

# Debating the Power and Scope of Adaptation

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## 1 Adaptation and Adaptationism

Adaptationism refers to an unruly family of views about the power, prevalence, methodological privilege or explanatory importance of natural selection (see also Dietrich, this volume). Yet the contemporary debate over perils and advantages of this collection of views, including the effort to disentangle them, is peculiarly shaped around a single paper: “The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme” (Gould and Lewontin 1979), known now simply as the *Spandrels* paper. By using architectural and anthropological examples with rhetorical flourish, Gould and Lewontin criticized the inference from current utility to evolutionary origin: “One must not confuse the fact that a structure is used in some way [...] with the primary evolutionary reason for its existence and conformation” (1979, p. 587). The problem that confronts the inference is that structures, objects, traits, and characters can be co-opted and put to uses different than their evolutionary origin.<sup>1</sup> Although analogies between artifacts and organisms can be misleading in a variety of ways (Kampourakis 2013), a simple one can help clarify the difference between origin and current use. I have co-opted my office chair to serve as an end table for stacks of paper and coffee mugs, and indeed this is the primary reason I keep an extra chair in my office, but that does not change the fact that the chair is supposed to serve as a seat for a person, not an end table for a disorganized philosopher. It is testament to the importance of this inference pattern to evolutionary biology, from current utility to origin, that it raises such broad concerns about evidence, method, and explanation.

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<sup>1</sup>Indeed, Gould and Vrba (1982) found this phenomenon so prevalent in evolutionary history that they recommended a new term for adaptations co-opted to play a different role: *exaptation*.

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Before investigating the controversy over adaptationism, we need to address the concept of *adaptation*. Let me start with some clarifications. The concept of adaptation has a rich history that reaches back before Darwin (see, e.g., Amundson 1996). The concept also suffers from a process/product ambiguity: it can refer to the process of natural selection adapting organisms to their environments, or to the evolutionary products of natural selection. Although both uses play important roles in evolutionary biology, I will focus primarily on the product sense of adaptation.

What, then, is an adaptation? Prima facie, an adaptation is a trait evolved via natural selection because it plays a particular role in the organism's struggle for existence, and plays this role well. Consider the following adaptive hypothesis: the bioluminescent light organ of the Hawaiian bobtail squid is an adaptation for camouflage against the night sky in their aquatic environment. Predators often lurk below, looking for shadows of passing prey against the sparkling night sky. The light organ provides bioluminescence to eliminate the shadow, allowing the squid to blend in with the stars and moon above. This adaptive hypothesis involves a rich set of empirical commitments about squid lifeways, their evolutionary history, and the nature of their environment. The squid should be nocturnal, face a predation risk from below, regulate their bioluminescence to blend in with the ambient light levels, and so on (see Nyholm and McFall-Ngai 2004). How to test the hypothesis is an important thread in the adaptationism debate (see below). How to determine the extent of the empirical commitments of an adaptive hypothesis is, in part, a matter of definition. One question about adaptation makes clear that the prima facie definition needs to be made more precise: can there be adaptations without selection?

If the definition of adaptation is *historical* then the answer must be no. Sober provides a canonical defense and formulation of the historical definition: "A is an adaptation for task *T* in population *P* if and only if *A* became prevalent in *P* because there was selection for *A*, where the selective advantage of *A* was due to the fact that *A* helped perform task *T*" (1984, p. 208). Thus, to say that some trait is an adaptation is simply to say that there is a history of selection for trait *A* (to do *T* in *P*). The historical definition has a number of advantages and has achieved something of a consensus (Lewens 2007; Kampourakis 2013). Despite this, there is an alternative definition that focuses not on the history of natural selection, but on the performance of an organism in its current environment.

