

## 5 Adaptation of Individuals and Groups

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Natural selection explains the apparent design of the living world. However, there remains considerable disagreement as to who wields this design, and for what purpose it is employed. The conventional view is to regard biological adaptation as occurring at the level of the individual organism, who appears designed to maximize her inclusive fitness (Hamilton 1963, 1964, 1970, 1996; Grafen 2006). This individual-adaptationist view has enjoyed huge empirical success, for example in the field of behavioral evolutionary ecology (Krebs & Davies 1978, 1984, 1991, 1993, 1997; Alcock 2005; Westneat & Fox 2010; Davies, Krebs, & West 2012).

However, in recent years there has been a resurgence of interest in group adaptationism, which regards social groups as designed entities that function to maximize their own fitness (Wheeler 1911; Marais 1925/1937; Wells, Huxley, & Wells 1929; Emerson 1932; Wynne-Edwards 1962, 1993; Seeley 1989, 1997; Wilson & Sober 1989; Hölldobler & Wilson 1990, 2009; Shapiro & Dworkin 1997; Shapiro 1998; Sober & Wilson 1998; Reeve & Hölldobler 2007; Wilson & Wilson 2007). This renewal of interest owes much to the recent reemergence of group selection theory, which now enjoys a mathematical respectability (Price 1972; Hamilton 1975; Wade 1985; Frank 1995, 1998; Okasha 2006). However, while the ideas of group selection and group adaptation are connected, they are conceptually distinct and require separate formalization.

Here, I review the theories of selection and adaptation of individuals and groups. I begin by reviewing the theory of Darwinian adaptation of individual organisms, showing how the concepts of selection and adaptation have been mathematically formalized and clarifying the foundations of kin selection and inclusive fitness theory. I then extend this view to encompass selection and adaptation at the level of the social group, reviewing the theory of group selection and clarifying its connection to the notions of group adaptation and the superorganism. Finally, I discuss general principles of adaptation that emerge at any level of biological organization.

## Adaptation of Individuals

### The Problem of Adaptation

The problem of adaptation is to explain the apparent design of the living world. This is an ancient problem, but it was most clearly formulated by William Paley in his book *Natural Theology* (1802). Paley famously likened organisms and their component parts to man-made contraptions, such as the pocket watch, in order to elucidate the fundamental principles of design. His important contribution was to reject the idea that design implies perfection of construction, or even optimality within physical or economic constraints. A watch may be constructed out of poor materials, or may even be broken, and yet still manifest design. Instead, he identified the hallmark of design as “contrivance and relation of parts.” Specifically, the parts of organisms and pocket watches appear contrived as if for a purpose and, moreover, all the parts of the organism or the pocket watch appear contrived as if for the same purpose. The problem of adaptation, then, is to explain the apparent coordinated purposefulness of the organism.

### Natural Selection

This problem was decisively solved by Charles Darwin in *The Origin of Species* (Darwin 1859). Darwin pointed out that those heritable variations that are associated with higher individual reproductive success will tend to accumulate in natural populations by a process of natural selection. Hence, he argued, the various parts of organisms will appear increasingly contrived as if for the purpose of maximizing the organism’s reproductive success (Darwinian fitness). Rather than deny the design of organisms, Darwin provided a naturalistic explanation for adaptation and, moreover, he clarified what it is that organisms are designed to do. Thus, Darwinism is the only scientific (i.e., predictive) theory of organism design.

The theory of natural selection was later captured in mathematical terms by R. A. Fisher, who synthesized Darwinism with Mendelian genetics in his book *The Genetical Theory of Natural Selection* (Fisher 1930; see also Fisher 1918). In particular, Fisher framed natural selection in terms of the genetic change of populations, and he clarified the idea of the individual’s fitness as her expected contribution of genes to generations in the distant future. These ideas were subsequently encapsulated in a simple covariance form by George Price (1970; box 5.1). These developments highlight the statistical nature of natural selection, and emphasize that natural selection will occur whenever there is heritable variation in fitness.

