

- (S before L) In the lineage leading to current mammals, first sutures evolved and then live birth evolved, where the sutures were part of the reason that there was selection for live birth.
- (L before S) In the lineage leading to current mammals, first live birth evolved and then sutures evolved, where live birth was part of the reason that there was selection for sutures.

These two hypotheses agree that the lineage began with organisms that didn't have live birth or sutures and ended with organisms that have both. They make different claims about what happened in between. The first says that there were organisms that had sutures but no live birth; the second says that there were organisms that had live birth but not the sutures. These are claims about organisms that are ancestral to current mammals. They make different predictions about what we should find in the collateral descendants – i.e., in current organisms that are *not* mammals. My suggestion is that Darwin's argument is that the observed features of reptiles and birds favor one of these hypotheses over the other:

$$\begin{aligned} & \text{Pr}(\text{reptiles and birds have sutures but no live birth} \mid \text{S before L}) \\ & > \text{Pr}(\text{reptiles and birds have sutures but no live birth} \mid \text{L before S}).^{103} \end{aligned}$$

This argument uses the fact of common ancestry to assess hypotheses about adaptation without using parsimony to reconstruct ancestral character states (Sober 2008b, pp. 259-261).

5.2. More on units of selection

One of the main conceptual questions that has exercised philosophers writing about the units of selection problem is realism versus conventionalism. The realist view of the evolution of a trait is that it is a factual question whether the trait's evolution is influenced by selection at each of several levels – group, individual, and genic. Conventionalists (Cassidy 1978, Sterelny and Kitcher 1988; Kitcher, Sterelny, and Waters 1990; Waters 1991; Sterelny and Griffiths 1999; Kitcher's comments in Gasper 2004; Waters 2005), argue that the biological facts do not settle the matter. For them, the relevant question concerns which type of explanation is most useful.¹⁰⁴ Conventionalists grant that it is sometimes true that a trait evolves because of group or individual selection, but then they claim that same processes

¹⁰³ Modern biology now recognizes that Reptilia is not a monophyletic group, though Reptilia+Aves is.

¹⁰⁴ Dawkins defends a position that resembles conventionalism in his second book, *The Extended Phenotype*, in which he proposes a modification of what he said in *The Selfish Gene*. Dawkins (1976) says that group selection is false and that genic selection is true; in the new book, Dawkins (1982) retains the thesis that group selection is factually mistaken, but says that the choice between individual and genic selection is a matter of convenience.

can also be correctly described as occurring because of genic selection. The converse, however, does not hold; some cases of genic selection can't be correctly described as cases of individual or group selection. So, for conventionalists, there is a pragmatic point in favor of the genic account – its generality. Conventionalism is not the position promoted by early foes of group selection such as Williams (1966), Maynard Smith (1964), and Dawkins (1976), who argued that group selection hypotheses are factually mistaken claims about nature. According to conventionalists, the battle concerning group selection that began in the 1960s was one big confusion. Biologists were wasting their time thinking that there is a substantive empirical issue here.

Figure 5.4: An individual's fitness depends on its own phenotype and on the phenotype of its partner.

		the individual's partner is	
		Altruistic	Selfish
the individual is	Altruistic	$x+b-c$	$x-c$
	Selfish	$x+b$	x

I describe the alternative to realism as *conventionalism*, not *pluralism*, because realism about *units of selection* and pluralism about *explanation* are compatible. Or, at least, I hope they are, because I embrace them both. The explanatory pluralism that I endorse holds that, for any event, there are different true stories that explain why the event occurred. Some describe more proximate causes while others describe causes that are more distal; some describe macro-causes while others describe causes that are more micro (Sober 1984, 1999). I doubt that there is an objective sense in which one of these is best; some are more useful than others, depending on our interests. For example, consider the evolution of altruism and selfishness in groups of size two¹⁰⁵ where the fitnesses of the two traits are the ones shown in Figure 5.4. If selection leads altruism to increase, the following explanations are both correct (Sober 1993, p. 114):

- (1) There is group selection favoring altruism and individual selection favoring selfishness, and the former cause is stronger than the latter.¹⁰⁶
- (2) $\Pr(\text{partner is } A \mid \text{individual is } A) - \Pr(\text{partner is } A \mid \text{individual is } S) > c/b$.¹⁰⁷

¹⁰⁵ The choice of $n=2$ is for convenience only.

¹⁰⁶ Price's (1970) equation decomposes the change in a trait's frequency produced by natural selection into the change due to group selection and the change due to individual selection. This is the device that is usually used to compare the magnitudes of the two processes, though contextual analysis offers a rival approach. For comparison of these two quantitative formats, see Okasha (2006) and Sober (2010b).