Gould and Lewontin opt for such an *ahistorical* definition of adaptation in the *Spandrels* paper. They claim that adaptation is "the good fit of organisms to their environment," and that selection can be "decoupled" from adaptation by other processes, such as developmental plasticity, that can produce the striking lock and key fit between a trait and the environment (Gould and Lewontin 1979, p. 592). Reeve and Sherman (1993) give one of the most thorough defenses of an ahistorical definition. They formulate the definition as follows: "An adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment" (Reeve and Sherman 1993, p. 9).<sup>2</sup> The rationale for removing history from the definition of

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<sup>2</sup>Evolutionary biologists take fitness to be a measure of reproductive success, usually expected number of offspring. However, there are a variety of fitness measures available and determining the correct interpretation of fitness is notoriously complex (see, e.g., Ariew and Lewontin (2004) or Beatty (1992)).

adaptation is that we usually can determine fitness differences among variation in a population, but we usually do not have access to the evolutionary history. Getting that access to history is but one goal of evolutionary research. Another is explaining why certain traits do better than others in a given environment, irrespective of history. Reeve and Sherman argue that focusing on these “phenotypic existence” questions structures evolutionary research in the right way: first we establish current utility, then we can evaluate whether and how that counts as evidence for past selection processes.

Must adaptations always play their role well? In short, no. Consider Gould’s (1980) example of the panda’s thumb. The so-called thumb evolved from a wrist bone, forming a notch that pandas use to strip leaves from bamboo shoots. Pandas spend most of their day occupied with this activity. An opposable thumb would do better at this task, but due to the contingencies of history and the constraints of the ancestral morphology this evolutionary innovation was unavailable to panda ancestors. Another set of examples, discussed originally by Darwin, concern the contrivances of orchids. Different orchid species have converged on various petal arrangements, but achieved these arrangements via the evolution of different developmental pathways. Some species evolved an efficient unfolding, whereas others evolved a more tortuous pathway to achieve the same result. Such developmental disparity evolved despite the species sharing a common ancestor.<sup>3</sup> Judgments about how well a trait may play its role depend on contrasts with biological structures that, due to the contingency of history, are not available to particular lineages. Notice that the panda’s thumb and the contrivances of orchids still count as adaptations on the historical definition, for there are histories of natural selection for those traits. However, they only count as adaptations on the ahistorical definition when we artificially constrain the set of variants to just those historically available. That is, we make a covert appeal to history to get the classification right.

That adaptations need not play their role well is a primary reason for adopting the historical definition, thus divorcing the concept of adaptation from any notion of design. Yet, as Lloyd (2007, p. 52) argues, some notion of design is often connected to the concept, and this leads her to distinguish between a *product of selection* (historical) sense and an *engineering* (ahistorical) sense of adaptation. The engineering sense of adaptation is perhaps better construed as *adaptedness*. As Brandon (1990) makes clear, the relative adaptedness of a trait must be evaluated within a specific selective environment, and it is differential adaptedness that drives evolution by natural selection. I find the historical definition of adaptation to be the best explication of the concept of adaptation, reserving the concept of adaptedness to capture ahistorical notions of performance, fitness advantage, and fit to the environment. So I will follow consensus and adopt the historical definition: a trait *A* is an adaptation (to do task *T* in population *P*) if and only if there is a history of direct selection for that trait *A* (to do *T* in *P*). Notice that the claim some trait is an adaptation applies to a single population. A trait being an adaptation in one lineage (e.g., the light organ for camouflage in bobtail squid) does not entail that similar traits are adaptations in other lineages (e.g., light organs in deep sea fishes); these are separate empirical claims.

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<sup>3</sup>Beatty (2004) and Beatty and Desjardins (2009) provide excellent discussion of this case in support of their analysis of why evolutionary history matters.

While adaptationism, in its many guises, is intimately connected with natural selection, the debate does not engage the nature of the process. Some version of a standard recipe is presupposed: evolution by natural selection occurs when there is variation in some trait, when that variation translates into differences in evolutionary fitness, and when that variation is heritable. It turns out that this standard recipe makes some interesting idealizations, and it does not line up exactly with more mathematical treatments of natural selection (Godfrey-Smith 2009). I suspect there are links between foundational issues about the nature of natural selection and aspects of the adaptationism debate, a suspicion I explore below. Yet much of the debate is independent of the foundational concern, and I will focus on those aspects first.

## 2 Different Kinds of Adaptationism

There are a number of ways to disentangle the knot of issues tied up in the adaptationism debates and these ways differ in the grain of resolution they impose on the debate. The most important coarse-grained distinction separates *empirical* from *methodological* issues. We might ask an empirical question about the prevalence of adaptation across the biological world, or about the power of the process of natural selection. Or we might ask methodological questions about how we should go about investigating the world. While the answers to the empirical questions may inform our methods for investigating the world, there is some important separation. We need to first adopt methods of investigation in order to answer the empirical questions and so we should expect broader concerns to enter into debate over methodological views.

