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# BIOLOGICAL FUNCTION, ADAPTATION, AND NATURAL DESIGN*

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Recently something close to a consensus about the best way to naturalize the notion of biological function appears to be emerging. Nonetheless, teleological notions in biology remain controversial. In this paper we provide a naturalistic analysis for the notion of natural design. Many authors assume that natural design should be assimilated directly to function. Others find the notion problematic because it suggests that evolution is a directed process. We argue that both of these views are mistaken. Our naturalistic account does not simply equate design with function. We argue that the distinction between function and design is important for understanding the evolution of the physical and behavioral traits of organisms.

**1. Introduction.** The last half century, especially the last quarter century, has seen the accumulation of a large and diverse literature about the use of teleological notions, such as function, design, and adaptation, in biology. Contributors to this literature include both theoretically oriented biologists and biologically oriented philosophers. In a recent survey of this literature (Allen and Bekoff 1995), we developed a classification scheme identifying nine distinct views about teleology in biology, among contributors as diverse as Ernst Mayr, Robert Hinde, George Williams, Richard Dawkins, Ernest Nagel, Larry Wright, Rob Cummins, and Ruth Millikan.

These authors disagree over questions such as whether teleological notions are essential or merely heuristic for understanding biological phenomena and whether biological explanation has a fundamentally different form from explanations in other sciences. For example, despite criticizing the way many biologists use the concept of adaptation, Williams (1966,11) writes, "I have stressed the importance of the use of such concepts as biological means and ends because I want it clearly understood that I think that such a conceptual framework is the essence of the science of biology." In contrast, Nagel writes (1961/1984, 346) that "the use of such explanations in biology is not a sufficient reason for maintaining that this discipline requires a radically distinctive logic of inquiry."

Originally, teleology was controversial because it was associated with pre-Darwinian, creationist views about organisms. Mayr (1974/1988, 40) identifies four reasons to be suspicious of teleological notions, namely (i) vitalism, (ii) incompatibility with mechanistic explanation, (iii) backwards causation, and (iv) mentalism. To Mayr's list we added a fifth category of methodological concerns about the empirical testability of teleological claims (Allen and Bekoff 1995). These categories may be related; for instance, backwards causation might be incompatible with mechanistic explanation and would entail methodological difficulties. Although concerns centering on vitalism and creationism no longer pose a serious worry for most biologists and philosophers, continuing controversy about teleological notions is attested by the high volume of theoretical papers in the literature.

Even a cursory scan of the theoretical literature reveals that biologists have found it difficult and even undesirable to eliminate teleological notions from their discussions of biological phenomena. Despite this, it is relatively difficult to find *explicit* claims about function or design in articles that primarily report empirical data. English, however, provides a variety of ways for making *implicit* functional claims without using the word "function" (Van Parijs 1982) and it is not difficult to find implicit claims about function. For example, in a paper titled "What is the function of encounter patterns in ant colonies?", Gordon et al. (1993) make no explicit statements about function, but they do say (p. 1099) "An ant that suddenly encounters alien ants may be in danger . . . the increase in [antennal] contact rate, though short-lived, may be sufficient to generate a defensive response to the intruders." This contains an implicit suggestion about the function of antennal contacts, but the authors exercise notable caution in avoiding any explicit claims. Another example is provided by Holley (1993), who writes about the bipedal stance that brown hares assume when confronted by red foxes. He says (1993, 21), "The functions of this behaviour are considered and competing hypotheses of Predator Surveillance and Pursuit Deterrence are examined by testing predictions against

results obtained. The results suggest that by standing erect brown hares signal to approaching foxes that they have been detected." In other words, a function of standing erect by brown hares is to deter pursuit by foxes. Implicit claims about function are also relatively common in textbooks of animal behavior (e.g., Drickamer and Vessey 1992; Alcock 1993). In discussing the classic work of Tinbergen and his colleagues, Drickamer and Vessey (1992, 23) note the plausible hypothesis that "Parents remove white eggshells to protect their young;" clearly they could just as well have written that for these birds a function of eggshell removal behavior is to protect their offspring.