This pluralism about explanation is perfectly compatible with the realism I prefer in connection with units of selection. As noted in §2.4, I define group selection as variation in fitness among groups and individual selection as fitness variation among organisms in the same group. A natural definition of genic selection is that it occurs precisely when there is fitness variation among genes in the same organism.¹⁰⁸ I'll use the term "MLS theory" (meaning multi-level selection theory) to label these definitions. According to MLS theory, a given trait may evolve because any or all of these processes is underway. The units of selection problem is as real as the question of how fitnesses vary.

Conventionalists argue for their position by pointing to the fact that group properties *supervene* on the properties of individuals. This means that the properties of a group at a given time are determined by the properties of the individuals in the group at that time.¹⁰⁹ For example, in standard models of the evolution of altruism, the trait that is relevant to a group's fitness is the percentage of altruistic individuals it contains; this property of the group is fixed once you specify, for each individual in the group, whether it is altruistic or selfish. The *supervenience argument for conventionalism* goes as follows:

- (a) Group properties supervene on properties of individuals.

- (b) Therefore, anything that group properties explain also can be explained in terms of properties of individuals.

- (c) Therefore, whenever group selection explains a trait's evolution, individual selection does too.

- (d) Therefore, it is a matter of convention, not fact, whether a trait evolves by

¹⁰⁷ Proposition (2) can be derived from the fitnesses given in Figure 5.4. We need to compute the fitnesses $w(A)$ and $w(S)$ of altruism and selfishness. Each is an average. Altruists sometimes live with other altruists and sometimes they live with selfish individuals. The fitness of the trait is an average over the fitnesses it has in these two contexts, and the same is true of the fitness of selfishness:

$$w(A) = Pr(\text{partner is } A \mid \text{individual is } A)(x-c+b) + Pr(\text{partner is } S \mid \text{individual is } A)(x-c)$$

$$w(S) = Pr(\text{partner is } A \mid \text{individual is } S)(x+b) + Pr(\text{partner is } S \mid \text{individual is } S)(x).$$

Let $p = Pr(\text{partner is } A \mid \text{individual is } A)$ and let $q = Pr(\text{partner is } A \mid \text{individual is } S)$. Then $w(A) > w(S)$ precisely when

$$p(x-c+b) + (1-p)(x-c) > q(x+b) + (1-q)x.$$

A little rearranging of this inequality yields proposition (2).

¹⁰⁸ This definition of "genic selection" is not the one used in Sober and Lewontin (1982) or in Sober (1984), which I abandoned as from Sober and Wilson (1994).

¹⁰⁹ Of course the fitness of a group depends on its environment, and so do the fitnesses of the individuals in it. The supervenience thesis does not deny this point.

group or individual selection.

I grant, for the sake of argument, that (b) follows from (a).¹¹⁰ However, I deny that (c) follows from (b), as does Okasha (2006, pp. 105-107). Why do conventionalists think that (c) is a consequence of (b)? Everything depends on how they define group and individual selection. If the groups in the metapopulation vary in fitness because they have different frequencies of altruism and selfishness, and the frequencies of the traits change for that reason, then it must also be true that altruistic and selfish individuals in the metapopulation vary in fitness. Conventionalists then define individual selection as variation in fitness among individuals in the metapopulation, and declare a victory. Their concept of individual selection differs from the one used by MLS theory, according to which individual selection means variation in fitness *within groups*, not in the *global metapopulation*. A similar ambiguity attaches to the concept of “genetic selection.” When selection causes gene frequencies in the metapopulation to change, conventionalists define genetic selection to mean variation in the fitness of genes in that global population; it then follows that all changes wrought by selection (even by group selection) are instances of genetic selection. MLS theory, on the other hand, restricts the term “genetic selection” to variation in fitness that occurs within individual organisms; it occurs when there is meiotic drive or intragenomic conflict,¹¹¹ but not universally. Figure 5.5 provides a translation manual for MLS theory and conventionalism. The key difference is that the former defines group, individual, and genetic selection so that they are logically independent, while the latter defines them so that they are linked by entailment relations.¹¹²

¹¹⁰ Granting this contradicts an influential argument against reductionism due to Putnam (1975), which I’ll discuss in the next section.

¹¹¹ Cancer is a third example of genetic selection in the sense of that term used in MLS theory. Cancers often result from mutations that cause cells with mutant genes to divide more rapidly than cells in the same organism that missed the mutation event; in addition, cancer cells often evade the programmed cell death that limits normal cells. Within-organism selection favors the cancer, but selection at the organismic level acts in the opposite direction.

