

## COMMENTARY

**Adaptation and Natural Selection revisited**

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**Abstract**

In *Adaptation and Natural Selection*, George C. Williams linked the distinction between group and individual adaptation with the distinction between group and individual selection. Williams' Principle, as we will call it, says that adaptation at a level requires selection at that level. This is a necessary but not a sufficient condition; for example, group adaptation requires group selection, but the fact that group selection influences a trait's evolution does not suffice for the resulting trait frequency to be a group adaptation. What more is required? In this paper, we describe an answer to this question that has been developed in multilevel selection theory. We also discuss an alternative framework for defining units of adaptation that violates Williams' Principle.

**– Dedicated to George C. Williams (1926–2010) –**

George C. Williams' 1966 book *Adaptation and Natural Selection* was a landmark in the development of evolutionary theory. For those who agree with Williams' critique of group selection, the book remains a paradigm of how to think rigorously about evolution. For those who disagree, the book remains a powerful force that cannot be ignored. We count ourselves in this second category, but our disagreement with Williams (1966) about group selection (Sober, 1984, 1993, 2010; Sober & Wilson, 1998; Wilson & Wilson, 2007) is not the subject we want to discuss here. Rather, we want to revisit Williams' ideas about the concept of adaptation. This is one of Williams' enduring contributions, something that critics and proponents of group selection should both endorse.

It is central to the conceptual framework of *Adaptation and Natural Selection* that adaptations must be distinguished from fortuitous benefits (*aka* 'incidental effects'). The book abounds with illustrative examples. Here are two:

- Worms improve the soil, but that does not mean that their digestive systems are adaptations for soil improvement; rather, the worm gut evolved to help

individual worms survive and reproduce. The benefit that the ecosystem receives is a fortuitous benefit – a useful side effect unrelated to what caused the trait to evolve. The gut's ability to extract nutrition for individual worms is what the gut is an adaptation for (Williams, 1966, p. 18).

- Flying fish eventually fall back into the water after they have glided over the waves, but their doing so is not an adaptation for keeping them alive. Rather, their falling back into the water is a physical inevitability. There was no selection process in which fish with mass competed with fish that were weightless. The return to the water is thus a fortuitous benefit; it is not an adaptation (Williams, 1966, p. 11).

Whether or not Williams is right about the details of worm digestion and flying fish trajectories, he is right to draw this important distinction. Here is a definition that captures what Williams is after:

A trait *T* is now an adaptation for doing *X* in a lineage if and only if *T* evolved in the lineage because there was selection for *T*, and there was selection for *T* because having *T* promoted doing *X* (Sober, 1984, p. 208).

Fortuitous benefits are not *adaptations*, although they are *adaptive*. Adaptation is a concept that looks to the past; to say that a trait is now an adaptation is to make a claim about its history. Being adaptive (or advantageous) is a concept that looks to the future; to say that a trait is now adaptive is to say that it promotes survival and/or

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reproductive success. The title of Williams' book was well chosen – adaptation is a concept that is fundamentally linked to the concept of natural selection.

This simple but powerful idea played an important role in Williams' discussion of group selection. The fact that a trait now benefits groups does not entail that it evolved *because* it was beneficial to groups. The distinction between group adaptation and fortuitous group benefit is vital. The above definition of adaptation can be used to articulate the difference between group and individual adaptation:

Trait *T* is now a group adaptation in a lineage if and only if *T* evolved in that lineage because there was group selection for having trait *T*.

Trait *T* is now an individual adaptation in a lineage if and only if *T* evolved in that lineage because there was individual selection for having trait *T* (Sober, 1993, p. 85).

If the worm's gut evolved purely by individual selection, it is not a group adaptation, although it may now benefit groups of organisms (whether these are groups of conspecific worms or multispecies communities). If the flying fish's eventually falling back into the water once it is aloft did not evolve by a selection process, then it is not an adaptation, individual or group. The general definition of adaptation entails the more specific definitions of group and individual adaptation once we add the following connecting idea. Group adaptations are adaptations for helping the group; individual adaptations are adaptations for helping the individual. These conceptual points come together in what we will call:

*Williams' Principle*: adaptation at a level requires that there was selection at that level.

