

Engineering Design and Adaptation

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Reverse engineering is a matter of inferring adaptive function from structure. The utility of reverse engineering for evolutionary biology has been a matter of controversy. I offer a simple taxonomy of the uses of engineering design in assessing adaptation, with a variety of illustrations. The plausibility of applications of engineering design reflects the specific way the models are elaborated and derived.

1. Introduction. *Reverse Engineering* is a matter of inferring adaptive function from structure. This leaves it deliberately ambiguous whether *function* is intended as *historical function* or as *anatomical function*. In the first case, the function of a trait is what it was selected for in the past, however, it may be used in the current economy of the organism. In the latter case, the function involves how the trait is currently used, whatever its historical function might have been. In its most contentious form, reverse engineering aims to infer the historical causes from observed organic form. If *adaptive thinking* begins with the ecological “problems” an organism confronts and explains or infers the “solution” based on the problem, reverse engineering turns the reasoning around, beginning with the “solution” and inferring what the ecological problem must have been (cf. Griffiths 1996).¹

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1. I favor the view held by Amundson, Godfrey-Smith, and George Lauder that there are two legitimate uses of “function” within biology. The first is the relatively familiar etiological view that “proper” functions are what was selected for in the past—the products of natural selection in the sense that they antecedently were selected *for*. The other is more common among anatomists and physiologists than with evolutionary biologists, and looks to current causal role as definitive of function. The issues I raise here survive either reading, though the historical use would make things more difficult for reverse engineering.

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D. C. Dennett claims this is *the* central “feature of the Darwinian Revolution: the marriage, after Darwin, of biology and engineering” (1995, 186). Here’s one example he uses:

Did *Archaeopteryx*, the extinct birdlike creature that some have called a winged dinosaur, ever really get off the ground? Nothing could be more ephemeral, less likely to leave a fossil trace, than a flight through the air, but if you do an engineering analysis of its claws, they turn out to be excellent adaptations for *perching on branches*, not for *running*. An analysis of the claw curvature, supplemented by aerodynamic analysis of archaeopteryx wing structure, makes it quite plain that the creature was *well designed for flight*. (1995, 233)

As a historical matter, this is surely not the central feature of the Darwinian Revolution. The evidence concerning *Archaeopteryx* also will not support Dennett’s arboreal conclusion, for a variety of reasons (see Ostram 1994, or Prum and Brush 2002). We need not settle either of these issues. Even if reverse engineering is problematic in inferring evolutionary origins, it may nonetheless be an important aspect in the understanding of adaptation. I am interested here in the inferential structure, and that is displayed clearly by Dennett. Engineering design is designed to take us from structure to function. We are supposed to infer that *Archaeopteryx* was airborne from the structure of the foot.

The study of adaptation within an evolutionary framework involves inferring historical process from contemporary products. The focus is on historical sequence and causal antecedents, emphasizing prior conditions as determinants of contemporary patterns (Lewontin 1969; Lauder 1996). This is a difficult task, since information concerning ancestral environments, variability, social structure, and other relevant features are often not available. Some biologists, especially evolutionary ecologists and behavioral ecologists, focus instead on questions of current form and function, abstracting from the historical paths that produced them. Models developed for parental investment, reciprocal altruism, and for inclusive fitness are extensions of the theory of natural selection, and are species of optimality models. In such applications, as in reverse engineering, the focus is not primarily historical, but rather concerns the extent to which a trait optimizes fitness among a specified set of variants and within a specific environment. The standard for fitness is optimality of design, measured by current utility.² Adding the historical dimension

2. Many of the architects of evolutionary psychology resist such an ahistorical approach to the study of adaptation, but the method has left its mark, and certainly has a salient place in biological research, including the work of R. A. Fisher (1990) and that of R. H. MacArthur (1957, 1960) on evolutionary ecology.

necessary for adaptation explanations makes the explanatory task more demanding.