¹¹² If evolution is defined as change in gene frequencies, then evolution caused by natural selection must be labeled as “genetic selection,” according to the definitions that conventionalists adopt. This means that group selection is a kind of genetic selection and therefore that genetic selection is not a real alternative to group selection. Notice how far we have strayed from the idea that group selection is factually incorrect and that genetic selection is correct.

Figure 5.5: M is an evolving metapopulation that is divided into groups, which contain organisms, which contain genes. MLS theory and conventionalism assign different meanings to “individual selection” and “genic selection.” They agree about what “group selection” means.		
	MLS theory	Conventionalism
Group selection	Variation in the fitnesses of groups in M	Variation in the fitnesses of groups in M
Individual selection	Variation in the fitnesses of organisms within groups	Variation in the fitnesses of organisms in M
Genic selection	Variation in the fitnesses of genes within organisms	Variation in the fitnesses of genes in M

At first glance, conventionalism about units of selection seems to resemble conventionalism about space-time theories in physics (Sterelny and Kitcher 1988, p. 359) in that both claim that there is “no fact of the matter” as to which of several hypotheses is true. However, there is an important difference. Conventionalists and realists who debate the geometry of physical space discuss the same alternatives – Euclidean and non-Euclidean geometries. In contrast, when MLS theorists discuss individual and genic selection, they mean something different from what conventionalists mean when they use the same words. Conventionalism and realism about geometry are incompatible philosophies, but conventionalism and realism about units of selection, apparently, are not, once the ambiguities are recognized. This polysemy is exasperating, but does it hold out the hope that we can all be friends? Well, I am happy to be a conventionalist about the descriptors that *conventionalists* use. What I don’t see is why conventionalists are entitled to take a conventionalist view of the distinctions that *realists* want to draw.

Kitcher says that “one can tell all the facts about how genotype and phenotype frequencies change across the generations – including the causal explanations of the changes – without any commitment to a definite level at which selection acts (Gasper 2004, p. 89).” Notice that Kitcher does not reject the factuality of causal talk in general; his scruples are more specific, in that he thinks that causal explanations can be given without invoking a uniquely correct “level.” Consider how Kitcher’s position applies to propositions (1) and (2). It is true that the evolution of altruism can be explained by citing proposition (2), which does not mention opposing selection processes that occur at different levels. But that does not address the question of why the claim made by proposition (1) is nonfactual. Nor does it address the more general question of why the distinctions described in Figure 5.5 that MLS theory wishes to deploy are nonfactual. Sterelny and Griffiths (1999, p.169) present an argument for conventionalism that makes the same mistake. They discuss two possible explanations for why beavers build dams. The

first invokes group selection while the second describes why dam-building beavers are, on average, fitter than non-builders. Waters' (2005) argument that "it makes no sense to say true causes are at higher levels and not lower levels" likewise ignores how MLS theorists define levels of selection. Pluralism about explanation does not entail conventionalism about units of selection, at least not when the units of selection question is understood in the way that MLS theory proposes.

I began this section by describing what realism and conventionalism each say about the evolution of a given trait. Does this mean that we have the option of being realists about the evolution of some traits and conventionalists about the evolution of others? On its face, picking and choosing in this way seems wrong. Realism and conventionalism are supposed to be *general* theses, so perhaps we are obliged to be realists about *all* traits, or about *none*. I don't think so; I am a realist 99.44% of the time. The exceptions I see have nothing to do with the pluralism about explanation on which conventionalists have rested their case. Rather, the exceptions involve special features of the evolution of neuter workers (§2.5) and sex ratio (§3.7). I'll discuss sex ratio here; the same points apply to the evolution of sterility. Suppose each nest in a species of social insect is founded by a single fertilized female who controls the sex ratio of her progeny and that nests with female-biased sex ratios are more productive than nests with even sex ratios. Is this group selection on nests for female-biased sex ratios or individual selection on foundresses for producing one mix of sons and daughters rather than another? I see no need to choose (Sober 1984, p. 348).¹¹³ This example is enough to show that the distinction between group and individual selection is *sometimes* a matter of convention. But that is a far cry from conventionalism, which holds that it is *always* a matter of convention whether group selection has occurred.¹¹⁴

Unlike the conventionalist philosophers whose views I just discussed, the biologists I now want to consider (West, Griffin and Gardner 2006, Gardner and Grafen 2008, and Wild, and Gardner and West 2009, whom I'll call GGGWW) do not deny that it is a factual question whether groups are ever units of selection. They agree with the viewpoint described in Chapter 2, that group selection means fitness variation among groups and individual selection means fitness variation within groups; it is hard to be a conventionalist about whether fitness varies among and within groups. Instead, GGGWW argue that units of *selection* must be distinguished from units of *adaptation* and that multi-level selection theorists

¹¹³ With more than one foundress, the ambiguity disappears.