Those who think that there are group adaptations in nature and those who deny that this is so should use this principle as common ground.

Williams' Principle (Gross, 2004 uses this phrase to label a different idea – that 'reproduction has not only a benefit but also a cost to lifetime fitness') says that group selection is a necessary condition for group adaptation. The principle does not say that group selection suffices for group adaptation. And it is not sufficient. To explain why, let's consider an example – a metapopulation divided into groups, where the groups vary in the percentage of altruistic and selfish individuals they contain. For the purposes of this example, we can define altruism and selfishness as follows: altruists are less fit than selfish individuals in the same group, but groups with higher frequencies of altruists are more fit than groups with lower frequencies. There are some fine points here – e.g. the difference between strong and weak altruism, on which see Grafen (1984), Nunney (1985), and Wilson (1980, 1990) – but these will not affect the point we want to make. There are also disagreements among 'contextualists' and followers of

the Price equation approach (to be discussed soon) as to how group and individual selection should be defined in general, but these disagreements also will not matter to the point we want to make about this example. In this example, contextualists and Priceans agree that there is both group and individual selection. Group selection promotes the evolution of altruism, and individual selection promotes the evolution of selfishness. Both the group and the individual are 'units of selection' in this process, because both group and individual selection influence trait evolution. When the metapopulation evolves to some stable trait configuration, how should that end result be described? It is here that the term 'adaptation' may apply. When should that end result be called a group adaptation and when should it be called an individual adaptation?

Suppose, in this example, that group selection 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 occurred along the way. This is why the occurrence of group selection in a process does not suffice for the product of that process to be a group adaptation. This point is reflected in the definitions given earlier. When selfishness becomes common, this is not because the trait provided a *group* advantage; it did not. Universal selfishness evolved *in spite of* group selection, not *because* of it. So, 100% selfishness is not an adaptation for helping the group; it is not a group adaptation.

Generalizing from this one example, how should group and individual adaptation be defined? Given Williams' Principle, answering this question requires a general definition of group and individual selection. Here, we encounter controversy. One standard definition is that individual selection occurs precisely when there is fitness variation within groups and group selection occurs precisely when there is fitness variation among groups. This qualitative statement is a consequence of using the Price (1970, 1972) equation to partition the amount of change in trait frequency that is due to group and individual selection. We propose to use the qualitative definition in what follows; this does not commit us to the Price equation's quantitative decomposition. Contextualists (e.g. Heisler & Damuth, 1987 and Goodnight *et al.*, 1992) disagree with the Price equation approach and have their own quantitative decomposition. It is a consequence of their framework that group selection can occur when there is just one group (and so no variation in fitness among groups). This is not the place to explore the strengths and limitations of the two approaches (see Okasha, 2006 for discussion), but we do want to reply to one objection to the Price approach that many find compelling. We describe this objection by way of another simple example. Suppose that zebras either run fast or run slow, that fast zebras are fitter than slow

ones, and that a zebra's fitness depends just on its own speed, not on the speed of the other zebras in its herd. Now, imagine a metapopulation in which there are groups of zebras where each group is internally homogeneous for running speed. All the variation in fitness is among groups, but it seems wrong to conclude that there is group selection and no individual selection in this case (Sober, 1984, pp. 257–262; Heisler & Damuth, 1987; Okasha, 2006). We believe that the solution to this problem does not require jettisoning the definition of group and individual selection stated above; rather, what is needed is attention to the meaning of 'group' in the sense relevant to questions about units of selection. The herds in this example are not groups with respect to the trait of running speed precisely because a zebra's fitness is not influenced by how fast other zebras run (Sober & Wilson, 1994, 1998). True, the zebras in a herd may reproduce together, and they may influence each other's fitness relative to other phenotypes. Trait groups are defined one trait at a time, in terms of fitness influence.