### Adaptation of Individuals

A fully satisfying resolution of the problem of adaptation must engage with the notion of design. The formal basis for ideas of design, purpose, and function lie in

#### Box 5.1

##### Natural Selection

The action of natural selection is defined as the genetic change of a population that owes to the differential reproductive success of individual organisms (Fisher 1930). From Price’s (1970) theorem, this is given by

$$\Delta_s E(g) = \text{cov}(v, g), \quad (5.1)$$

where  $g$  is the individual’s genetic value for the character of interest (i.e., the heritable portion the character);  $v$  is the individual’s relative fitness or reproductive value (formally, this is an expectation taken over future uncertainty);  $E$  is the arithmetic average taken over the set of all individuals in the population (formally, it is the expectation of the random variable defined as the property of interest of a random individual drawn from the population, with all individuals having the same probability of being drawn); and  $\text{cov}$  is the statistical covariance taken over the set of all individuals in the population (formally, it is the covariance of the two random variables defined as the properties of interest of a random individual drawn from the population, with all individuals having the same probability of being drawn).

Thus, if genes for a character of interest are positively associated with relative fitness ( $\text{cov}(v, g) > 0$ ), then natural selection acts to increase the average value of that character in the population ( $\Delta_s E(g) > 0$ ); whereas if genes for a character of interest are negatively associated with relative fitness ( $\text{cov}(v, g) < 0$ ), then natural selection acts to decrease the average value of that character in the population ( $\Delta_s E(g) < 0$ ); and if there is no association between genes for the character of interest and relative fitness ( $\text{cov}(v, g) = 0$ ), then natural selection does not act upon this character ( $\Delta_s E(g) = 0$ ).

Assuming nonzero heritable variation in the character of interest, the action of natural selection can be written as the product of the heritable variance and a multiplying coefficient:

$$\Delta_s E(g) = \beta(v, g) \text{var}(g), \quad (5.2)$$

where  $\beta(v, g) \equiv \text{cov}(v, g) / \text{var}(g)$ . It happens that this coefficient has a useful interpretation: if we were to collect all the  $(g, v)$  data of all the individuals in the population, then  $\beta(v, g)$  is the slope of the straight line fitted through these data by the method of least-squares, i.e.:

$$E(v | g) = E(v) + \beta(v, g)(g - E(g)). \quad (5.3)$$

This slope provides another way of thinking about the relationship between the heritable character and relative fitness. The condition for natural selection to occur is that there is heritable variation ( $\text{var}(g) > 0$ ) for a character that is (positively or negatively) correlated with relative fitness ( $\beta(v, g) \neq 0$ ). The multiplicative partition (5.2) of natural selection obtains irrespective of the relationship between the heritable character and fitness: the linearity of the regression model should not be confused with any assumptions of additivity in the underlying evolutionary model (reviewed by Gardner, West, & Wild 2011).

**Box 5.1**  
 (continued)

Natural selection can occur through two distinct routes: direct selection, mediated by an individual's own genes ( $g$ ) for the character of interest; and indirect selection, mediated by the genes ( $g'$ ) of the individual's social partners (Fisher 1930). We can separate these effects by least-squares linear regression:

$$E(v|g, g') = E(v) + \beta(v, g|g')(g - E(g)) + \beta(v, g'|g)(g' - E(g')). \quad (5.4)$$

Substituting regression model (5.4) into equation (5.1), the action of natural selection can be expressed as

$$\Delta_s E(g) = \beta(v, g|g') \text{cov}(g, g) + \beta(v, g'|g) \text{cov}(g', g), \quad (5.5)$$

i.e., separated, on the right-hand side, into its direct (first term) and indirect (second term) components. Thus, the condition for natural selection to favor an increase in any character of interest is that the right-hand side of equation (5.5) is greater than zero or, equivalently,

$$\beta(v, g|g') + \beta(v, g'|g) \frac{\text{cov}(g', g)}{\text{cov}(g, g)} > 0. \quad (5.6)$$

This is Hamilton's (1963, 1964, 1970) rule,  $-c + br > 0$ , where  $\beta(v, g|g') \equiv -c$  is the impact of the individual's heritable character on her own fitness, holding fixed the heritable character of her social partner;  $\beta(v, g'|g) \equiv b$  is the impact of the social partner's heritable character on the focal individual's fitness, holding fixed her own heritable character; and  $\text{cov}(g', g)/\text{cov}(g, g) = \beta(g', g) \equiv r$  is the kin selection coefficient of genetic relatedness. Here, Hamilton's rule is expressed in its "neighbor-modulated fitness" form, which examines the impact of heritable traits of self and social partners on a focal recipient's own fitness. Equivalently, we may consider the inclusive-fitness form of Hamilton's rule, which examines the impact of the heritable trait of the focal actor on her and her social partner's fitness:

$$\beta(v, g|g') + \beta(v', g'|g') \frac{\text{cov}(g', g)}{\text{cov}(g, g)} > 0, \quad (5.7)$$

where  $v'$  is the fitness of the focal actor's social partner (Hamilton 1963, 1964, 1970; Queller 1992; Frank 1998; Rousset 2004; Gardner et al. 2011).

optimization theory and, in particular, are captured in the form of an optimization program. This posits an agent, with an agenda, and an instrument wielded by the agent in pursuit of her agenda (box 5.2).