Stephen Jay Gould and Richard Lewontin famously—perhaps infamously—have attacked what they call the “adaptationist program,” the view that natural selection is “so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function and behavior” (1979, 76). Instead of a commitment to adaptation as *the* explanation of organic form, Gould and Lewontin argue for a more pluralistic approach to evolutionary biology, in which a wider array of alternatives to natural selection need to be systematically considered. Showing some trait is the product of natural selection requires eliminating alternative explanations, or at least showing that they are less likely. Gould and Lewontin offer a variety of alternatives to natural selection, including genetic drift, but the image of the spandrels of San Marco suggests strongly the role that developmental or structural constraints might play in evolutionary processes (cf. Alberch 1982; Gould 1977; Maynard Smith, et al. 1985). The attraction of the idea is not difficult to see. The construction of a phenotype from a genotype is a complex affair, and the idea that the phenotype could be indefinitely molded to meet the demands of the environment, is unrealistic. Pleiotropy and epistasis, furthermore, entail that there are nonlinear, and nonadditive, interactions among genes. There are dependencies in ontogeny that entail that characters cannot be readily decoupled (cf. Schank and Wimsatt 1987; Wimsatt and Schank 1988). Suites of characters evolve in concert, in ways that are impossible to predict in the absence of specific developmental information. What has emerged in the twenty years since the “Spandrels” paper, though by no means solely as a result of that paper is, in fact, a much more eclectic, more pluralistic, research program in evolutionary biology, with more sensitivity to problems involving developmental limitations, more awareness of the deep conservatism in underlying genetic mechanisms, the significance of phylogenetic analysis, stochastic effects on evolution, and at the same time a more nuanced understanding of the action of natural selection.

The reliance on optimality and reverse engineering in the analysis of adaptation is perhaps the clearest example of the sort of research Gould and Lewontin criticize. They claim that the “adaptationist program” typically involves two steps. First, an organism is “atomized” into traits that are explained as independent structures optimally designed by natural selection. This often amounts to assuming that genetic variation is both extensive and additive, and that as a consequence phenotypes are almost indefinitely malleable. Second, since assuming traits are independent is generally unrealistic, interaction effects are incorporated as trade-offs. Competing demands on organismal design are acknowledged, but without compromising the

commitment to optimal design.³ The focus on current function, and the use of abstract design criteria, they contend, obscures the role of history.

So while Dennett finds reverse engineering essential to good Darwinism, Gould and Lewontin see it as inimical to it. Other responses to engineering design arguments have been equally varied. Some regard it as good science. Others regard it as little more than a sham. Here is what G. C. Williams says, even in the context of emphasizing how difficult it is to show that some trait is an adaptation:

Adaptation is demonstrated by observed conformity to *a priori* design specifications. This is the main method used by Galen and Paley . . . and recently advocated by Thornhill (1990). The hand is an adaptation for manipulation because it conforms in many ways to what an engineer would expect, *a priori*, of manipulative machinery; the eye is an optical instrument because it conforms to expectations for an optical instrument. (Williams 1992, 40)

We find Steven Vogel offering this somewhat more limited approval:

[M]uch of the design of organisms reflects the inescapable properties of the physical world in which life has evolved, with consequences deriving from both constraints and opportunities. (1988, 4)

These sentiments contrast sharply with the verdicts offered, for example, by Michael Ghiselin:

Panglossianism is bad because it asks the wrong question, namely, What is good? . . . The alternative is to reject such teleology altogether. Instead of asking, What is good? What has happened? The new question does everything we could expect the old one to do, and a lot more besides. (1983, 363)

The divergence of opinion should give us some pause. How could there be such a wide divergence of opinion? I think it is useful to distinguish a number of applications of engineering design in the understanding of adaptation. I will offer a simplified scheme here, with some biological illustrations. These cases differ strikingly in how compelling they are, and that might, in turn, explain the divergence of opinion. The first thing to notice is that we can begin in different places. On the one hand, we can begin with an analysis of environmental structure, looking to the demands the environment places on the organism to infer organismic function. This is often called “adaptive thinking.” Such adaptive thinking can involve significant appeal to design. On the other hand, we can begin with an analysis of organ-

3. It is tempting and common, to treat this complaint as if it were one over the failure of falsifiability. I think this is not the most fruitful rendering, to say the least.

ismic structure, looking to the structure of the organism to determine the organismic function, and from that infer the environmental demands. There is an equally fundamental difference in approach that is independent of this first distinction. There are very different roles for the constraints that give substance to these models (see Amundson 1994; Amundson 1996; Amundson and Lauder 1998). The issue is whether the constraints defining what counts as optimal form are prior to the assessment of fit between form and function. On the one hand, information concerning constraints can be incorporated into evolutionary models as prior constraints on the available range of biological form. It is useful to think of this as an a priori structuring of the “problem,” in the way Williams embraces it. Environmental information then gives a structure to the problem, constraining the alternatives systematically.⁴ On the other hand, we can develop design constraints a posteriori, using the performance of the phenotype to determine the environmental factors that shaped that design (see Beatty 1980). This is the most restrictive case of reverse engineering.

