober and Wilson review self-sacrificial altruism among multicellular parasites. They specifically use the example of the lancet liver fluke (*Dicrocoelium dendriticum*), a parasite that creates a *brain worm* within ants, which induces parasitized ants to rise high and lock their jaws around a grass blade, making it more likely that they will be eaten by a ruminant, such as a sheep. From thence, the parasite can infect the ruminant liver, and exit as feces, which are eaten by snails. Thereafter, the parasite comes out in a mucus envelope, which is then eaten by ants; and so, the life of these parasites cycle between ants, ruminants, snails, and back again. The ant phase is focused on by many ecologists and evolutionists, for it is an account of behavioral change induced by a parasite on its host. From a group selectionist perspective, however, the point of interest is not the manipulation of the host, but the self-sacrificial process by which that manipulation is accomplished. The *brain worm* is, in effect, an altruistic volunteer member of the parasitic population, which generates the ant's behavioral change at the cost of its own reproductive potential. As per an individual selectionist view, brain worms should decrease and disappear. However, the key to understanding why this does not happen is to consider the individual ant with its population of fifty odd parasites inside, vying in competition against conspecific parasite populations sequestered in other ants. Within the ant, brain worms have lower fitness. However, parasitic populations with brain worms, because they manipulate their host ants into being reliably eaten by ruminants, have higher fitness than parasitic populations without brain worms. Thus, there is an individual selection pressure opposing a group selection pressure. The very existence of brain worms, in this sense, may be taken as evidence of group selection's ability to overcome individual selection. What looks to be something impossible to explain, Sober and Wilson (1998) conclude, becomes easy to explain.¹²

Though ecological exigencies are among the other factors inducing cooperation, competition and cooperation may have been its main drivers. This is evident even in the laboratory. Release a predatory small mouth ciliate into a population of single-celled algae (*Chlorella*), and witness those algae form into eight-celled units (Bahar, 2017), with predation inducing de novo multicellular clustering.

Think of what is happening—a predator creates a pressure to which there is an adaptive response toward cooperative aggregation. We witness the rudiments of complexity through cooperation among organisms against other organisms—a point we return to in Chap. 4 when describing how large-scale cooperative societies begin ratcheting toward complexity.

Evolution is famously directionless. It is a branching bush not a ladder. Lay descriptions, especially those perverting evolutionary science to the ends of ideology, often conceive of a teleological evolution replete with levels of hierarchal organization. Such levels then are understood as improvements on prior forms all progressing to a platonic ideal of perfection. Evolution, of course, is nothing of the sort. It is, rather, a blind bottom-up process of continual adaptation. However, that is not to say that evolution is absent trends. There is a robust trend toward complexity, when taking the overarching view of life as a whole (Bonner, 1988; Wilson & Kirman, 2016; Yaeger, Griffith, & Sporns, 2008). Most simply, time affords the evolution of complex forms (McShea, 1994). Yet, trends toward complexity are not simply a matter of endless iterations of integrational evolutionary cycles. Complexity comes of competition (Robson, 2005). Biotic competition, life struggling against life, both within and between species, tends, all else being equal, to augment complexity (Brockhurst et al., 2014). To be sure, the Cretaceous-Tertiary extinction ending eons of evolutionary complexity is only one of many examples of long-evolving and slowly won complexity being suddenly stricken from the evolutionary record by a sharp reversal in the prevailing selective regime. Nevertheless, complexity has a way of reasserting itself and will do so as long as complexity is a viable mode of competition (Benton, 1987). Thus, prokaryotes were joined by eukaryotes, multicellularity evolved, organisms developed lungs rather than relying on diffusion, and competition for light caused plants to invest in costly trunks

and the complex plumbing known as xylem and phloem. That is to say, complexity is ratcheted up by competition via a red queen effect in an evolutionary arms race between life forms. To competition must be added cooperation, an equally powerful spur toward complexity, as seen among the many intricate mutualisms (Thrall, Hochberg, Burdon, & Bever, 2007) ranging from multicellularity to eusociality (Thorne, Breisch, & Muscedere, 2003).

The foregoing examples all illustrate that the dynamics of multilevel selection generalize across a wide array of different levels of biological organization as well as different taxa.