The standard Darwinian view of adaptation regards the individual as striving to maximize her fitness. Alan Grafen has mathematically captured this idea using an optimization program, in which the agent is the individual organism, her instrument

**Box 5.2**  
 Individual Adaptation

The formal basis for ideas of design, function, and purpose lies in optimization theory. These ideas are formally captured as an optimization program, which takes the following form:

$$s \max_{s \in S} \mathcal{F}(s), \quad (5.8)$$

where  $S$  is the strategy set,  $s$  is the employed strategy, and  $\mathcal{F}$  is a real-valued objective function defined over the whole strategy set. The optimization program sets the idea of an agenda, whereby we have an agent who, within the confines of the strategy set, is striving to maximize the value of the objective function, a greater obtained value corresponding to the agenda being better realized.

The analogy of the individual organism as an inclusive-fitness maximizing agent has been formalized by Grafen (2002, 2006) using this optimization-program approach. Here, the agent is represented by an individual organism, the strategy by the individual's phenotype, the strategy set by the set of possible phenotypes the individual might exhibit, and the objective function by the individual's inclusive fitness. This mathematical analogy permits formal statements of the purpose or function of the phenotype: that is, the idea the phenotype functions to maximize inclusive fitness. It also permits formal notions of optimality and suboptimality: an optimal strategy is one, belonging to the strategy set, that maximizes the objective function; and a suboptimal strategy is one that results in an objective function value that is lower than this maximum. Hence, an optimal phenotype is one that achieves maximal inclusive fitness, and a suboptimal phenotype is one that achieves submaximal inclusive fitness.

The optimization program defines the notion of purpose or function or design, but it does not in itself provide justification for viewing organisms and their phenotypes in this way. Formal justification for the individual-as-maximizing-agent analogy comes from relating the mathematics of the optimization program to the mathematics of natural selection. Grafen (2002, 2006) has done this, effectively revealing an isomorphism between the dynamics of natural selection as captured in equation (5.1) and the idea of phenotype optimization as captured in the expression (5.8).

In particular, the following links have been established: if all agents are optimal, there is no scope for selection and no potential for new genetic variants to increase from rarity under the action of selection; if all agents are suboptimal, but equally so, there is no scope for selection, but there is potential for new genetic variants to increase from rarity under the action of selection; if agents vary in their optimality, there is scope for selection, and the change in all gene frequencies and in the average of any heritable character is equal to its covariance with relative maximand value, taken across all individuals in the population; and if there is no scope for selection nor potential for new genetic variants to increase from rarity under the action of selection, then all agents are optimal (Grafen 2002, 2006).

This clarifies that natural selection acts according to the design objective of inclusive-fitness maximization. Hence, all heritable traits are moulded according to this design principle, and this accounts for the contrivance and relation of parts of the individual organism; that is, the appearance of design that defines the problem of adaptation (Gardner 2009). This is separate from the claim that organisms achieve maximal inclusive fitness: the optimization program specifies a purpose or goal, without implying that this goal is realized and optimality attained.

is her phenotype, and her agenda is to maximize her fitness (Grafen 2002; box 5.2). Grafen (2002) has shown that there is a strong mathematical connection (isomorphism) between this optimization program and the dynamics of natural selection, in a wide class of models that exclude social interaction between relatives. This mathematically captures the sense in which the action of natural selection corresponds to a design objective of fitness maximization. All parts of the organism become contrived according to this same design objective, and this accounts for the contrivance and relation of parts that Paley identified as the hallmark of design (Gardner 2009).