This would give us a four-way categorization, as illustrated in Figure 1. On both dimensions, the differences are probably better thought of as matters of degree rather than kind. As a useful approximation, I’ll treat them as if they are qualitative differences. The issues are considerably more complex than this simple taxonomy allows. There is another dimension to the problems that ideally would be recognized. One introduces depth to the understanding of organismic analysis; the other brings depth to the environment. George Lauder (1996) emphasizes that there is often no ready connection between an analysis of structure, behavior, and (physiological) function. He considers four taxa among salamanders: *Abbystoma*, *Cryptobranchus*, *Necturus*, and *Siren*. There are significant differences among the three groups. Considered from the point of view of structure, *Siren* and *Abbystoma* are indistinguishable, while *Necturus* and *Cryptobranchus* are differentiated. Behaviorally, *Abbystoma* and *Necturus* are indistinguishable while *Siren* and *Cryptobranchus* are differentiated. And in terms of function, *Necturus* and *Cryptobranchus* are indistinguishable while *Abbystoma* and *Siren* are differentiated. So even though *Siren* and *Abbystoma* are similar in morphology, they differ with respect to both behavior in feeding and in physiological function. And even though *Abbystoma* and *Necturus* are similar, they are functionally distinct. Lauder concludes from this that “It is clear that an analysis of any one level alone is an insufficient description of the design of the feeding system in salamanders, and that prediction of behavior or physiological function

4. It is difficult to use this approach generally. Such a priori optimization requires substantive knowledge of the environmental “problem” to be solved, the range of phenotypic variation, their relative efficiency, and much more (cf. Lauder 1996).

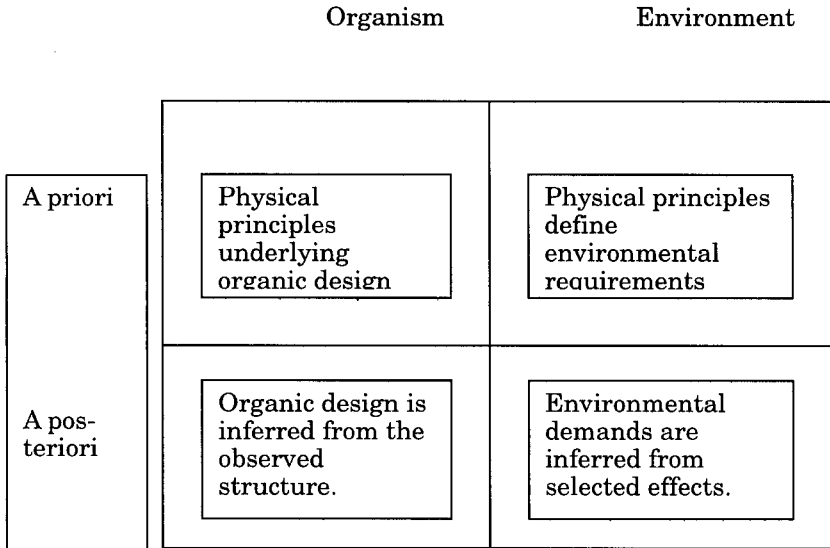


Figure 1

from structure alone in this case study is effectively impossible” (1996, 70). Structure, behavior, or (physiological) function each could be targets for evolutionary explanation.

Similarly, Robert Brandon provides an articulation in the understanding of the environment. The entry point is that natural selection, and adaptedness, are relative to a *common environment*. Brandon offers a simple argument for this conclusion. Given two different plants, with dispersal of seeds by wind a disproportionate number of one type may by chance land on fertile ground. This will result in a differential increase of that plant. This is not natural selection. The differences in realized fitness are not due to differences in adaptedness. Brandon concludes that “in order to explain differences in realized fitness in terms of differences in adaptedness one must compare organisms in common environments” (1990, 46–47). Brandon’s example is one that could naturally be treated as simply a chance effect in a heterogeneous environment, and that, as he says, is not a straightforward result of natural selection. It is not obvious to me that the example Brandon offers is one in which the organisms lack a common environment. Brandon is nonetheless correct. A simpler, but analogous, argument yields the same conclusion. A plant in Borneo might differ in any number of ways from another in Haiti, or they might be genetically identical; but, lacking a common environment, they simply cannot be compared with respect to fitness. Even though one may proliferate, and the

other might decline in numbers and finally go extinct, this is not a difference in their relative adaptedness, and the process is not one of natural selection. Population pressures may differ, a drought may cause a population crash on one island, or there may be different competitors. Any comparison of their *relative* adaptedness is empty. As Brandon sees, though two plants in different environments may differ in reproductive success, the two seed types might not differ at all, and whatever differences there are between them should not be seen as due to natural selection without a common environment.