The distinction between empirical and methodological strands is apparent in the *Spandrels* paper itself. Part of Gould and Lewontin's argument attempts to show that evolutionary factors other than natural selection are often in play. Neutral molecular evolution and constraints imposed by genetic and developmental structure are two important alternatives they cite (see also Dietrich, this volume; Love, this volume). Another part of their argument is independent of these empirical concerns. They criticize the methods deployed by so-called adaptationists to test their hypotheses, arguing that they fail to provide adequate evidence for natural selection.

There are a variety of finer-grained typologies for distinguishing different flavors of adaptationism (see, e.g., Amundson 1988, 1990; Sober 1996; Godfrey-Smith 2001; Lewens 2009; Orzack and Forber 2010). For my purposes, Godfrey-Smith (2001) provides a useful way to untie that knot that distinguishes between three kinds of adaptationism. The three kinds are (quoted from Godfrey-Smith 2001, pp. 336–337)<sup>4</sup>:

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<sup>4</sup>While the definitions are directly quoted from Godfrey-Smith (2001), I have changed to order to fit my exposition.

*Empirical adaptationism*: Natural selection is a powerful and ubiquitous force,<sup>5</sup> and there are few constraints on the biological variation that fuels it. To a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by selection. No other evolutionary factor has this degree of causal importance. [...]

*Methodological adaptationism*: the best way for evolutionary science to analyze biological systems is to invoke adaptation and natural selection; alternatives to natural selection need not be considered in most cases. [...]

*Explanatory adaptationism*: The apparent design of organisms, and the relations of adaptedness between organisms and their environments, are the *big questions*, the amazing facts in biology. Explaining these phenomena is the core intellectual mission of evolutionary theory. Natural selection is the key to solving these problems—selection is the *big answer*. Because it answers the biggest questions, selection has unique explanatory importance among evolutionary factors.

In short, the empirical kind makes a claim about the world, the methodological kind makes a claim about how best to conduct evolutionary inquiry, and the explanatory kind makes a claim about the philosophical priority of certain explanations. While there are natural lines of support between positive and negative positions on the three kinds of adaptationism, they are logically independent (Godfrey-Smith 2001). So, for example, even if adaptations are rare we might still reasonably think that looking for them first is a good method, or that explaining these rare adaptations is the intellectual mission of evolutionary biology.

In the sections that follow, I will discuss issues raised by each kind of adaptationism with the goal of revealing the importance and diversity of lessons one can learn from scientific controversy.

### 3 Making Claims About the World

The thesis of empirical adaptationism makes a claim about the world, and so to resolve controversy on this front we simply need to check the world. Unlike the other kinds, we can *test* empirical adaptationism. Of course, how to test the thesis is a difficult issue and involves making some methodological commitments. So there are covert connections between empirical and methodological theses that prevent controversy from disappearing completely, connections that will surface over the next two sections. Despite complications, there is a clear and useful proposal on how to go about checking the world to see if empirical adaptationism is true.

Orzack and Sober (1994a, b, 1996) develop an ensemble test of (empirical) adaptationism. The ensemble test works by identifying what it means for natural selection to provide a sufficient explanation for a single trait, then evaluating whether this is true for most biological traits (see Potochnick, this volume for explanation in biology). To get clear on the test we need to analyze what it means to count as a sufficient explanation, and how an evaluation of the entire wide and wild biological world is supposed to go.

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<sup>5</sup>See Depew this volume on this topic.

Consider three claims of increasing strength about some trait  $T$  of an individual member of some population (quoted from Orzack and Sober 1994, p. 362):

(U) Natural selection played some role in the evolution of  $T$ . (U stands for ubiquitous since we believe this proposition applies to most traits.)

(I) Natural selection was an important cause of the evolution of  $T$ . (I stands for important.)