### Inclusive Fitness

The only revision of the basic theory of Darwinian adaptation that has occurred in its 150-year history is a change in our understanding of the purpose of adaptation, which becomes apparent in the context of social interaction between relatives. Darwin (1859) noticed that a problem is posed by the exquisite adaptations of sterile workers in social insect colonies: how to explain their adaptations, given that they have no reproductive success, and hence cannot be directly acted upon by natural selection? His solution was to notice that natural selection can act indirectly upon such traits, through the reproductive success of the workers' fertile family members, who Darwin supposed carry the heritable tendencies for the worker traits in latent form.

This idea was expanded upon and formalized more than a century later by W. D. Hamilton (1963, 1964, 1970), who captured the combined direct and indirect effects of natural selection in the famous inequality  $rb - c > 0$ , now termed "Hamilton's rule" (Charnov 1977). This rule denotes the direct fitness effect of a trait on the actor by  $-c$ , the fitness effect of the trait on the actor's social partner by  $b$ , and the genetic relatedness of the two individuals by  $r$ . Thus, Hamilton (1963) showed that altruistic behaviors that incur a direct fitness cost,  $c$ , for the actor can be favored owing to the indirect fitness benefit  $rb$  that the actor experiences through the increased reproductive success of a genetic relative. More generally, Hamilton's rule reveals that the basic condition for natural selection to favor any trait is not to increase the individual's direct fitness but rather to increase her inclusive fitness, i.e.,  $rb - c > 0$ . The indirect component of selection has been termed "kin selection" (Maynard Smith 1964), and so inclusive-fitness theory is sometimes referred to as kin-selection theory.

Hamilton's original contribution was to realize that indirect fitness effects impact upon the purpose of adaptation. The basic condition for natural selection to favor any trait is that the individuals who carry genes for this trait are, on average, fitter than those who do not. However, the adaptations that subsequently evolve are not designed for maximizing the individual's personal fitness, but rather her inclusive fitness, i.e., the sum of all the fitness effects that she has on all of her genetic

relatives, each increment or decrement being weighted by the corresponding coefficient of genetic relatedness (Hamilton 1964). In other words, the adaptive agent remains the same as in the traditional Darwinian view (i.e., the individual organism), but the adaptive agenda is changed. This idea has subsequently been formalized by Grafen (2006), who has shown the mathematical connection between the dynamics of natural selection and an optimization program in which the individual strives to maximize her inclusive fitness, for a wide class of models, including those that allow for social interaction between relatives.

### Adaptation of Groups

#### Group Selection

In *The Origin of Species*, Darwin (1859) laid the first foundations of kin-selection theory in order to understand the social adaptations of insects. Later, in *The Descent of Man* (Darwin 1871), he took an alternative, group-selection approach to understand the social evolution of humans. Darwin (1871) noted that certain moral behaviors would place individuals at a relative disadvantage to the other members of their social group, but nevertheless these behaviors could be selectively advantageous if they provided a large enough benefit to the group in its competition with other groups. Interestingly, Darwin appears not to have considered kin selection and group selection as altogether distinct processes, and he emphasized the role for blood relationship within groups to provide an incentive for group-beneficial behavior.

The theory of group selection has had a checkered history, mainly owing to lazy thinking in the first half of the twentieth century, which held that between-group selection would always win out against within-group selection, leading to all organismal traits being adapted for the good of the group, or even the species. These ideas culminated in Vero Wynne-Edwards' infamous *Animal Dispersion in Relation to Social Behavior* (Wynne-Edwards 1962), which was pilloried by George Williams' (1966) *Adaptation and Natural Selection*. Williams' critique was very persuasive, and led many researchers to reject the idea that group selection could have any impact on the evolutionary process.

Subsequently, George Price (1972; and see Hamilton 1975) showed that natural selection can be partitioned into within-group and between-group components, and that there is a priori no reason why either of these should be zero (Rousset 2004; box 5.3). It is now increasingly understood that separation of natural selection into within-group and between-group components (the "group-selection partition") is a perfectly appropriate alternative to the separation of natural selection into direct and indirect components (the "kin-selection partition"): both add up to the same thing, and both approaches should always give exactly the same predictions (Price 1972; Hamilton 1975; Wade 1985; Frank 1986, 1995, 1998; Queller 1992; Gardner,