In both the theoretical and empirical literatures, explicit claims about design are even harder to find than claims about function. However, for numerous mammals it has been hinted that play signals may be designed to initiate and to maintain social play, and that developmental scheduling and structural sequencing of play (e.g., duration, the interval between play-bouts, the different motor patterns that are used, how they are organized in sequence, and where bites or other actions are directed) are designed to fulfill various functions (e.g., Rasa 1973; Bekoff 1977, 1982, 1988, 1989a,b, 1993; Leyhausen 1979; Bekoff and Byers 1981; Fagen 1981; Martin and Caro 1985; Hass and Jenni 1993; Pellis 1993; Watson and Croft 1993).

Reluctance to discuss design may be due to a couple of factors. First, the notion of design may be considered metaphorical and offputting because it suggests a strong directional component in the evolution (or development) of a behavioral phenotype (Dawkins 1986). Second, many authors seem to accept a principle that straightforwardly assimilates the notion of design to that of function such as:

> [ND = F] T is naturally designed for X if and only if X is a biological function of T.

Some authors make their allegiance to something like ND = F explicit. For example, Kitcher (1993, 379) writes: "the function of an entity *S* is *what* S *is designed to do*" and Millikan (1984, 17) states that "Having a proper function is a matter of having been 'designed to' or of being 'supposed to' (impersonal) perform a certain function." Other authors write as if they implicitly accept ND = F (e.g. Williams 1966, 9). Further below, we shall argue that this identification ought to be rejected.

2. **Naturalizing Biological Function.** Like many authors, it is our view that successful naturalization of teleological notions in biology requires that one give an account of these notions that does not involve the goals or purposes of a psychological agent. With respect to the term "function," we agree with Millikan (1989; see also Godfrey-Smith 1994) who refers to

an ambiguity in its biological uses, and argues that there is room in biology for at least two different notions—etiological functions (Wright 1973, 1976) and Cummins-functions (Cummins 1975). Kitcher (1993, 395) also notes that "Philosophical discussions of function have tended to pit different analyses and different intuitions against one another without noting the pluralism inherent in biological practice."

Although Millikan and Godfrey-Smith endorse the pluralistic view, they believe, and we agree, that an etiological approach to function, based on Wright (1973), gives the best account of the majority of uses of the notion of function within evolutionary biology. The number of philosophers of biology converging on etiological accounts of function justify our labelling it "the standard line" (Allen and Bekoff 1995); in addition to Millikan and Godfrey-Smith, proponents of the standard line include Ayala (1977), Griffiths (1993), Mitchell (1993), and Neander (1991a,b). The standard line has these three components (from Allen and Bekoff 1995):

(1) Functional claims in biology are intended to explain the existence or maintenance of a trait in a given population;
(2) Biological functions are causally relevant to the existence or maintenance of traits via the mechanism of natural selection;
(3) Functional claims in biology are fully grounded in natural selection and are not derivative of psychological uses of notions such as design, intention, and purpose.

Variants of the standard line differ mostly over how to make component (2) precise. There is also some discussion of (1) with respect to the importance of distinguishing, on the one hand, initial spread of a new phenotypic trait in a population from, on the other hand, the maintenance of traits in populations (Gould and Vrba 1982; we discuss their distinction between adaptation and exaptation below).

**3. Function and Adaptation.** Tinbergen (1963) is widely regarded as having set the agenda for ethology—the study of the evolution of behavior—by identifying the four areas of evolution, causation, adaptation (or function), and development, as the major areas of concern for ethological study. Ethologists and behavioral ecologists typically follow his identification of function and adaptation (see, for example, Marler and Hamilton 1966; Brown 1975; Eibl-Eibesfeldt 1975; Manning and Dawkins 1992; Drickamer and Vessey 1992; Alcock 1993).