With these definitions of individual and group selection in hand, we turn to the concepts of group and individual adaptation. These may be defined by identifying the group optimum and the individual optimum. The group optimum is the trait frequency that is predicted to evolve when group selection, but no individual selection, is at work. Symmetrically, the individual optimum is the frequency that is predicted when individual selection, but no group selection, is at work. When the evolving traits are altruism and selfishness, the group optimum is 100% altruism and the individual optimum is 100% selfishness. 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 & Wilson, 1998, pp. 10–12, pp. 101–107). Should we say that these compromises are group and individual adaptations simultaneously, or that they are neither, or is there another way to classify them that is better? If the equilibrium trait frequency is closer to one of the optima, do we want to quantify the degree to which it is a group and an individual adaptation? How these questions should be answered will not affect the argument in what follows. Obviously, the boundary between 'extreme' trait frequencies and ones that are 'intermediate' is vague, but there is no helping that.

Although discussions of group and individual selection have often focused on the evolution of altruism and selfishness, we want to emphasize that group selection can promote the evolution of traits that are not altruistic. For example, traits that have multiple adaptive peaks can be affected by group selection, although they are not altruistic (Boyd & Richerson, 1992; Samuelson, 1997; Sober, 2010). Individual and group optima can be

defined for traits other than altruism and selfishness, so group adaptations can fail to be altruistic.

Williams' Principle, as noted earlier, is something that critics and proponents of group selection should embrace. If so, what is the point of preaching to a universal choir? The point is that a number of evolutionary biologists have recently developed definitions of group and individual adaptation that differ from the ideas just described. Their proposals, it turns out, contradict Williams' Principle. It is ironic that these biologists see themselves as continuing the individualist tradition that Williams helped initiate. It is doubly ironic that we two anti-individualists need to defend Williams against his own followers.

The biologists we have in mind are West *et al.* (2006), Gardner & Grafen (2009), and Wild *et al.* (2009). We will call this group GGGWW. They do not deny that group selection is conceptually coherent or that it actually occurs in nature. In this respect, they have moved far away from Williams (1966). They do so in part because they take the Price (1970, 1972) equation to provide a useful formalism for separating group and individual selection, although Gardner & Grafen (2009, p. 9) acknowledge that there are some limitations in using the Price equation to define this distinction; these limitations will not be relevant in what follows. GGGWW grant that there are cases in nature in which the addend in the Price equation that represents the change in trait frequency owing to group selection is nonzero.

To explain GGGWW's ideas about adaptation, we begin by noting that they assert (correctly, in our view) that there is an equivalence between inclusive fitness theory and the Price equation formalism (Gardner & Grafen, 2009, p. 5). To see what this means, let's once again consider an altruistic and a selfish trait that are evolving in a metapopulation. GGGWW interpret inclusive fitness theory in such a way that the following proposition is true:

Altruism has a higher inclusive fitness than selfishness if and only if group selection is stronger than individual selection.

To secure this equivalence, the coefficient of relatedness  $r$  that Hamilton (1964) used to describe inclusive fitness must be interpreted broadly; it is defined as the correlation among interacting individuals, not as the probability that their genes are identical by descent. Understood in this way, inclusive fitness has nothing essential to do with 'kin selection,' if 'kin' means genealogical relatives. The above equivalence, we hasten to note, is not an argument against group selection nor do GGGWW suggest that it is.

As described so far, the GGGWW position is a repudiation of Williams' attack on group selection, and we are in full agreement with this part of what they say. The picture clouds when we turn to what they say about the

concept of adaptation. They argue that units of *selection* must be distinguished from units of *adaptation* and that multilevel selection theorists (such as Sober & Wilson, 1998) fail to recognize this distinction, which leads them to fall into a 'logical error' (Gardner & Grafen, 2009, p. 666).

Gardner & Grafen (2009) assert that multilevel selectionists have never characterized what it takes for the individual or the group to be a 'unit of adaptation,' and 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 we said above 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, we part ways with GGGWW when they define what it means for the *individual* to be 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. More generally, GGGWW maintain that the individual is *always* a unit of adaptation no matter what the mix is of group and individual selection. They hold this position because *individuals are predicted to maximize their inclusive fitness*, and this point holds regardless of the strengths of individual and group selection.