¹¹⁴ In addition to the qualitative question of what the units of selection are in the evolution of a trait, there also is the quantitative question of how the total change in trait frequency produced by natural selection should be decomposed into the amount of change due to group selection and the amount due to individual selection. For discussion of realist and conventionalist positions on this quantitative question, see Okasha (2006) and Sober (2010b).

fail to recognize this distinction, which leads them to fall into a “logical error” (Gardner and Grafen 2008, p. 666).

GGGWW point out that multi-level selection models of the evolution of selfishness and altruism that separately represent the contributions of individual and group selection are predictively equivalent with models of kin selection that describe the inclusive fitnesses of the two traits; these kin selection models do not separate individual from group selection (see, for example, Gardner and Grafen 2009, p.660). To make precise the sense in which this claim of equivalence is true, let’s consider what inclusive fitness means. Given the fitnesses shown in Figure 5.4, the usual representation of the old-fashioned Darwinian fitnesses of altruism (A) and selfishness (S) in groups of size 2 is as follows:

$$(3) \quad w(A) > w(S) \text{ if and only if } \Pr(\text{partner is } A \mid \text{individual is } A) - \Pr(\text{partner is } A \mid \text{individual is } S) > c/b.$$

The inclusive fitnesses of the two traits are:

$$I(S) = x$$

$$I(A) = x - c + rb,$$

from which it follows that

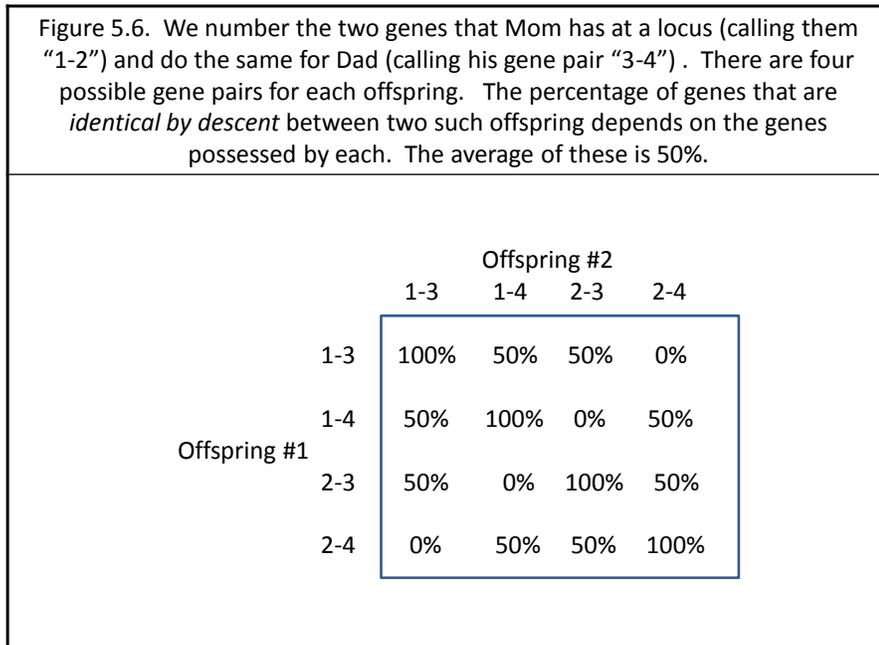
$$(4) \quad I(A) > I(S) \text{ if and only if } r > c/b.$$

The quantity r is the coefficient of relatedness and the right-hand side of (4) is Hamilton’s inequality. Propositions (3) and (4) each describe what it takes for altruism to have a higher fitness than selfishness; the one is stated in terms of Darwinian fitness, the other in terms of inclusive fitness. In each case, the fitness ordering is taken to predict which trait will increase in frequency. It is in this sense that propositions (3) and (4) make predictions. The two criteria will be predictively equivalent precisely when

$$(5) \quad r = \Pr(\text{partner is } A \mid \text{individual is } A) - \Pr(\text{partner is } A \mid \text{individual is } S).$$

Under what circumstances is proposition (5) true? The coefficient of relatedness r describes the probability that a gene found in an individual will be *identical by descent* with a gene found in the individual’s partner. The right-hand side of (5) says nothing about genes or identity by descent; rather, it

describes how the phenotypes of the two individuals in a pair are related. Let us explore each of the concepts used in proposition (5) in the context of a simple example – where the individuals in each pair are full sibs whose parents are not genealogically related to each other and there is a dominant gene for altruism.