The assimilation of adaptation and function is a characteristic not only of behavioral scientists. For example, Sober (1993, 84) offers this definition of adaptation:

Characteristic C is an adaptation for doing task T in a population if and only if members of the population now have C because, ances-

trally, there was selection for having C and C conferred a fitness advantage because it performed task T.

If the phrase "is an adaptation for doing task T" is replaced in this definition with the phrase "has task T as a function," then we have an instance of the standard account of function, and in this sense the two notions are assimilated. Sober's definition is cited approvingly by many biologists (but see Reeve and Sherman 1993 for dissent). We believe, however, that it represents a considerable divergence from normal biological usage. Specifically, nothing in Sober's definition captures the idea of modification in form or structure that is an important component of many notions of adaptation. This is not automatically a criticism. It might be argued that biological usage should be reformed. However, we believe that it is *prima facie* preferable to elucidate scientific usage rather than attempt to reform it. We believe that the notion of an adaptation is better understood in the context of an analysis of natural design than than by assimilating it to biological function.

**4. Naturalizing Natural Design.** If most uses of the notion of biological function are successfully naturalized by the standard line, then the principle ND = F provides a cheap way to naturalize the notion of natural design. We share the goal of naturalizing the notion of design, but we do not believe that it is necessary or desirable to conflate function and design in order to do so. We advocate rejecting ND = F while still basing the analysis of natural design on natural selection. This distinguishes our view from that of Ollason (1987, 549) who claims that "Optimal foraging theory has nothing to do with the theory of evolution: it has to do with the science of design," which entails that the science of design has nothing to do with the theory of evolution.

   We claim that uses of the notions of design and function in biological contexts should be understood in ways that do not make biological teleology derivative of psychological teleology. Nonetheless, we shall argue that analysis of *psychological* teleology can, with care, motivate distinctions that are useful for understanding the use of teleological notions in the study of evolution. The methodological principle here is that biological practice provides the stronger constraints on analyses of teleological notions in biology, while considerations from psychological usage provide (at best) weak constraints.

**5. Design in Psychological Contexts.** Our strategy, then, is to apply what we learn about ordinary psychological usage to help develop a useful account of natural design. We start by noticing that psychological uses of "design" are ambiguous; the term "design" has at least two different but related senses when applied to human activity. The first sense, that we

label "goal-driven design," coincides with detailed planning before or during a sequence of behaviors geared to a specific goal. In this sense, architects design buildings and football coaches design plays. Goal-driven design involves the attempt to shape an object or behavior in the light of explicit functional desiderata. Products of goal-driven design are properly called artifacts. The process of design frequently involves successively modified versions of a product that are tested by trial and error. The second sense of "design" is close in meaning to "intentional," and is accordingly labeled "intent design." Someone who is rude intentionally can be said to have been rude by design. Actions may be intentional even when little thought has been given to the action's point or consequences; intentional rudeness very often occurs even when one has not considered what objectives are served by it, or what the aftermath will be. Goal-driven design entails intent design, but the converse is not generally true. Goal-driven designers generally try to anticipate factors which threaten the success of the project, whereas this need not be true of intentional actions, which may occur with relatively little forethought. When talking about design in psychological contexts, we should be understood as using "design" in the goal-driven sense, unless specifically noted.

With respect to goal-driven design, (a) design determines function, but (b) not everything that has a function is designed (for that function). Consider (b) first. Many people use natural objects (driftwood, seashells, heads of game animals, etc.) for decorating rooms and buildings. These objects are clearly not designed for that purpose (although they are presumably placed in strategic locations by design, in the sense of intent-design). A rock on a desk may function as a paperweight, but unless the rock has had a flat base chiselled into it, or other similar modification, it is not appropriate to say that this object was designed for the purpose of holding down papers. A taxidermist may design a ferocious pose for a stuffed grizzly bear; in this case the pose is designed to titillate, but it is not true to say that the bear was designed for this purpose. Thus, function does not entail design for that function.