GGGWW's permissive view concerning the individual as unit of adaptation violates Williams' Principle. Consider the evolution of selfishness and altruism in a metapopulation in which there is no phenotypic variation within groups; each group is either 100% selfish or 100% altruistic. This means that there is no individual selection, and the result is that the metapopulation evolves to 100% altruism. In this case, 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. To be sure, GGGWW do discuss the evolution of altruism in a metapopulation composed of clonal groups and correctly call the result a group adaptation. We agree with *this* description. Our point is that their framework also entails that the evolution of 100% altruism in this circumstance is an *individual* adaptation. This is where they come into conflict with Williams' Principle. Gardner & Grafen (2009, p. 666) acknowledge this consequence of their proposal when they say that 'the function of individual-level adaptation is to maximize inclusive fitness and ...

this obtains irrespective of the relative strength of within-group vs. between group selection.'

If an inclusive fitness model predicts the same outcomes as a multilevel selection model that explicitly recognizes the separate roles of group and individual selection, why should the fact that an outcome is correctly predicted by these two models be taken to show that the *individual* is always a unit of adaptation, but that the *group* is a unit of adaptation only in special circumstances? A motivation for this curious asymmetry can 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 often can predict which traits will evolve by imagining rational agents who are trying to get what they want (for cases in which this heuristic goes wrong, see Sober, 1998). Inclusive fitness seems like a natural generalization of this idea – individuals are 'trying' to maximize the representation of their genes in future generations, where it is recognized that your genes can be found in your genetic relatives as well as in your own offspring. The idea then gets broadened further, by taking into account the fact that nonrelatives sometimes have copies of your genes (although here 'your genes' means genes that are identical by type, not identical by descent); this means that helping nonrelatives can also be a way to get your genes represented in future generations. The net result is that *any* helping behaviour that evolves because of natural selection 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, as 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 of organization. What is good for the individual can conflict with what is good for the group. The 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 (or any mixture thereof), we think it more useful to use 'group adaptation' to label traits that evolved because group selection dominated the selection process and 'individual adaptation' to label traits that evolved because individual selection was in the driver's seat. Why have two labels if one of them applies no matter what? Here, we follow the lead provided by population geneticists who use a symmetric criterion for saying when selection dominates drift and when drift domi-

nates selection (see, for example, Roughgarden, 1979, p. 78).

Gardner & 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 just about gene survival, it provides no basis for saying that individuals, rather than groups, are units of adaptation.

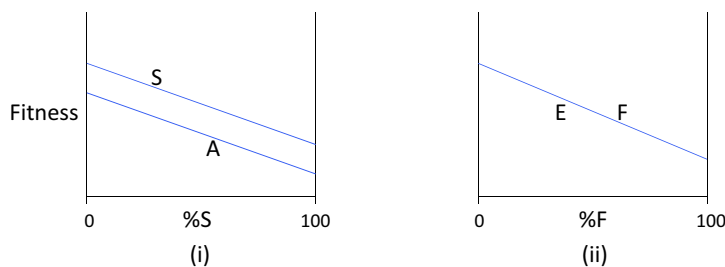
As mentioned earlier, Gardner & Grafen (2009, p. 666) think that multilevel selection theorists have failed to recognize the difference between unit of selection and unit of adaptation and therefore have fallen into a 'logical error.' The logical error that Gardner and Grafen have in mind, allegedly committed by Sober & 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 view that multilevel selection that includes a within-group component *sometimes* causes group adaptations to evolve or is the error supposed to be the view that multilevel selection *always* has this outcome? The latter *is* an error, but it is not one that Sober and Wilson commit; 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.

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 & 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).' Their argument for this thesis is that 'the superorganism comes into existence after these mechanisms [policing, punishing, etc.] are already established (p. 667).' To analyse this argument, 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 (where the punishing benefits the group although it imposes a cost on the punisher) is an altruistic act and requires group selection to evolve (Boyd & Richerson, 1992; Sober & Wilson, 1998, pp. 142–149). If altruistic punishing evolves to fixation or near fixation, it is a group adaptation.