If the individuals in each pair are full siblings and their parents are unrelated, $r = 0.5$.¹¹⁵ To see why, consider Figure 5.6. The coefficient of relatedness does not represent how probable it is that the genotypes of two siblings will be similar. For example, in a population in which a given gene is close to 100%, two full sibs will almost certainly have the same genotype at the locus in question, but r is still equal to 0.5. Identity by descent (IBD) isn’t about similarity (which geneticists call *identity by state*); rather, for full sibs whose parents are unrelated, the question is whether genes in the two siblings trace back to the same genes in their parents. In Figure 5.6, I have numbered the four genes that Mom and Dad have at the locus in question (ignoring whether they are in the same or different state). There are four possible gene pairs that an offspring might have; with fair meiosis, they are equiprobable. There therefore are 16 possible pairings of a gene pair in the first offspring with a gene pair in the second. In some of these pairings, all the genes in the two offspring are IBD. In other pairings, half the genes are IBD. And

¹¹⁵ If the parents are themselves full sibs, the r value for their offspring will be greater than 0.5 (Hartl and Clark 1997, pp. 258-259).

in still others, none of the genes are IBD. The average value, $(4/16)(100\%) + (8/16)(50\%) + (4/16)(0\%)$, is 0.5. That's why $r = 0.5$ for full siblings whose parents are unrelated.

Figure 5.7. Values for $\Pr(\text{partner is } A \mid \text{individual is } A)$ and for $\Pr(\text{partner is } A \mid \text{individual is } S)$ when A is rare and when A is common. Altruists have genotype aa or as ; selfish individuals have genotype ss .

	Probable genotype for individual	Probable genotype for parents	$\Pr(\text{partner is } A \mid -) =$
individual is A ; A is rare	as	$as \times ss$	0.5
individual is S ; A is rare	ss	$ss \times ss$	0
individual is A ; A is common	aa	$aa \times aa$	1
individual is S ; A is common	ss	$as \times as$	0.75

Now let's consider the right-hand side of proposition (5), which says nothing about identity by descent of genes. Still assuming that the individuals in each pair are full sibs, our task is to ascertain when the right-hand side equals 0.5. This will be true when altruism is caused by a dominant gene and the gene is rare; in this case, $\Pr(\text{partner is } A \mid \text{individual is } A) = 0.5$ and $\Pr(\text{partner is } A \mid \text{individual is } S) = 0$. However, these probabilities change value as the gene changes frequency. When the gene for altruism is common, $\Pr(\text{partner is } A \mid \text{individual is } A) = 1.0$ and $\Pr(\text{partner is } A \mid \text{individual is } S) = 0.75$. These numbers are explained in Figure 5.7. So proposition (5) is sometimes true, but sometimes it isn't; the criterion for when altruism will evolve, stated in terms of old-fashioned Darwinian fitness, doesn't always coincide with the one stated in terms of inclusive fitness.¹¹⁶

Hamilton (1964) developed his theory of inclusive fitness by considering a special case in which proposition (5) is true. However, by the time he wrote his 1975 paper, he had come to see that identity by descent isn't what is essential for altruism to evolve; he realized that what is crucial is that altruists tend to interact with other altruists, whether or not the interacting individuals happen to be closely related genealogically. This is why I said in §2.4 that kin selection is a special kind of group selection, one in which groups of interacting individuals are composed of genetic relatives. This point led Hamilton and his successors to give the coefficient of relatedness r a wider interpretation than the one I just described.

¹¹⁶ Here's another example that shows why proposition (5) can be false. Suppose there are 20 unrelated individuals, 10 altruists and 10 selfish, and that like pairs with like, yielding 5 pairs of altruists and 5 of selfish individuals. Since the individuals in each pair are genealogically unrelated, $r=0$. However, the difference in the two conditional probabilities on the right-hand side of proposition (5) equals 1.

Instead of defining r in terms of identity by descent, the idea is to let proposition (5) define what r means. If r is interpreted in this way, propositions (3) and (4) are predictively equivalent. With this wider interpretation of r , kin selection theory (stated in terms of inclusive fitness) is predictively equivalent with a multi-level selection theory (stated in terms of Darwinian fitness) in which group and individual selection are represented as separate processes. This wider interpretation, I take it, is what GGGWW intend. I have no objection to this, though it needs to be remembered that the predictive equivalence of kin selection with individual+group selection means that the “kin” in kin selection don’t need to be genealogical relatives.

In the parlance of multi-level selection theory, both the group and the individual are said to be “units of selection” if group and individual selection each influence the evolution of the trait in question. The term “unit of selection” therefore characterizes the *processes* that govern trait evolution. When the metapopulation evolves to some stable trait configuration, how should we describe that end result? It is here that the term “adaptation” should apply. When should that end result be called a group adaptation and when should it be called an individual adaptation? The fact that group selection influences a trait’s evolution (however weakly) is obviously not enough to say that the product of that process is a group adaptation. For example, suppose group selection occurs but is so weak that it is overwhelmed by the much stronger influence of individual selection, with the result that altruism is driven to zero. It would be absurd to call the result (100% selfishness) a group adaptation just because group selection was one of the processes that influenced what happened. The following definition of adaptation explains why. Suppose trait X becomes common in a lineage. When is X an adaptation, and what is X an adaptation for?