(O) Natural selection is a sufficient explanation of the evolution of  $T$ , and  $T$  is locally optimal. (O stands for optimal)

Notice that these claims do not deny the operation of other evolutionary processes. Drift, mutation, constraints and other factors are always at play to some degree in any natural population (see Pigliucci, this volume; Dietrich, this volume for the concept of drift). Instead, these claims focus on the relative importance of natural selection versus other non-selective factors for the evolution of trait  $T$ , and identify important benchmarks on this spectrum.

Determining relative importance involves assessing the sufficiency of an evolutionary explanation for trait  $T$  that invokes only natural selection. Obviously, a sufficient explanation is not a complete explanation. Complete explanations are rarely useful—they include every detail, no matter how minute—and so we often seek explanations that invoke one or a few factors that made the difference. Thus, Orzack and Sober devote a majority of their analysis to providing an account of when natural selection *alone* made the difference; that is, to distinguishing (O) from (I) for a given trait  $T$ . Briefly, they argue that the appropriate test for (O) contrasts the predictions of an uncensored evolutionary model with a censored model. An uncensored model includes *all* evolutionary factors, from natural selection to mutation pressures, drift, constraints, etc. A censored model, on the other hand, only includes natural selection. Optimality models, an important tool for representing fitness differences among traits in a given environment, are examples of censored models.<sup>6</sup> If the predictions of the censored model fit the observations (in a rigorous statistical way), then (O) is taken to be true.

Brandon and Rausher (1996) raise two interesting objections to Orzack and Sober's analysis that track contours in the adaptationism debate. The first objection concerns the inclusion of the claim that  $T$  is locally optimal in the formulation of (O). The use of optimality models is generally associated with adaptationist views; the very idea that evolution optimizes traits to the prevailing environmental conditions seems to presume the truth of empirical adaptationism. While optimality models do presume that natural selection is operating, sophisticated application of the models cannot be dismissed in this way. Such models must incorporate underlying constraints, and they can provide quantitative predictions that can be tested rigorously. As Orzack and Sober (1994b, 1996) argue, mere qualitative fit between model and data is not rigorous enough. So, for example, in the squid bioluminescence case, observing that squid increase bioluminescence in the presence of predators provides a qualitative test of the adaptive hypothesis. Observing that squid finely tune

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<sup>6</sup>For canonical defenses of optimality modeling see Parker and Maynard Smith (1990) and Seger and Stubblefield (1996).

bioluminescence to ambient light levels, and that this degree of fine-tuning correlates with decreased predation risk provides a better, quantitative test. Jones and Nishiguchi (2004) conducted just such a test and their results support the adaptive hypothesis. Furthermore, while optimality modeling may be a natural tool for an adaptationist, many uses of the modeling technique in biology need not make strong adaptationist commitments (Potochnik 2009).

A second, related objection concerns the contrast between censored and uncensored models as a testing protocol for determining whether natural selection provides a sufficient evolutionary explanation for some trait *T*. As Brandon and Rausher put the problem, "...failing to reject the selection (O-type) model says nothing about whether there are other, I-type or U-type models that might also fail to be rejected when their predictions are compared with observations" (1996, p. 190). This raises deep issues about the nature of scientific testing that I will discuss in more detail in the next section, but let me mention two points here. First, the effectiveness of a testing protocol is limited by the alternative hypotheses considered. Second, testing protocols should balance complexity of the model and fit to data.<sup>7</sup> This is because more complex models face a higher risk of *over-fitting* the data and compromising predictive accuracy. Recall that the uncensored model includes all the evolutionary factors and the censored model includes only selection, excluding many other factors. Thus, the comparison between uncensored and censored models involves a difference in complexity that can complicate the test. As Godfrey-Smith (2001, p. 344) suggests, perhaps a better testing protocol would contrast models of comparable complexity.

In short, determining whether natural selection provides a "sufficient explanation" for some trait is truly difficult. The difficulties arise in the implementation of the testing protocol for individual traits. Bracketing these for a moment let me focus on how the analyses of individual traits function in the overall test of adaptationism. Orzack and Sober sharpen the (empirical) thesis as a generalization of (O): "Natural selection is a sufficient explanation for most non-molecular traits, and these traits are locally optimal" (1994, p. 364). This is an empirical claim about the relative frequency of (sufficient) natural selection explanations for traits, and so requires an ensemble of individual cases to test.

