

*Opinion piece***Adaptation as organism design**

The problem of adaptation is to explain the apparent design of organisms. Darwin solved this problem with the theory of natural selection. However, population geneticists, whose responsibility it is to formalize evolutionary theory, have long neglected the link between natural selection and organismal design. Here, I review the major historical developments in theory of organismal adaptation, clarifying what adaptation is and what it is not, and I point out future avenues for research.

Keywords: Darwinism; natural selection; population genetics; optimization

1. INTRODUCTION

Charles Darwin's *The Origin of Species* (Darwin 1859) made three major contributions to biological understanding. First, by amassing diverse evidence from a range of different disciplines, Darwin firmly established the fact of biological evolution. Since his time, there has been no serious challenge to the view that organisms have evolved, and this insight now forms the foundation for all of the biological sciences. Second, Darwin proposed natural selection as a mechanism to explain evolutionary change. We now understand that other factors also contribute to the evolutionary process and that natural selection may not even be the main driver of evolutionary change, particularly at the level of DNA sequence evolution. Nevertheless, natural selection is undoubtedly a major driver of phenotypic evolution.

Third, Darwin explained how natural selection could give rise to the apparent design of organisms. This may be the greatest of his three contributions; certainly it is the most far reaching. The theory of Darwinian adaptation knocks the foundation out of the Teleological Argument for the existence of God, or the 'argument from design'. Prior to Darwin, the apparent design of organisms had represented among the most convincing evidence for a divine creator and was instrumental in making natural history—then styled as 'natural theology'—a respectable pursuit for generations of British gentlemen.

Despite the importance of this third contribution, and despite the fact that it underlies a great deal of biological research—from functional anatomy to behavioural ecology—the link between natural selection and organism design has been almost completely neglected by population geneticists, who are charged with the task of formalizing all aspects of evolutionary theory. Indeed, many researchers in this discipline regard the notion that natural selection leads to optimization of the phenotype as naive. I suggest that this

paradoxical situation—whereby the core of evolutionary theorists reject the core result of evolutionary theory—is owing to a misunderstanding of what biological design (adaptation) really entails, and I suggest that getting the definition right resolves controversies such as the long-running 'group-selection' debate.

2. THE PROBLEM OF ADAPTATION

Darwin showed that adaptation results from natural selection and, since then, many researchers have defined adaptation as *any* response to natural selection. However, this definition confuses the original empirical problem (adaptation) with its solution (natural selection). To avoid this confusion, it is helpful to consult pre-Darwinian commentators on the problem of adaptation. Although the problem of adaptation is an ancient one, perhaps its clearest formulation was given by William Paley (figure 1a) in his book *Natural Theology* (Paley 1802). Importantly, this book provided the key stimulus for Darwin's focus on the problem of organismal design, so Paley's account provides a natural starting point for any discussion of Darwinian adaptation.

Paley explicitly framed the problem of adaptation as the need to explain the empirical fact of apparent organismal design. Importantly, Paley began his argument by giving a considered account of how adaptation manifests and how it can be recognized as such. Drawing upon an analogy between an organism and a pocket watch, as a conceptual aid, Paley firmly rejected the idea that adaptation implies perfection: one recognizes the design of a watch, even if it is constructed from poor materials. He also rejected the idea that adaptation implies optimality within given (physical or economic) constraints: even a broken watch evidences design. Instead, Paley identified two defining characteristics of biological adaptation. First, he recognized that the various parts of both organisms and watches appear contrived as if for a purpose. Second, he recognized that all of the parts of the organism or watch appear contrived as if for the *same* purpose. Paley termed these two properties 'contrivance' and 'relation'. Put another way, the problem of adaptation is to account for the empirical fact that living material is packaged into units of common purpose (organisms).

3. DARWIN'S SOLUTION

If Paley clearly formulated the problem of adaptation, then Darwin (figure 1b) decisively solved it, with the theory of natural selection. Those heritable characters that are correlated with individual reproductive success are expected to accumulate in natural populations. Hence, Darwin argued, over successive generations, organisms should appear increasingly well designed for the purpose of achieving reproductive success, or 'Darwinian fitness'. In particular, following Paley, Darwin framed the notion of adaptation in terms of the apparent design of the organism: the contrivance of parts as if for a common purpose.