X is an adaptation for task T in a lineage if and only if X became prevalent in the lineage because there was selection for X , and the selective advantage of X was due to the fact that X helped perform task T (Sober 1984, p. 208; Sober 1993, p. 85).¹¹⁷

When selfishness becomes common, this is not because the trait provides a *group* advantage; it therefore would be wrong to regard 100% selfishness as an adaptation for helping the group. So it is not a group adaptation.

More generally, group and individual adaptation may be defined by identifying the group optimum and the individual optimum. The group optimum is the trait frequency that is predicted to

¹¹⁷ This definition could be generalized to cover the evolution of a stable polymorphism.

evolve if group selection, but no individual selection, is at work; this is why the group optimum is 100% altruism. Symmetrically, the individual optimum is the frequency that is predicted when individual selection, but no group selection, is at work; this is why the individual optimum is 100% selfishness.¹¹⁸ If altruism evolves to fixation or nearly so, the result is a group adaptation (not an individual adaptation). If selfishness evolves to fixation or nearly so, the result is an individual adaptation (not a group adaptation). And if the metapopulation settles down around 50/50, the result is a compromise (Sober and Wilson 1998, pp. 10-12, pp. 101-107).¹¹⁹ Obviously, the boundary between an “extreme” trait frequency and one that is “intermediate” is vague, but there is no helping that.

Gardner and Grafen (2009) complain that multi-level selectionists have never characterized what it takes for the individual or the group to be a “unit of adaptation,” and proclaim that they are the first to take this important step. They are wrong about the history, but, more importantly, the way they address this question goes awry. GGGWW agree with what I just said concerning *group* adaptation; if the model they describe (which separately represents group and individual selection via the Price equation) predicts that the metapopulation should evolve to 100% altruism or nearly so, and this is what we observe, then the group is a unit of adaptation; and if the model predicts that the system will evolve to 100% selfishness or nearly so, and this is what we observe, then the group is not a unit of adaptation. However, when it comes to defining when the *individual* is a unit of adaptation, GGGWW say that this is *always* true, provided that the metapopulation exhibits the predicted trait frequency. This has a peculiar consequence. Suppose the metapopulation is predicted to evolve to 100% altruism and this is what happens; the GGGWW proposal concludes that the individual is a unit of adaptation in this case. Why do they think that any mix of group and individual selection is compatible with the individual’s being a unit of adaptation? The reason is something I mentioned before — the predictive equivalence of a multi-level selection model with one stated in terms of inclusive fitness. Regardless of what the mix is of individual and group selection, *individuals are predicted to maximize their inclusive fitness*.

GGGWW’s permissive view concerning the individual as unit of adaptation violates one of Williams’ (1966) most important insights concerning the concept of adaptation — that adaptation at a

¹¹⁸ Notice that when selfishness evolves to fixation in a single group (and so there is no group selection), the individuals in the group are less fit at the end of the process than they were at the start (Figure 2.2). Selfishness may be said to be “optimal” for the individual nonetheless, if this means merely that it is better for an individual to be selfish than altruistic.

¹¹⁹ One possibility is to describe such compromises as embodying both group and individual adaptations; another is to say that it involves neither; a third is to say that the upshot is an individual adaptation if the final frequency of the trait is closer to the individual optimum, and to say that it is a group adaptation if the final frequency is closer to the group optimum. This choice won’t be relevant to my argument in what follows.

level requires selection at that level. Williams' thesis entails that group adaptation requires group selection (§2.1), but it applies to other levels as well. The GGGWW proposal violates Williams' requirement that individual adaptations must evolve by individual selection. If the metapopulation involves groups that are internally homogeneous (and so there is no individual selection), with the result that the metapopulation evolves to 100% altruism, it still is true that the trait with the higher inclusive fitness evolves; the GGGWW proposal concludes from this that the individual is a unit of adaptation — never mind the fact that no individual selection has occurred.¹²⁰