6 Conclusions

Together, Chaps. 1 and 2, traversing selfish genes and kin selection, and thereafter colonial organisms and eusocial insects, were so organized as to alert readers from an essentialist torpor wherein clear boundaries separate organisms and their constituent cells. To the contrary, as we have seen, aggregations exist at various hierarchical levels of biological organization, forming temporary federations, lasting associations, or permanent mutualisms. Aggregation at any of these levels represents selection favoring group formation in reaction to some selective pressure. When we see associations ranging from complex multicellularity, to colonial organisms, to eusocial colonies, we are observing, in some sense, degrees of aggregation reflective of the levels of selection within multilevel selection theory. Genetic relatedness among group members, rather than being an alternative explanatory framework, is simply an auxiliary adjunct, perhaps necessary but not sufficient for group formation. This principle is illustrated by the aforementioned uncoupling of eusociality and relatedness wherein the co-occurrence of eusocial insect communities comprising individuals that are not closely related exist alongside populations of closely related individual insects that are not eusocial. Genetic information briefly occupies and animates individual organisms. With the death of the organism comes the dissolution of the genetic aggregation. Yet, genetic information recombines generation after generation, allowing for stable aggregation at the group level.

Notes

1. <https://evolution-institute.org/blog/the-tide-of-opinion-on-group-selection-has-turned/>
2. *Haystack Model*: Hamilton's theory of inclusive fitness was brought forth and framed as a competitor to group selection, a view reinforced by John Maynard Smith's *Haystack Model*. The Haystack Model makes assumptions that maximize the force of individual selection and minimize the force of group selection, in addition to confusing some concepts, as discussed by Sober and Wilson (1998, p. 71).
3. Sober and Wilson (1998) explain *Simpson's paradox* when discussing altruism and group selection. Simpson's paradox, or the *Yule-Simpson effect*, is a phenomenon in probability and statistics wherein a trend appears in several different groups of data but disappears or reverses when these groups are combined, which is also why some additionally use the terms *reversal paradox* or *amalgamation paradox* synonymously. From one factor pulling in this direction and another factor pulling in that direction can come a cancellation of effects. So, Simpson's paradox is a myopic focus on outcome that fails to appreciate how that outcome came about. This is relevant in a multilevel selection model as individual selection and group selection are often thought to be working at odds. Take the example of a tug of war where the flag marking the rope's center hovers in the middle, not because it is at rest but because pull on one side is correspondingly countered by pull on the other.
4. Bourke, A. F. (2007). Social evolution: Community policing in insects. *Current Biology*, 17 (13), R519–R520.
5. (<https://www.wolf.org/wolf-info/basic-wolf-info/biology-and-behavior/hunting-feeding-behavior/>)
6. "Richard Dawkins agreed, writing that the Nowak, Tarnita, and Wilson paper was "no surprise" since "Edward Wilson was misunderstanding kin selection as far back as this seminal 1975 work, *Sociobiology*." David Sloan Wilson leapt into the mix, writing an "open letter to Richard Dawkins" titled "Why Are You Still In Denial about Group Selection"? Mutual allegations of ignorance of the literature are a common motif. "Your view is essentially pre-1975", wrote Wilson, "a date that is notable not only for the publication of *Sociobiology* but also a paper by W. D. Hamilton, one of your heroes, who correctly saw the relationship between kin selection and group selection thanks to the work of George Price."

7. These three characteristics were defined by Richard Lewontin and were described by Okasha on page 13 of the following work:
Okasha, S. (2006). *Evolution and levels of selection*. New York: Oxford University Press.
8. Fishman and Jainike (2014) also provide the example of selfish genetic elements among stalk-eyed flies. In this case selfish genetic elements bias toward female production, so that when males and females mate, they produce a preponderance of females. As males become rare, it becomes extremely advantageous to rid oneself of the burden of these distorting elements. Stalk eyes are actually associated with not having these selfish genetic elements; they are a marker of being free of them; therefore they give rise to female preference for stalk eyes. Thus, you have sexual selection driven by selfish genetic elements.
9. It seems that rabbits were brought in cages on the First Fleet from England, and so it was their escape into the wild that was accidental.
10. See Bahar (2017, p. 188) for an interesting image depicting the stages of amoeba collectivization: growth, aggregation, differentiation, migration, and culmination.
11. Interestingly, in the course of this presentation, Bahar describes *persisters*, which might first sound like antibiotic-resistant bacteria. However, these persisters are more common where the biofilms are denser, and thus their presence and numbers appear to be density dependent. They are quite good at founding the colony anew where it has been decimated. They have a slower metabolism allowing them to exist in a sort of stasis or diapause so that they are not ingesting toxins to lethal rates.
12. It should be noted that, when first explaining the significance of the aforementioned parasite, Sober and Wilson do not mechanistically explain how the selfishness in the group does not entirely displace the altruistic. In other words, how within-group selfishness does not undermine between-group fitness. By the end of page 31, these authors begin to broach this subject. Sober and Wilson essentially argue that there will be a stable polymorphism and then, without using the word, at least just then, make an argument about an evolutionarily stable strategy maintained by negative frequency-dependent balancing selection. However, there is no actual evidence of the presence of this polymorphism; it is only posited.

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