The theory of natural selection—the 'survival of the fittest'—is regularly accused of being an empty tautology. The argument is that, if an organism's Darwinian fitness is defined as its ability to 'survive' (and reproduce), then the concept of natural selection is

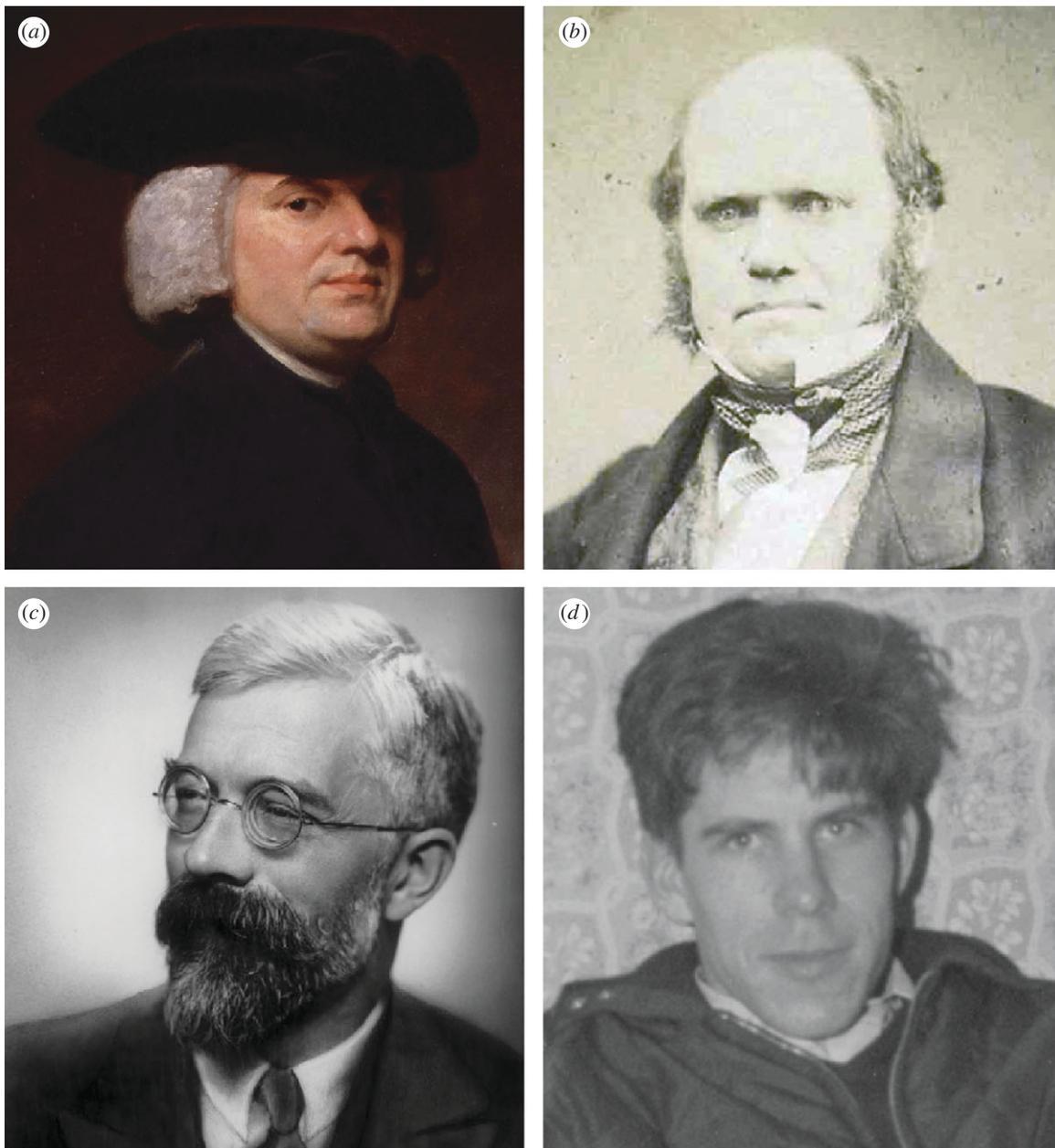


Figure 1. Key developments in adaptationism. (a) William Paley (1743–1805) formulated the problem of adaptation as the need to explain the apparent design of organisms (image courtesy of the National Portrait Gallery, London). (b) Charles Darwin (1809–1882) solved the problem of adaptation with the theory of natural selection. (c) R. A. Fisher (1890–1962) framed Darwinism in population-genetical terms (image courtesy of the National Portrait Gallery, London). (d) William D. Hamilton (1936–2000) developed the theory of social adaptation (image courtesy of the family of W. D. Hamilton).