**Box 5.3**

## Group Selection

Box 5.1 detailed how the action of natural selection is formally captured by Price's (1970) equation, and how it may be partitioned into its direct and indirect components (the kin-selection partition). An alternative partition separates natural selection into within-group and between-group components (the group-selection partition). This is most readily illustrated by assuming that individuals occur in equal-sized groups, with each group being assigned a unique index  $i \in I$  and each individual being assigned a unique index  $j \in J$  within its group. Then, the total action of natural selection can be expressed as

$$\Delta_S E(g) = \text{cov}_I(v_i, g_i) + E_I(\text{cov}_J(v_{ij}, g_{ij})), \quad (5.9)$$

where the first term on the right-hand side is the genetic change owing to differential reproductive success of groups, and defines "between-group" selection; and the second term on the right-hand side is the genetic change owing to differential reproductive success of individuals within groups, and defines "within-group" selection (Price 1972; Hamilton 1975). Importantly, the right-hand side of equation (5.1) is exactly equal to the right-hand side of equation (5.9). The former defines natural selection (or "individual" selection or "between-individual" selection). The latter breaks this into between-group and within-group components. There is no a priori reason why either between-group selection or within-group selection should be zero (Rousset 2004). Thus, ignoring either of these processes may lead to an incomplete account of natural selection.

Moreover, the right-hand side of equation (5.5) is exactly equal to the right-hand side of equation (5.9). Thus, kin-selection and group-selection accounts of social evolution are exactly equivalent and, if conducted properly, should lead to exactly the same predictions (Hamilton 1975; Wade 1985; Queller 1992; Frank 1995, 1998; Gardner & Grafen 2009). An altogether separate issue is whether the kin-selection and group-selection approaches to social evolution theory are equally useful, in terms of ease of generating empirically testable predictions. West, Griffin, and Gardner (2008) have argued that, even in fields such as sex allocation where researchers have long been aware of the equivalence of approaches, the kin-selection approach has been most successfully employed to develop empirically useful theory.

West, & Barton 2007). Importantly, irrespective of the strength of group selection, individuals are adapted to maximize their inclusive fitness (Gardner 2009; Gardner & Grafen 2009; Wild, Gardner, & West 2009, 2010).

**Group Adaptation**

An interesting question arises as to whether social groups can be considered adaptive entities in their own right. In *The Descent of Man*, Darwin (1871) suggested that in the case of the social insects (and them alone) we should perhaps recognize

that natural selection operates through and for the good of the colony, not the individual organism. This idea of the social-insect colony as a "superorganism" was later elaborated by William Morton Wheeler (1911) and Eugene Marais (1925/1937) and, more recently, by Bert Hölldobler and Ed Wilson in *The Superorganism* (2009). The idea of group-level adaptation frequently arises in discussions of group-level selection and, indeed, the two concepts are often confused. For example, group adaptation has sometimes been defined as any response to group selection (Wilson & Sober 1989).

A more appropriate approach to formalizing group adaptation is to capture the idea of the social group as a fitness-maximizing agent within an optimization program and see when this corresponds to the dynamics of natural selection. This was done by Alan Grafen and myself (Gardner & Grafen 2009), and we found that such mathematical links do exist, but only in special circumstances (box 5.4).

**Box 5.4**

## Group Adaptation

If individual adaptation concerns the apparent design of the individual organism, then group adaptation concerns the apparent design of social groups. This idea is formally captured using an optimization program:

$$s \max_{s \in S} \mathcal{F}(s), \quad (5.10)$$

in which the social group is conceived of as an intentional agent employing its group phenotype  $s$ , within the constraints of the group-phenotype set  $S$ , in pursuit of the maximization of its own fitness  $\mathcal{F}$  (Gardner & Grafen 2009). This mathematical analogy permits formal statements of the purpose or function of the group phenotype; that is, the idea the group phenotype functions to maximize group fitness. It also permits formal notions of optimality and suboptimality: an optimal group phenotype is one, belonging to the set of possible group phenotypes, that maximizes group fitness; and a suboptimal phenotype is one that achieves submaximal group fitness.