An ensemble test is no easy undertaking; we need to conduct a large number of evolutionary studies and resolve the explanation for each individual (non-molecular) trait studied. As Orzack and Sober (1994, p. 378) recognize, this test must overcome an ambiguity that faces any ensemble test: how to count the instances. A standard statistical approach to the problem would recommend a random sample of independent data points. But this recommendation is hard to follow. We do not have a good grasp on the sample space of *all* biological traits. Indeed, how to individuate biological traits is one strand of the adaptationist controversy. Part of the *Spandrels* critique attacks the strategy of "atomizing" the organism into optimized traits (Gould and Lewontin 1979, p. 585). Further, in biology the data points are not independent due to common ancestry, a problem familiar in phylogenetics (Felsenstein 1985).

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<sup>7</sup>Sober (2008) provides a precise analysis of testing in evolutionary biology that takes these model selection issues seriously.



To illustrate, recall the bobtail squid with its bioluminescent light organ. We can adopt a coarse-grained description of the trait: bioluminescence is an adaptation for camouflage against the night sky. Yet this description can be made more fine-grained. The light organ is a complex structure made of many mechanisms that foster the colonization and control of the symbiotic bioluminescent bacteria. The squid must acquire the right bacteria at the right time to develop a functioning light organ. In some sense these fine-grained features of the light organ are independent, for selection may have had varying roles in the evolution of each component; (O) may be true for some structures, whereas (I) or (U) may be true for others. But in another sense these fine-grained traits share an evolutionary history, for they are all features of individuals belonging to a single lineage. There is also a hierarchical part-whole relationship between the coarse and fine-grained trait descriptions. Wilkins and Godfrey-Smith (2009) argue that differentiating between various “grains of resolution” helps mitigate some of the disagreements over empirical adaptationism, for the thesis may be true at more coarse-grained levels of description and false at more fine-grained levels.

The contrast between morphological and molecular levels may provide just such an example. Notice that the Orzack-Sober ensemble test focuses on non-molecular traits. While the adaptationist debate has tended to focus on the morphological traits of organisms, accelerating research in molecular evolution has raised some of the same issues (see Dietrich, this volume). But at the molecular level neutral evolution is a viable alternative, so we must consider another claim about the role of selection: (N) Natural selection played no role in the evolution of  $T$  (N denotes neutral). Even supposing (empirical) adaptationism is true at the morphological level, the case for adaptationism at the molecular level is an open question (see Orzack and Forber 2010).

While the strategy for evaluating empirical adaptationism is clear—we simply check the world—how to implement that strategy is a genuine challenge. The implementation raises issues that penetrate deep into evolutionary theory, concerning the standards for identifying traits, for evaluating the role of selection in the evolution of those traits, and for assessing the relative frequency of selection actually shaping aspects of the biological world. And the truth of empirical adaptationism is very much an open question. Despite the rhetorical element in the *Spandrels* paper and replies (see, e.g., Queller 1995), discussion about how to evaluate the empirical thesis produced scientific progress of a sort. As Rose and Lauder (1996) put it, the need to formulate a “post-spandrels adaptationism” led to both conceptual and practical innovations for investigating the truth of (empirical) adaptationism. Some of those innovations are methodological, and to those questions I now turn.

## 4 Getting the Method Right

The thesis of methodological adaptationism makes a claim about how best to investigate the world. Of course, assessing the methodological thesis depends, in part, on the way the world is. If empirical adaptationism were true, if natural selection provided a



sufficient evolutionary explanation for most traits, then looking for adaptations first would be an effective method. But the assessment also depends, in part, on broad concerns about the nature of scientific methodology, and on more precise concerns about testing practices in evolutionary biology.

One broad concern about methodology involves whether there should be a single consensus method for evolutionary investigation. Mayr (1983) replies to the *Spandrels* paper in this way, arguing that biologists should look first and foremost for adaptive explanations and only resort to non-adaptive explanations when all else fails. Looking for non-adaptive explanations first would, on Mayr's view, be bad evolutionary science and impede epistemic progress.