If an inclusive fitness model predicts the same outcomes as a multi-level selection model that explicitly recognizes the roles of group and individual selection, why should the fact that an outcome is correctly predicted by group+individual selection entail that the *individual* is always a unit of adaptation, but that the *group* is a unit of adaptation only in special circumstances? GGGWW's answer is to be found in a certain intuitive idea. Before inclusive fitness came along, it was natural to think about individual selection by imagining that individuals “try” to maximize their Darwinian fitness. Although “trying” can't be taken literally, the as-if quality of this thought is often heuristically useful; we can predict which traits will evolve by imagining rational agents who are trying to get what they want.¹²¹ Inclusive fitness seemed like a natural generalization of that idea — individuals are “trying” to maximize the representation of their genes in future generations, where it is recognized that an individual's genes can be found in her genetic relatives as well as in her own offspring. The idea can be broadened further, by taking on board the fact that nonrelatives sometimes have copies of one's genes;¹²² this means that helping nonrelatives can also be a way to get one's genes represented in future generations. The net result is that *any* helping behavior that evolves gets viewed as a form of genetic self-interest. This may seem like a pleasing consequence until it is realized that “self-interest” has now become an all-encompassing category. When altruism evolves, this is consistent with the heuristic idea of self-interest, since altruists are getting their altruistic genes into the next generation by helping other altruists. The idea that altruism is good for the group but bad for the individual has been lost. The way to recovery is to set aside the metaphor of “trying” and focus on the fact that there can be conflicts of interest between different levels

¹²⁰ Gardner and Grafen (2009, p. 666) seem to endorse the part of Williams' thesis that concerns group adaptation when they say that “a character that has not been selected according to this principle [i.e., the “principle of group-fitness maximization”], but which incidentally improves group reproductive success, can be described in terms of ‘group optimality,’ but does not constitute a group adaptation.”

¹²¹ I argue in Sober (1998a) that this heuristic sometimes yields the wrong answer.

¹²² In the narrower case of one's genes also being present in kin, these genes will (with some probability) be *identical by descent*; in the broader case in which kin and nonkin alike have copies of “one's genes,” the genealogical idea is discarded and one is simply talking about genes that are of the same type. This corresponds to the narrower and broader definitions of r , the coefficient of relatedness, discussed earlier.

of organization. What is good for the individual can conflict with what is good for the group. Our concept of adaptation should reflect this fact. Rather than use “individual adaptation” as an all-encompassing label that is defined so that it applies to *all* adaptations, regardless of whether they evolve by group or individual selection, I think it more useful to use “group adaptation” to name traits that evolve when group selection dominates the selection process and “individual adaptation” to name traits that evolve when individual selection is in the driver’s seat. Why have two labels if one of them applies no matter what?¹²³

Griffiths and Grafen (2009, p. 659) start their paper by quoting, apparently with approval, a remark of Dawkins’:

I have characterized inclusive fitness as “that property of an individual organism which will appear to be maximized when what is really being maximized is gene survival’ ... One might generalize this principle to other ‘vehicles’. A group selectionist might define his own version of inclusive fitness as ‘that property of a group which will appear to be maximized when what is really being maximized is gene survival’ (Dawkins 1982, p. 187)!

Individual selection and group selection both involve “gene survival.” In a haploid metapopulation, if altruists have gene *a* and selfish individuals have gene *s*, the evolution of altruism means that gene *a* outsurvives gene *s* and the evolution of selfishness means that *s* outsurvives *a*. If inclusive fitness is really about gene survival, it provides no basis for saying that individuals, rather than groups, are units of adaptation.

As mentioned earlier, Gardner and Grafen (2009, p. 666) think that multi-level selection theorists have failed to recognize the difference between unit of selection and unit of adaptation and therefore have fallen into a “logical error.” The logical error they have in mind, allegedly committed by Sober and Wilson (1998), is “the view that multilevel selection (including within-group selection) leads to the emergence of group adaptation.” Their phrasing is ambiguous – is the error supposed to be the idea that

¹²³ There is one remark that Gardner and Grafen (2009, p. 666) make that seems to me to be at odds with the position they take in the rest of their paper. They say that “... a character that has evolved according to the principle of group optimization, but which does not achieve optimality (for example, owing to insufficient time), is nevertheless a group adaptation.” This seems to mean that if there is solely group sel for a second, and the metapop remains at 99%*S*, that this configuration is a group adaptation.]

multi-level selection that includes a within-group component *sometimes* brings about group adaptation, or is the error supposed to be the claim that multi-level selection *always* has this outcome? The latter *is* an error, but it is not one we have committed; the former is not an error at all. Altruism can evolve to near fixation even when there is *some* individual selection; it isn't essential that there be zero. This point is illustrated by the example explored earlier in which groups are sibships of size two and there is a dominant gene for altruism; in this case, altruism evolves to near fixation when the cost/benefit ratio is small enough ($c/b < 1/4$). This example includes mixed groups, and so, as GGGWW agree, it follows that individual selection is part of the process.¹²⁴