The optimization program defines the notion of purpose, function, or design, but it does not in itself provide justification for viewing social groups and their phenotypes in this way. Formal justification for the group-as-maximizing-agent analogy comes from relating the mathematics of this optimization program to the mathematics of natural selection. Gardner & Grafen (2009) have done this, effectively revealing an isomorphism between the dynamics of natural selection as captured in equation (5.9) and the idea of group phenotype optimization as captured in the expression (5.10), but only in very special circumstances. In particular, this isomorphism only holds in those scenarios where the within-group component of selection is guaranteed to be zero ( $E_J(\text{cov}_J(v_{ij}, g_{ij})) = 0$ ). This occurs in the context of clonal groups ( $g_{ij} = g_i$  for all  $j \in J$ , and hence  $E_J(\text{cov}_J(v_{ij}, g_{ij})) = 0$ ) and in groups where all differences in (expected) fitness are abolished ( $v_{ij} = v_i$  for all  $i \in I$ , and hence  $E_I(\text{cov}_I(v_i, g_i)) = 0$ ). More generally,

**Box 5.4**  
(continued)

for groups comprising genetically variable individuals with the possibility of achieving differential (expected) fitness, within-group selection cannot be assumed absent, and no isomorphism holds in this case.

This clarifies that natural selection acts according to the design objective of group-fitness maximization when within-group selection is abolished by mechanisms such as clonality or complete repression of internal competition (Gardner & Grafen 2009). In these extreme scenarios, all heritable traits are moulded according to this design principle, and this accounts for the contrivance and relation of parts of the social group; that is, the appearance of design that defines a superorganism (Gardner 2009). This is separate from the claim that superorganisms achieve maximal group fitness: the optimization program specifies a purpose or goal, without implying that this goal is realized and optimality attained.

This mathematical result provides the formal justification for Williams' and Maynard Smith's principles of adaptation: adaptation of an entity at any level of biological organization requires selection between, and the absence of selection within, entities at that level of biological organization. Formal justification is necessary, because different researchers use the same words to mean different things, and so a purely verbal argument is liable to cause semantic confusion. For example, Sober & Wilson (2011) employed Williams' principle to argue that individuals cease to be adaptive units when all selection occurs at the between-group level. This relies upon their interpretation of between-individual selection to mean that which is due to individual fitness differences within groups. However, the above formal analysis clarifies that the appropriate between-individual selection is that which is due to fitness differences between all individuals in the population: that is, both within and between groups. Consequently, between-group selection is a component of between-individual selection and, irrespective of the strength of the former, individual organisms are adapted to maximize their inclusive fitness.

In particular, if all of natural selection occurs at the level of the social group, then natural selection does act according to a design objective of group fitness maximization. Hence, mechanisms that abolish within-group selection—such as clonal relatedness of group mates or strict policing to prevent unsanctioned reproduction—do permit group-level adaptation. This explains why clonal groups, such as the Portuguese Man o' War, and groups characterized by repression of internal competition, such as the honeybee hive, do have the appearance of super-organismality, and why most other social groups do not (Gardner 2009; Gardner & Grafen 2009).

This formal analysis allows us to distinguish between traits that are the cause of group adaptation and those that are the consequence of group adaptation. Mechanisms of conflict resolution such as high genetic relatedness and worker policing

have sometimes been suggested as examples of group-level adaptations (Wilson & Sober 1989; Wilson & Hölldobler 2005; Wilson & Wilson 2007). However, insofar as they have evolved to suppress internal conflict, these traits must have evolved in the context of within-group conflict, and hence in circumstances that do not allow for a group-adaptationist interpretation (Gardner & Grafen 2009). Also, because the formal approach that connects an optimization program to the dynamics of selection engages with the issue of what adaptations are *for*, rather than what they *do*, we can mathematically distinguish true group adaptations from those phenotypes that increase group fitness merely by incidental effect or as a means to an end of inclusive-fitness maximization. Unless selection is abolished within groups, then—from an ultimate (teleological) perspective—adaptations do not function for the good of the group, but rather to maximize the individual's inclusive fitness.

### A General Theory of Adaptation

Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations.

—G. C. Williams (1966, pp. 92–93)

The achievement of individuality at the higher level has required that the disruptive effects of selection at the lower level be suppressed.

—J. Maynard Smith (1988, p. 230)

### General Principles of Adaptation

The above discussion of adaptation of individuals and groups can be applied to any two adjacent levels of biological organization. This suggests two extremely general principles of adaptation, which we may term Williams' principle and Maynard Smith's principle, respectively. These are:

*Williams' principle* Adaptation of an entity at any level of biological organization requires selection *between* entities at that level of biological organization.

*Maynard Smith's principle* Adaptation of an entity at any level of biological organization requires the absence of selection *within* entities at that level of biological organization.