This version of the thesis is problematic. As Kitcher (1993) argues, dividing our cognitive labor among competing research programs actually encourages progress towards our epistemic goals. Given that certainty is a luxury we seldom have in science, allowing diversity among methods, programs, and agendas of members of the scientific community hedges our epistemic bets. Such diversity increases the power of the community to solve outstanding problems (see also Potochnick, this volume). Forcing the community to adhere to a single method destroys this advantage. Thus, strong methodological adaptationism, interpreted as a thesis about how the community of evolutionary biologists should conduct their investigations, is probably false.

The need for diversity of methods is compatible with a weaker form of (methodological) adaptationism. Mayr's methodological recommendation could be correct for *some* evolutionary biologists. In fact, the point that Kitcher makes about the social structure of science provides support for the claim that some individual evolutionary biologists *should* accept methodological adaptationism, so long as other evolutionary biologists are following alternative programs that focus on (say) developmental and genetic constraints. The recently emerging field of evolutionary-developmental biology is arguably such an alternative program (see Love, this volume). Of course, the existence of a diversity of methodologies raises the possibility of conflicts between them. Ideally we will have the capabilities to integrate the products of different methodologies, but how exactly we should resolve such conflicts when they occur is an open question.

A more narrow methodological concern involves what testing protocols within evolutionary biology should look like. The discussion of the Orzack-Sober test of adaptationism raised connected issues about what the testing protocol for selection as a sufficient evolutionary explanation for some trait *T* should be, and whether optimality models provide the right tool for such a test. This issue can be connected to a more general moral about the nature of testing: *evidence is contrastive*. For a testing protocol to provide evidence *for* some hypothesis, it must provide evidence *against* rival hypotheses. To clarify the consequences of this point, let me approach it from a more philosophical angle.

Any scientific discipline must confront the problem of *underdetermination of theory by evidence*. This is a problem for theory choice. Evidential support is the primary criterion for making these choices. Yet how should we proceed when all the available evidence we have *fails* to discriminate between competing theories?

We might appeal to pragmatic concerns or other virtues of the theories, such as simplicity. While that is a plausible response to the problem, let me, for the sake of the argument, hold to the empiricist commitment that evidence and evidence alone should guide theory choices. How, then, should an empiricist proceed?

In principle, the solution is obvious: gather more data. In practice, it is precisely those factors that generate the problem that make executing the solution so difficult. We lack perfect epistemic access to the world. In evolutionary biology the problem is particularly acute since one primary aim of the discipline is to reconstruct the deep past. A significant part of the science endeavors to create better and more precise access to evolutionary history (Forber and Griffith 2011; see also Pigliucci, this volume). This search for evidence is guided by the formulation of competing evolutionary accounts with the goal of uncovering data that will discriminate between the rival hypotheses. If we do not have the right rival hypotheses on the table then the search may not provide the right evidential support.

One way to interpret the *Spandrels* critique is that it accuses adaptationists of ignoring rival evolutionary hypotheses that invoke drift or constraint (Forber 2009). This is subtly different than the methodological point in response to Mayr. Getting the set of rival hypotheses right is a prerequisite for testing adaptive hypotheses properly. Without contrasting an adaptive hypothesis against a non-adaptive hypothesis, there is a risk that the apparent evidential support for the adaptive hypothesis may be misleading.

To illustrate the problem, consider the testing protocol proposed by Sober (2008) to contrast directional selection (plus some drift) with pure drift (no selection) for a quantitative phenotypic trait. Sober works with the length of polar bear fur. The protocol assumes an optimality model that specifies the optimum mean fur length for the polar bear environment. Suppose we send an expedition into the far north and they return with observations that fit the predictions of the optimality model.<sup>8</sup> Sober (2008, p. 200) argues that this fit confirms the selection hypothesis over the pure drift hypothesis because such observations are much more likely given selection for fur length. Notice the contrastive element to the test.