circular and has no empirical value. The error here is to suppose that Darwinism is simply a theory of evolutionary dynamics, and the apparent tautology vanishes when one understands that Darwinism is really a theory of organismal design. It is possible to imagine worlds where organisms are designed to boil water or write poetry. The empirical value of Darwinism owes to it identifying that, in this world, organisms are designed to achieve reproductive success. Thus, Darwinism not only explains the origin of adaptation, but also its ultimate function.

4. FORMAL DARWINISM

A shortcoming of Darwin's argument is that it is given verbally. Today, evolutionary theory is properly framed

in mathematical terms and with reference to the genetics of populations. The formal link between mathematical population genetics and Darwinism was developed by R. A. Fisher (figure 1c), in his book *The Genetical Theory of Natural Selection* (Fisher 1930). Together with J. B. S. Haldane and Sewall Wright, Fisher is celebrated for synthesizing Darwinism with Mendelism, revealing that these are complementary—not conflicting—theories of the evolutionary process.

However, Fisher also made two further crucial contributions to the theory of Darwinian adaptation. First, he made the notion of Darwinian fitness concrete, by defining it as the organism's expected asymptotic contribution of genes to future generations or 'reproductive value'. Second, he showed that natural selection always acts to increase the mean fitness of

the population, in what he termed the ‘fundamental theorem of natural selection’ (FTNS). Fisher interpreted this as proof that organisms will appear increasingly designed as if to maximize their Darwinian fitness.

The FTNS has suffered a chequered history. For a long time, it was widely interpreted as a naive statement that populations evolve in the direction of increasing mean fitness, as captured in the notion of the ‘adaptive landscape’ (which Fisher detested). Models incorporating non-selective effects, such as recombination between interacting loci, were devised to show that the fitness of populations may decrease (e.g. Moran 1963). Thus, the FTNS was rejected, and with it any notion of fitness maximization. Since then, population geneticists have regarded branches of evolutionary biology that make use of fitness-maximization principles as deeply suspect, despite their empirical success. More recently, population geneticists are coming to appreciate the correctness of the FTNS, on the understanding that it describes the action of natural selection only, and not the whole of evolutionary change in fitness (see Crow 2002 for a review)—although the usefulness of such a partial result is disputed. The importance of the FTNS is that it isolates the part of evolutionary change that constitutes adaptation.

Fisher employed the FTNS as if it were formal justification for seeing organisms as economic, fitness-maximizing agents. However, the mathematical structures that properly capture such concepts rest in optimization theory, whereas the FTNS speaks only of dynamics. So, while the FTNS is correct, it does not quite realize Fisher’s goal. Recently, a formal link between natural selection and optimization theory has been established by Alan Grafen (reviewed in Grafen 2007). Specifically, Grafen has demonstrated a mathematical equivalence (isomorphism) between the dynamics of gene-frequency change under the action of natural selection and the optimization view of organisms as fitness-maximizing agents. Echoing Paley, this work makes no claim that natural selection results in optimality, but rather it accounts for the contrivance exhibited by the organism: the heritable component of the phenotype is moulded—through the medium of gene-frequency change—according to a design objective of fitness maximization. And it accounts for the relation (common purpose) of the component parts of the organism: all gene-frequency change is governed by the *same* design objective, under the assumption of Mendelian inheritance. However, this formal approach has also clarified that the maximand is not always the individual’s personal fitness: a more general design objective emerges if social interaction is permitted.