As an antidote against lazy adaptationist thinking that was so prevalent in the early and middle years of the twentieth century, Williams (1966) argued that there is an onus on anyone who invokes an adaptive explanation for a biological character to identify a corresponding selective advantage that could be responsible for driving genetic change in the population. In particular, he pointed out that group

adaptationists who invoke benefits to the population or species must explicitly frame their explanations of phenotypic evolution in terms of selective processes operating between groups. Between-group selection was therefore taken to be a necessary—but not sufficient—condition for group-level adaptation, and the Williams' principle given here generalizes this insight to cover all levels of biological organization (see also Sober & Wilson 2011).

John Maynard Smith (1988; see also Maynard Smith 1987 and Maynard Smith & Szathmáry 1995) framed major transitions in individuality in terms of the interests of group members becoming aligned such that the social group could be considered an adaptive unit in its own right. He pointed to within-group selection as the source of internal conflict, and hence the suppression of within-group selection as a necessary—but not sufficient—condition for a major transition in individuality. Maynard Smith particularly emphasized the potential for within-group selection to oppose between-group selection. However, as discussed in the previous section, even if within-group selection and between-group selection act in the same direction, the resulting adaptation will not be for the group per se, but rather for the individual. Any benefit arising for the group is not part of the adaptation's ultimate design objective. Rather, it is an incidental effect or a means to the end of maximizing the individual's inclusive fitness.

Both Williams' and Maynard Smith's principles provide necessary conditions for a biological entity to be considered an adaptive unit. If there is between-group selection, but within-group selection has not been abolished, then there can be a response to selection, but this must be understood in terms of adaptation at a lower level. Conversely, if within-group selection has been abolished, and there is also no between-group selection, then there can be no adaptation at any level of biological organization. This raises the question as to whether the two principles, taken together, represent a sufficient condition? That is, does the presence of between-group selection plus the absence of within-group selection provide justification for regarding the group as an adaptive unit? Unfortunately, the answer appears to be no.

A key assumption of the analysis of Gardner & Grafen (2009), which provides the formal justification for both Williams' and Maynard Smith's principles, is that all social interaction occurs within groups. However, if social interaction also extends between groups, then the unity of purpose of the group cannot be guaranteed even in the presence of between-group selection and the absence of within-group selection. This is because, while individuals are unable to improve their personal fitness independently of improving the fitness of their group, they may be able to improve their inclusive fitness by providing help to genetic relatives in other groups. If different members of the same group have different degrees of genetic relatedness to these extra-group recipients, then they may come into conflict with each other over

the enactment of between-group social behaviors, preventing adaptive integrity at the group level.

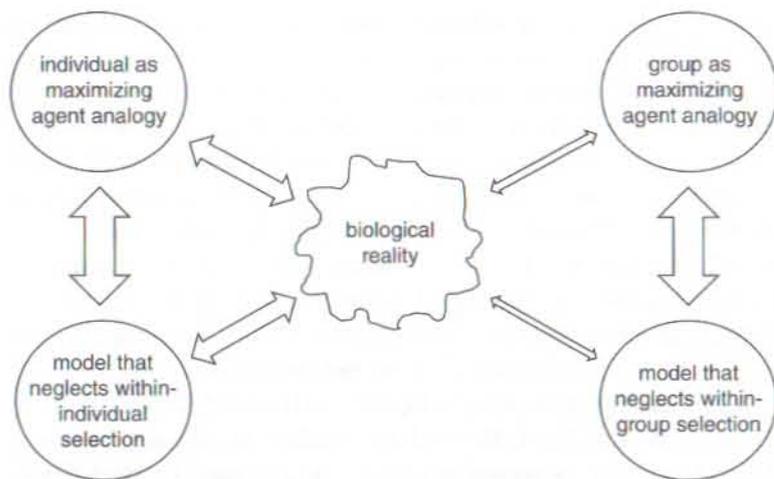
A concrete example of this is genomic imprinting, whereby maternal and paternal genes at a particular locus have consistently different levels of expression. For example, in a species where females mate multiply, a juvenile individual sharing a nest with maternal siblings may be more related to her nestmates via her maternal genes than her paternal genes (Haig 2002). Hence, her maternal genes are favored to have the individual behave relatively kindly to her nestmates, whereas her paternal genes are favored to have the individual behave relatively selfishly. Consequently, even though there is between-individual selection, and there is no within-individual selection, such traits may have no individual-level rationale, and must be understood in terms of gene-level adaptation (Haig 1997, 2002; Burt & Trivers 2006; Gardner & Welch 2011). Beyond the nuclear family, sex biases in dispersal, mortality, and variance in reproductive success can lead to asymmetric relatedness between social partners from the perspective of their maternal and paternal genes (Úbeda & Gardner 2010, 2011, 2012). Thus, while the evolution of social behavior has usually been considered a first step toward a major transition from organism to superorganism, social interaction can reignite conflicts between genes that break down the unity of the individual organism.