Natural selection is thus relative to a common environment. Brandon distinguishes three concepts of the environment. The *external environment* is partitioned on the basis of independent physical or biotic factors, such as rainfall, temperature, food sources, or predators; any differences can be used to discriminate parts of the external environment. The *ecological environment* is partitioned on the basis of differences in the performance of organisms, and thus is dependent upon only those factors that affect fitness; the ideal measure of differences in the ecological environment is the performance of the same type across space or time. Finally, the *selective environment* is partitioned on the basis of relative differences in the performance of organisms, and thus is dependent upon only those factors that *differentially* affect fitness; the proper measure is the relative performance of different organisms within the same ecological environment. It is an important part of Brandon's work that there be ways of distinguishing differences in the environment that are methodologically tractable, and Brandon spends considerable energy explaining how we can discriminate such differences. Thus, if local variations in the bacterial concentrations in the soil do not affect adaptedness within a population of plants, then though they are part of the external environment they are not part of the ecological environment for those plants. This could be observed by comparing the reproductive output of genetically identical plants in different ecological environments. If these variations do affect the adaptedness of different plants, but do not change their relative fitness, then they are part of the ecological environment but not of the selective environment. This could be seen by comparing strains across environmental variation. If these variations affect the relative fitness of the plants, then these are differences in the selective environment as well. Brandon says that from "the point of view of the theory of natural selection, the relevant environment is the selective environment" (1990, 66). If we are to infer from environmental structure to organismal function, or *vice versa*, it is important to distinguish in which sense the environment is being used.

I think that the differences observed by Lauder and Brandon could be used to give us a yet more complicated picture of the forms of engineering design. It may well be that acknowledging these differences would affect

our verdicts on the quality of the inference. For the most part, I will ignore these additional dimensions and focus on the more superficial differences. So let's look at some examples from each of the four quadrants in the more simplified scheme. In the first quadrant, we have a priori constraints on organismic design. Vogel recognizes that the designs of nature are imperfect and incomplete. He nonetheless finds the assumption that there is a "decent fit between organism and habitat a useful working hypothesis" (1988, 10). He has a number of fascinating cases. One vivid illustration of physics at work in the biological world derives from Bernoulli's principle (after Daniel Bernoulli 1700–1782). The principle essentially says that the pressure from a fluid decreases as the rate of flow increases. So consider a simple plane surface with a hole and fluid flowing horizontally (it could be liquid or gas, but it must be a fluid with low viscosity). As the fluid moves more rapidly across the opening, the pressure from the fluid will decrease. If we start at equilibrium above and below the surface, the result would be to draw from below to above at a rate proportional to the difference in rate of motion. As it turns out, we find something akin to this in prairie dog burrows. Burrows have more than one opening. Changing the shape and height of the openings will bring Bernoulli's principle into play. Flow will be more rapid for raised openings, which will create a pressure differential with air motion through the burrows. A slight breeze will then draw air through the burrow. Showing exactly how this works depends on burrow lengths, depths, and the distance between openings. Prairie dogs evidently work to maintain a difference between the openings in such a way as to maintain air flow. This has the consequence that the animals are not asphyxiated in the bottom of the burrows. Sponges similarly use pressure differentials to move water through for filtration.

Here is another simple example from Vogel (1998). Leaves are flat, and that results in a problem with bending. A flat surface is generally not rigid. One solution is to impose "beams." The veins on leaves provide simple support structures that make them relatively rigid, as does introducing curvature. The veins effectively increase thickness, with the result that tension can resist bending. Curvature along the midrib results in a mildly concave curvature that also resists bending. The flexibility in turn allows some leaves to fold when the wind increases, reducing drag and damage. In such cases, the constraints on design derive from the physical demands.

In the second quadrant, we have cases in which there are a priori constraints on environmental structure. In this use of engineering design, information concerning constraints is incorporated into evolutionary models as constraints on the available range of biological form, specified prior to the assessment of adaptation. Thus, the ubiquitous marine water striders, *Halobates*, can move across the surface of seawater with amazing quickness, and also can jump and land on the surface of the water. There

are two physical constraints that make this remarkable trick possible. First, like many insects, the water strider has a coating that makes it resistant to surface wetting. Second, there is a match between the total perimeter of its feet (which determines the contact line for the striders) and surface tension (which varies with salinity). With a mass of roughly ten milligrams, the contact line would need to be roughly 1.3 millimeters total to move about and roughly 13 millimeters of contact line to sustain a jump (cf. Vogel 1988). *Halobates* meets the expectation from the physical model. It has specialized hairs to increase its total contact, thus making both movement and jumping possible. In cases such as this, the constraints are easily defined beforehand, since they depend on physical parameters (body mass and surface tension). This use of constraints is, in itself, not objectionable. It amounts to using environmental or developmental information to structure the problem, constraining the alternatives systematically. It is, though, difficult to use this approach generally. George Lauder observes:

The claim that relevant design criteria can be specified *a priori* to allow the analysis of biological design amounts to a claim that we can specify in advance the problem or problems that the design is supposed to solve. Although it is almost always possible to specify *some* design criterion, the more complex the design, the less likely it is that we will be able to determine what the relevant performance and mechanical functions are that any given structure needs to solve. And furthermore the less likely it is that we will be able to meaningfully weigh alternative performance goals. (1996, 71)

The difficulty is simply that *a priori* design constraints are often not specified, and in many cases cannot be specified before the fact. A turn toward historical function would make the difficulties even greater.

In the third quadrant, we have *a posteriori* constraints on environmental structure. The point of MacArthur's (1957, 1960) classic work on the abundance of species in the "broken stick" model was that the existing data on relative abundance of species fit better with a model based on nonoverlapping niches. These data, MacArthur concluded, fit better with an analysis that assumes competitive exclusion than with an analysis that assumes species distribution patterns are caused by, say, abiotic factors. The analysis of pattern is, for MacArthur, a vehicle for understanding evolutionary history. MacArthur finds a rough qualitative fit between the observed distribution of species and a competitive model. The fit is by no means perfect, though. Common species are more abundant than the models would predict, and rare species are less abundant than predicted. MacArthur points out that if the environment is heterogeneous, then it is possible to improve the fit between data and model. He goes on to reverse the dependence: "The divergence from the ideal curve may, in fact, be

regarded on this hypothesis as a measure of heterogeneity. Experimentally, for bird communities, this appears to explain most of the ‘steep’ curves” (MacArthur 1957, 293). This is a standard strategy in handling a mismatch between model and prediction, in order to explain apparent lack of optimal design. A deviation from initial predictions is explained by superimposing a second application of the same optimization model, taking up the slack in the fit by *assuming* optimal design. In such a posteriori applications, the degree of mismatch with the predicted optimum is used as a measure of the significance of the constraint. We no longer test for adaptation or optimality, but assume it.⁵

Finally, in the fourth quadrant, we find a posteriori constraints on physiological design. Williams uses the human hand as a consequence of selection, recognizing that this depends on the sort of variation that was historically present and recognizing that there are alternative “designs” that might work equally well for grasping. This could explain, for example, the presence of five digits (even if six or four might result in a better-engineered tool for grasping), partly as a result of frequency-dependent selection. It could also explain quantitative characters, such as digit length. Williams does not claim any of these actually were selected as illustrative, but, as far as I can tell, he intends them to be so. Lauder takes the example to task, as one for which there is too much freedom in defining the constraints on design. The hand is certainly a complex device, with twenty-six separate bones, nerves, blood vessels, and tendons. There are five metacarpals, fourteen phalangeal elements that constitute the fingers, and seven carpal bones. The hand is evidently designed for grasping. But what of these structures are adaptations for grasping? It is at least clear that much of the structure reflects ancient features common to vertebrate forelimbs. They are surely independent of the need for manipulation. As Lauder says:

[I]t is clear that the possession of independently mobile jointed elements (“fingers”) is not a design component that could be linked to any specific function that is unique to the human hand: fingers are an ancient design feature of the vertebrate forelimb . . . and occur in many animals that do not have the manipulative abilities of the human hand. (1996, 75) Of course, the hand is used for manipulation. Beginning here, though, leaves us short of anything resembling a principled analysis of design.

Given these different applications, what can we conclude? I think that, following the simplified scheme I’ve offered, we can begin to sort out the

5. As Gould and Lewontin observed, this kind of retrofitting does insure that there will be some optimal model for the behavior in question. Responses to the challenge of finding an analysis that makes a trait optimal depend primarily on the creativity of the theorist.

cases. Where we have significant a priori constraints, offering principled reasons for recognizing either organismic or environmental limitations, then the case for adaptation is relatively compelling. It is not decisive in the absence of historical information, but such cases do offer some support for adaptive conclusions. Where we have only a posteriori constraints on environmental structure, adaptation (or adaptiveness) is not so much tested as assumed. This is exactly what some defenders of optimality and adaptationism have insisted upon (e.g., Mayr 1983). Finally, when we have only a posteriori constraints imposed after the fact on organismic structure, there is little substantial support for adaptive hypotheses.

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