5. SOCIAL ADAPTATION

Organisms do not always appear designed to maximize their personal reproductive success. Sterile workers in social-insect colonies display exquisite adaptations that benefit other members of their community, rather than promoting their own reproductive success. Darwin suggested that the traits of sterile workers are shaped by natural selection operating upon the

reproductive members of the colony who, being their close relatives, are expected to carry heritable tendencies for such traits in latent form. This suggestion was developed into the modern theory of kin selection, by W. D. Hamilton (figure 1*d*) in the 1960s. Hamilton (1964) showed that the ultimate criterion for a trait to be favoured by natural selection is for it to increase the overall reproductive success of all the individual’s relatives (including itself), weighting each increment by the bearer’s genetic relatedness to the recipient. Thus, biological adaptation functions to maximize this ‘inclusive fitness’, rather than personal fitness.

Recently, the established inclusive-fitness paradigm has been challenged by proponents of multilevel selection (Wilson & Wilson 2007). However, the inclusive-fitness result is obtained irrespective of whether natural selection is considered as operating through direct- and indirect-fitness effects (the kin-selection approach) or through within-group and between-group fitness effects (the multilevel-selection approach). Irrespective of the strength of group selection, adaptation occurs at the level of the individual organism, where it functions to maximize the bearer’s inclusive fitness. By contrast, adaptation only rarely occurs at the level of the group: the action of natural selection only corresponds to the design principle of group-fitness maximization if within-group selection is absent (Gardner & Grafen 2009). This explains why honeybee hives and the Portuguese Man o’War have the appearance of ‘superorganisms’—here, within-group selection is largely abolished owing to policing mechanisms and clonal relatedness, respectively—whereas most social groups do not. Confusion between group-level selection (which is ubiquitous) versus group-level adaptation (which is rare) has been a major contributing factor to the longevity of the empirically vacuous group-selection controversy.

6. WEAK VERSUS STRONG ADAPTATIONISM

It is useful to make a distinction between ‘weak’ versus ‘strong’ forms of adaptationism. I have focused upon the weak form: i.e. recognition that organisms appear designed to maximize their inclusive fitness, without implying that they are optimally designed in this respect. This property of organisms is attributed to the action of natural selection, which need not be the sole (or even the main) driver of evolutionary change. The usefulness of weak adaptationism is that it permits biologists to describe organisms and their traits in purposeful, functional, intentional terms. Such language is not necessary, but it is extremely useful. Not only does it provide biologists with a powerful shorthand—which can be translated with fidelity into the mathematics of gene-frequency change—but it also defines whole (and successful) programmes of research. For example, on the evolution of altruism.

By contrast, strong adaptationism is the extreme view that organisms are optimally designed, owing to natural selection being the sole factor in evolution. This cannot be defended as an accurate view of the natural world, and indeed much anti-adaptationist literature has been directed against this caricature.

However, the assumption of optimality provides a powerful methodological tool for generating testable predictions. As with the hugely successful evolutionary-game-theoretic approach (Maynard Smith & Price 1973)—which focuses upon equilibria, despite real-world populations being in continual flux—the strong-adaptationist approach must ultimately be judged upon its ability to facilitate empirical testing of basic theory, and provide new biological insights, and not upon the biological face value of its underlying axioms.

7. FUTURE DIRECTIONS

Population geneticists, who are responsible for developing formal evolutionary theory, have neglected the design aspects of Darwinian theory. In the absence of a formal theory, biologists have employed ad hoc approaches, such as identifying adaptation as any response to natural selection (which confuses the problem with its solution), or else as degree of optimality (which conflates biological function and incidental effect). The task of achieving a more fundamental understanding of adaptation has largely been taken up by philosophers, with mixed results.

However, formal links between the genetics of populations and the design objectives for phenotypes have been established, and these permit mathematical inquiry into the nature of adaptation. So far, this programme of research has aimed at formally justifying existing results, such as those of inclusive-fitness theory (reviewed by Grafen 2007). However, the approach can be used to make progress on more controversial topics, such as disentangling the reality of between-group selection from the myth of group adaptationism (Gardner & Grafen 2009). An important goal for future research will be to rigorously examine claims of apparent purposefulness attached to other evolutionary entities—from selfish genes, and viral memes, to the ‘living Earth’ described by the Gaia

hypothesis. More generally, and especially in light of the current incarnation of creationism—which styles itself as ‘intelligent design’—evolutionary biologists should not shrink from addressing the central problem of adaptation. Indeed, we should make more of an effort to emphasize that Darwinism is the only scientific theory of biological design.

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