Clearly, an individual's maternal genes can only come into conflict with her paternal genes if they "know" they are maternal in origin, and vice versa. Thus, an important third general principle of adaptation may be the withholding of such divisive information from the members of the group (e.g., Bourke 2011, p. 160). Formalizing this third principle is difficult in the absence of a proper understanding of the links between information theory and natural selection (e.g., Edwards 2000; Frank 2009), and this represents a very exciting avenue for future exploration. Anticipating: the combination of three necessary conditions—concerning the presence of between-group selection, the absence of within-group selection, and the absence of divisive information—may provide a single, sufficient principle of adaptation (after Orwell 1949):

*Orwell's principle* War is peace, freedom is slavery, ignorance is strength.

### Simplified Models versus Biological Reality

The above account of levels of adaptation suggests that a necessary condition for adaptation is the absence of selection within entities at that level of biological organization. Taken literally, this would rule out traditional organisms as adaptive entities, because selection-like processes occur between cell lineages and genes within the organism. Clearly, this literalist view is not desirable. A better approach would



**Figure 5.1**

Simplified models versus biological reality. A population genetics model that neglects selection within individual organisms—i.e., the basis for the analogy of the individual organism as an inclusive-fitness-maximizing agent—does not capture the whole of biological reality, but provides a reasonably good fit (medium arrows). A population genetics model that neglects selection within social groups—i.e., the basis for the analogy of the group as a fitness-maximizing agent—provides a poorer fit with biological reality (small arrows). Theory clarifies what assumptions are needed in order to justify individual or group adaptationism, and empiricism determines which of these assumptions are valid.

be to allow entities that exhibit *negligible* internal conflict the property of adaptation. But what exactly is meant by negligible internal conflict?

The formal justification for the idea of individual organisms striving to maximize their inclusive fitness lies, as with all legitimate evolutionary theories, in theoretical population genetics. In particular, there is a strong mathematical correspondence between this idea of individual-level adaptation and population genetics models that neglect selection-like processes within the individual organism. Conversely, population genetics models that incorporate selection-like processes within the organism do not admit this individual-adaptationist perspective. However, all population genetics models are abstractions of reality (figure 5.1), and the ultimate justification for any theoretical model rests in its empirical usefulness. Thus, we can say that selection-like processes within the organism are negligible whenever a population genetics model that neglects such processes is empirically appropriate for whatever purpose we wish to put it. The massive empirical success of the individual-adaptationist perspective provides the ultimate justification for considering selection-like processes within the organism to be negligible.

Likewise, formal justification for the idea of social groups as superorganisms striving to maximize their fitness is granted if we feel that a population genetics

model that neglects within-group selection is empirically valid (figure 5.1). Sometimes, such an abstract model will be empirically valid (Gardner & Grafen 2009). For example, whether or not we allow for within-group selection is unlikely to impact meaningfully upon our predictions for the foraging behavior of honeybee hives. However, in very many cases we would expect within-group selection to play an important role in mediating the evolution of social and other adaptations (Gardner & Grafen 2009). For example, in determining the evolutionarily stable level of parasite virulence in structured populations (Wild et al. 2009, 2010). The ultimate justification (or repudiation) of group-adaptationism therefore rests in the empirical usefulness of population genetics models that neglect within-group selection. More generally, owing to its formal validity in a wider class of models, that subsumes the class of models in which within-group selection is neglected, individual adaptationism is more valid than group adaptationism (Gardner & Grafen 2009).

## Conclusions

Adaptation is the apparent design of the living world that owes to the action of natural selection. Two necessary conditions for adaptation to arise at any particular level of biological organization are: (1) that selection acts between such entities (Williams' principle); and (2) that selection does not act within such entities (Maynard Smith's principle). Group selection is ubiquitous in the natural world but, owing to the action of selection within groups, group-level adaptations and superorganisms are rare.

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