There is a world of difference between the philosophers and biologists I have discussed in this section. The philosophers are conventionalists about units of selection but the biologists are not; the biologists develop a view of what a unit of adaptation is, but this is not a topic that the conventionalist philosophers address. In spite of these differences, there is something the philosophers and biologists have in common. Both indulge in *semantic stretching*. The conventionalist philosophers define “genic selection” so that it applies to all of natural selection (even to group selection). GGGWW define “individual adaptation” so that it applies to all adaptations that evolve by any mix of group and individual selection (even to the evolution of 100% altruism by pure group selection). Semantic stretching has an older pedigree in this subject. Dawkins (1976) calls a gene that evolves because of natural selection “selfish” even when it cooperates with other genes in the same body and even when it leads the organism in which it lives to lay down its life and thereby help other organisms. If this is selfishness, “selfishness” is not an antonym for cooperation and altruism. You don't need to be a friend of group selection to think that something fishy is going on here. The group selection problem began as an empirical question. Is there selection among groups, just as there is selection among the individuals who live in the same group? Does group selection change evolutionary outcomes, just as individual selection does? Are there

¹²⁴ Although GGGWW emphasize the importance of not confusing the process of group selection with group adaptation, which is a possible product of that process, Gardner and Grafen's (2009) discussion of policing and punishment in superorganisms runs afoul of that distinction. They say that they have established that “mechanisms of conflict resolution such as policing cannot be regarded as group adaptations (p. 668).” What is their argument for this conclusion? A page earlier Gardner and Grafen assert that “the superorganism comes into existence after these mechanisms [policing, punishing, etc.] are already established” and claim that this point “suggests that phenomena, such as punishment, policing, and high genetic relatedness cannot be understood as group adaptations.” The shift from “suggesting” to “establishing” is odd. In any event, let's suppose that superorganisms, by definition, must police and punish defectors. However, this does not entail that policing cannot evolve by group selection. There is a difference between the existence of group selection and the existence of superorganisms. Superorganisms are a possible product of the group selection process, not a precondition for the process' occurring. Gardner and Grafen have done nothing to undermine the thesis that punishing defectors is an altruistic act and requires group selection to evolve (Sober and Wilson 2008, pp. 142-149). If the behavior evolves to fixation or near fixation, it is a group adaptation.

adaptations that evolve because they help groups, just as there are adaptations that evolve because they help individuals? Although each of these questions can be answered with a simple *yes* or *no*, it is better to take one's options to be *often*, *sometimes*, *rarely*, and *never*. And besides these global questions that encompass the whole of nature, there also are local questions about specific traits in specific populations. Of course, a set of definitions cannot, by itself, *suffice to answer* questions that are genuinely empirical. But definitions can *clarify* empirical questions, which we then seek to answer by making observations. Do the inclusive definitions just mentioned of "genetic selection," "individual adaptation," and "selfish gene" help clarify these questions? If all selection is genetic selection, if all adaptations are individual adaptations, and if all genes are selfish, it may seem to follow that group selection, group adaptation, and altruistic genes are all myths. In fact, none of these conclusions follows if we use the definitions that conventionalist philosophers, GGGWW, and Dawkins respectively deploy. The illusion that these conclusions *do* follow has allowed pseudo-solutions to pass for genuine solutions to biological problems.

I'll conclude this section with an analogy and a puzzle. Here's the analogy: suppose that an electron's trajectory is affected by a gravitational force and an electrical force. One way to model this situation is to describe each of these forces as components and then compute the resultant net force by vector addition. A second way to model what is going on is to set this decomposition aside and simply describe the net force. These two models are not in conflict. However, confusion is bound to arise if we announce that the net force described in the second model is "really" a kind of gravitational force. It is the *inclusive* gravitational force, which reflects both the old-fashioned gravitational force and the electrical force as well. This may tempt one to conclude that gravitational force is the real cause of the particle's acceleration, even though we began by granting that both forces are at work. And now for the puzzle: If individual+group selection = kin selection and kin selection is really just a kind of individual selection, should we conclude that individual+group selection is really just a kind of individual selection? If so, we also should be happy to conclude that a bag of apples and oranges is really just a bag of apples. Neither the analogy nor the puzzle is aimed at GGGWW, who know that kin selection is not an argument against group selection. Unfortunately, many foes of group selection seem not to have heard the news.

5.3. Evolutionary theory and the reality of macro-probabilities

Modern evolutionary theory is awash with probabilities. For example, natural selection occurs when there is variation in fitness, and fitness is standardly decomposed into two components, viability and fertility, each of which is understood probabilistically. With respect to viability, a fertilized egg is said to have a certain *chance* of surviving to reproductive age; with respect to fertility, an adult is said to

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