If we augment the set of rivals, the observations may no longer univocally support the selection hypothesis. Let us suppose further that there is a plausible constraint hypothesis: fur length, due to features of polar bear development, is deeply entrenched and there is little or no variation among the population. Then the precise fit between the trait and the environment may be due instead to the migration of polar bears north after the last ice age. The precise fit that favors selection over drift will not discriminate between selection and constraint. Both hypotheses predict, with high probability, the observed match between phenotype and environment. While this toy example of a constraint is perhaps a bit far-fetched, developmental constraints certainly affect the evolutionary trajectories of complex organisms. The squid's light organ is clearly an adaptation, but explanations of some fine-grained features of the organ may be better explained by developmental constraint. We need

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<sup>8</sup> Assume the fit is statistically rigorous. The protocol also assumes that sufficient evolutionary time has elapsed for selection to operate (Sober 2008, pp. 199–200).

to enrich the testing protocol to find evidence that will support selection over drift *and* developmental constraint.<sup>9</sup>

Disagreements about methodology are particularly sharp when evolutionary inquiry turns to human behavior. The research programs of sociobiology and evolutionary psychology offer adaptive evolutionary explanations for features of contemporary human behaviors and cognitive abilities that have generated enormous controversy (Kitcher 1985; Laland and Brown 2002; Buller 2005; Downes 2010). Part of the controversy concerns normal scientific issues about the nature of paleobiological evidence and the structure of our minds. But another part concerns the methodologies behind these programs, with many critics identifying a connection to (methodological) adaptationism that introduces biases into efforts to “evolutionize” the mind.<sup>10</sup> More sophisticated approaches to the evolution of cognition emphasize the subtle interaction between selection and non-adaptive processes (e.g., Sterelny 2003, 2012), and these show much more promise.

In sum, controversy over (methodological) adaptationism concerns grand issues about how to structure scientific inquiry, and more pedestrian issues about how to test adaptive hypotheses. While the grand issues may not intersect with daily scientific practice, the issues about testing certainly do. The emphasis on pervasive problems of evidence for evolutionary biology, and how testing protocols should be revised to handle these problems, is a beneficial feature of the debate, making adaptationism worthy of careful study.

## 5 A Philosophy of Nature

Explanatory adaptationism is the most contentious thesis, for it makes claims about the primacy of certain questions for making sense of the world. It is not about the prevalence of adaptations, nor about methodology for evolutionary inquiry. It is instead about adopting a particular conceptual lens through which we understand and explain the biological world. Dennett (1995) is one of the most enthusiastic proponents of the thesis, arguing that Darwin’s theory of evolution by natural selection extends beyond revolutionizing biology, generating far-reaching implications for our overall worldview.

A problem for evaluating explanatory adaptationism is that it appears to be a sort of aesthetic claim. The striking interest we take in the apparent design of organisms seems to be a fact about us, not a fact about the biological world or the nature of evolutionary inquiry (Amundson 1988, 1990; Godfrey-Smith 2001). An illuminating

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<sup>9</sup>Sober’s protocol is based on the law of likelihood and so can easily be extended to incorporate constraint hypotheses, so long as such hypotheses specify an appropriate likelihood function. Pigliucci and Kaplan (2000) have an alternative protocol for contrasting selection and constraint that compares the probabilities of transition between possible forms.

<sup>10</sup>Lloyd (2005) makes an interesting argument of this kind about how methodological biases obscured evolutionary research on human female orgasms.

way to contrast the explanatory thesis with its empirical and methodological relatives invokes a triad due to later work by Godfrey-Smith. When reflecting on the nature of the scientific enterprise we can distinguish between science, philosophy of science, and philosophy of nature. The contrast between science and philosophy of science should be relatively clear. We can ask questions about the world (science) or we can ask questions about the nature of the scientific enterprise (philosophy of science). There is interplay between the products of science and philosophy of science, for the latter seeks to develop normative strategies for evaluating the quality of science. This cannot be done without both consulting and revising the practice. Philosophy of nature, however, stands apart. As Godfrey-Smith describes it:

This is the project of taking science as developed by scientists, and working out what its real message is, especially for larger questions about our place in nature. So we aim to use scientific work to inform our view of the world, but we do not determine this view using science in its 'raw' form (2009, p.3).

With some simplification, we can treat empirical adaptationism as a thesis within the scope of science, and methodological adaptationism as a thesis within the scope of philosophy of science. Explanatory adaptationism, then, is primarily a thesis about philosophy of nature.