In criticizing the GGGWW framework, we have assumed, as they do, that group selection means fitness variation among groups and individual selection means fitness variation within groups. These definitions are consequences of using the Price equation to define what group and individual selection are. We now want to explain why our criticism of GGGWW does not depend on using this Pricean framework. Priceans say that there

**Box 1: Two pairs of fitness functions.** In (i), if groups vary in fitness but are phenotypically homogeneous (100% altruistic or 100% selfish), the Price approach says there is group selection but no individual selection; contextualism declines to say whether there is individual selection here. In (ii), E and F individuals in the same group have the same fitness. If groups vary in fitness and are phenotypically mixed, both the Price approach and contextualism say that there is group selection but no individual selection.



is individual selection but no group selection when groups vary in fitness but are phenotypically homogeneous. This is the case depicted in figure part (i) of Box 1 when each group is either 100% altruistic or 100% selfish. Contextualists provide a different description of this example; they say that there is no fact of the matter as to whether there is individual selection in this case, since one cannot compare the fitnesses of two phenotypically different individuals who live in the same group; for contextualists, whether there is individual selection in this case is *not defined* (Okasha, 2004, pp. 490–491). This means that contextualists should agree that the GGGWW framework conflicts with Williams' Principle – GGGWW say that there is individual adaptation in this case even though contextualism says that there is no fact of the matter as to whether there was individual selection.

A second example further substantiates our claim that the disagreement between contextualists and Priceans does not affect the point that the GGGWW framework conflicts with Williams' Principle. Consider the two traits, *E* and *F*, whose fitnesses are depicted in figure part (ii) of Box 1. An *E* and an *F* individual in the same group have the same fitness, although groups in which *E* is common are fitter than groups in which *E* is rare; this is the 'neutral pathway' discussed in Wilson (1980). Now, consider a metapopulation in which groups differ in their local frequencies of these two traits and there are some mixed groups. There is *phenotypic* variation within groups, but no *fitness* variation within groups. Contextualists and Priceans agree that there is group selection without individual selection in this case. The result is that trait *E* evolves to 100%. The GGGWW framework entails that this is an individual adaptation even though there was no individual selection.

The reader will notice that our definitions of group and individual adaptation, and our criticisms of the GGGWW framework, did not require the presentation of any equations. As mentioned earlier, the Price equation and contextualism address a *quantitative* question: how much of a trait's change in frequency can be attributed to group selection and how much to individual? We rely here on some simple clarifications of a *qualitative* question: when do group and individual selection occur? Obviously the quantitative and the qualitative questions are related, but the latter does not require heavy-duty mathematics to answer. Similarly, the question of when a trait is an individual or a group adaptation is a *qualitative* question; it is not a question about *how much*. Mathematics is important in evolutionary biology. But it is not true that *only* mathematics is important nor is it true that mathematics is *always* important.

In *Adaptation and Natural Selection*, Williams is a robust individualist (a position he tempers in Williams, 1992). He denies that group adaptations exist (Williams, 1966, p. 93) and he says that the Lewontin & Dunn (1960) study of meiotic drive in the house mouse is the only

well-documented case of group selection in nature (Williams, 1966, p. 117). GGGWW have abandoned this position, and rightly so. Although GGGWW have retreated from Williams' robust individualism, they retain a vestige of that individualism in their view of adaptation. In the evolution of altruism and selfishness in a metapopulation (or, indeed, of any pair of traits), GGGWW assert that the individual is *always* a unit of adaptation, regardless of what trait frequencies the process produces and regardless of whether there is any individual selection at all. This violates Williams' Principle. A more even-handed conception of adaptation is preferable, one in which group and individual selection are symmetrically linked to group and individual selection. Gardner & Grafen (2009, p. 7) say that they 'have formally separated the issues of levels of selection and levels of adaptation.' They are right that group selection can be part of a selection process without the product of that process being a group adaptation. They go wrong by embracing a framework in which individual adaptations can evolve without individual selection. There is nothing wrong with seeking a quantity that natural selection optimizes, and inclusive fitness provides a useful device for thinking in those terms (although it is important to remember that meiotic drive and intragenomic conflict can lead to results that are not maximizations of inclusive fitness, as Gardner & Grafen, 2009, p. 666 acknowledge). However, the maximization of inclusive fitness is not an argument for individualism with respect to units of selection *or* with respect to units of adaptation.

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