One may legitimately question the relevance of philosophy of nature, and whether it has, or should have, any interaction with scientific practice. One common view is that while philosophy of nature may be important for packaging and exporting the products of science to the broader public, it does not have anything of value to offer the practicing scientist. That is, it is part of science education, not science. This common view is right to emphasize the connection to science education, but science ignores philosophy of nature at its peril. Philosophy of nature provides perspective on the science, a perspective that students come to internalize as they become the next generation of scientists. Such perspective can interact with practice by making certain features of the world more or less perspicuous, by emphasizing certain causal factors and downplaying others.

Consider an example of philosophy of nature interacting with science. This example involves a foundational concept: *the replicator*. This concept rose to prominence with *The Selfish Gene* (Dawkins 1976), a popular presentation and extension of concepts found in Williams (1966). Roughly, replicators are entities of which copies are made and that can influence the rate or probability of being copied. Genes are the canonical replicators. Talk of replicators pervades biology and evolutionary biology, and there is a legacy of controversy over whether the concept unduly privileges genes, gene action, and genetic inheritance. I do not want to rehearse that here. Instead, let me point to an interesting feature of the replicator concept: the integral use of agential language—strategies, plans, interests, agendas—at the level of the gene to describe evolutionary phenomena. Such language treats genes as metaphorical agents. This metaphor can have enormous effects on the science, effects that can be problematic because genes are not agents in any literal sense. Godfrey-Smith (2009, pp. 10–14) calls the unregulated use of this language *Darwinian paranoia*, arguing that the peculiarly powerful agential language has obscured core Darwinian ideas. The focus on replicators in popular

presentations of evolutionary science has also misrepresented the science, for much of evolution proceeds without using any of this agential language. Of course, many find such language indispensable to evolutionary theorizing. Haig (1997) generalizes the concept of the selfish gene to that of the social or strategic gene. Dennett (2011) responds directly to Godfrey-Smith, embracing agential language for genes as the primary way we make sense of complex evolutionary ideas. This debate about the foundational consequences of agential language is particularly relevant to biological education, for most of us learn the basic evolutionary concepts in agential terms.

Another way philosophy of nature may interact with science involves the export and trafficking of concepts between disciplines within the broad field of biology. A prominent evolutionary biologist once famously remarked, “nothing in biology makes sense except in the light of evolution” (Dobzhansky 1973). The general idea is that evolutionary considerations frame questions in more proximal biological sciences, such as ecology and developmental biology, in an essential way. Griffiths (2009) puts a sophisticated twist on explanatory adaptationism by treating it as a thesis of this kind. More precisely, he argues that much of ecology and developmental biology needs to consider forward-looking evolutionary consequences when doing research because these considerations are necessary to ground the concept of biological function. Thus, evolution by natural selection provides something different than the big answer to the question about apparent design in nature; it provides the backdrop that structures whole biological disciplines.

Perhaps explanatory adaptationism is an aesthetic claim, or perhaps it is something more. Regardless, resolving debate over this thesis requires going beyond the usual scope of scientific inquiry. Our stance on explanatory adaptationism depends on views about how we tend to think, and how those tendencies interact with scientific practice. Such a stance also has consequences for biological education: should we teach evolution emphasizing the importance and ubiquity of natural selection? Or, should we draw attention to the roles of contingency, constraint, and historical accident? How we teach the science contributes to our perspective on philosophy of nature, and that perspective can (and indeed, often does) influence how research is conducted and disseminated in the future.

## 6 Science in Action

The adaptationism controversy is such a fascinating and instructive episode of science because it raises a truly diverse set of questions. There are empirical questions about the prevalence and power of natural selection. These questions are open. Science continues to investigate evolutionary lineages, providing better resources to answer these questions. There are methodological questions about how to test evolutionary hypotheses, and how to structure the community of evolutionary biologists. These questions are unresolved. Far from a source or sign of problems, continuing discussion and debate on methodological issues fashions

better testing protocols, advancing the scientific discipline. There are questions about the importance and status of foundational concepts in evolutionary science. These questions are dangerously philosophical. Yet they are relevant to the practice of biology, for they concern overall perspectives on the science that scaffold the education of future biologists. And while the rhetoric of the debate sometimes distracts from the core issues, it illustrates an indelible feature of science: it is an enterprise undertaken by humans, with human motivations, and bearing the influences of their culture and society (Shapin 2010). The debate over adaptationism is far from an unproductive distraction from real science—it is science in action.

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