Now consider (a). Knowing what something is designed for, one knows its (intended) function, even if the item does not and cannot perform that function. Prior to the 1903 Wright Flyer, many contraptions were designed for heavier-than-air powered flight, yet none of them flew. Modern aviation did not have to get off the ground (pun by design!) for it to be the case that the function of those remarkable contraptions was to fly. It *was* their function to fly because that is what they were designed (albeit poorly) to do. Biological functions are importantly disanalogous. Millikan is fond of pointing out that individual hearts (e.g., malformed or diseased ones) may fail to pump blood, but that these hearts would not have this function unless some of their predecessors had actually succeeded in pumping

blood. For a thing to possess a biological function, at least some (earlier) members of the class must have successfully performed the function. In cases of psychological design, the corresponding claim is not true. Such cases are called "deviant" or "marginal" by some authors (e.g., Wright 1976; Achinstein 1977; Van Parijs 1982). Nevertheless, they *can* arise in psychological teleology, but not in biological teleology.

**6. The Analysis of Natural Design.** These considerations about goal-driven design and function suggest two questions about the relationship of natural design to biological function: (1) Are there cases where it is appropriate to say that a trait is naturally designed for X even though it does not have X as a biological function?; and (2) Are there examples where it is appropriate to say that a trait has a certain biological function but is not a product of natural design for that function? Answers to these questions will, of course, depend on what account one gives of biological function and natural design. Accepting ND = F leads to the answer "No" in both cases. However, we believe that this result ignores an important distinction in evolutionary history. Our proposal is to analyze natural design according to this schema (Allen and Bekoff 1995):

> *Trait T is naturally designed to do X* if and only if
> (i)   X is a biological function of T, and
> (ii)  T is the result of a process of change of (anatomical or behavioral) structure due to natural selection that has resulted in T being more optimal (or better adapted) for X than ancestral versions of T.

Clause (i) should be understood according to the standard line, and it has the direct consequence that the answer to question (1) is that there are no cases where a trait is naturally designed for X even though it does not have X as a biological function. Clause (ii) is likely to be controversial because it involves the notions of optimality and adaptedness. The chief criticism of adaptationism in evolutionary biology is that it is Panglossian (Gould and Lewontin 1978)—i.e., it entails the belief that this is the best of all possible worlds. The "Panglossian Paradigm" is defended by Dennett (1983/1987), who claims that it involves an idealizing assumption about natural selection that is probably false, but that is necessary for making predictions using the theory of natural selection. Byers and Bekoff (1990) worry that arguments for optimality frequently involve logical errors and are bothered that in many cases empirical studies make an adaptationist assumption on the basis of inadequate empirical evidence.

Because it stresses *comparative* judgments, our clause (ii) avoids the charge that it is Panglossian. The required comparison is between the traits of extant organisms and the corresponding traits of their ancestors. For

instance, the wings of birds evolved from the forelimbs of their land-bound saurian ancestors. It is hypothesized that the lineage involves successive modifications of forelimbs into more aerodynamically efficient wings found in extant species of birds (ratites and penguins excepted). According to our analysis, to say that the wings of (most) birds are designed for flying is to say that (i) enabling flight is a biological function of birds' wings and (ii) extant morphological forms of such wings are the result of natural selection for variants that were better adapted for flying than earlier forms.

Comparative judgments do not require the Panglossian assumption. The claim that A is more optimal or better adapted than B with respect to some function does *not* entail that A is optimal or even good with respect to that function. A Rolls-Royce may consume more fuel per kilometer than a Cadillac, but it does not follow that the Cadillac has good, let alone optimal, fuel efficiency. (The theoretical optimum would be complete conversion of all the energy stored in the fuel into distance travelled.) This simple point about the logic of comparative statements is often overlooked. For example, during the confirmation hearings for U.S. Supreme Court Justice Clarence Thomas, one senator missed this point completely when he repeatedly claimed that Professor Anita Hill was being inconsistent by objecting to the nomination, given that she had told a newspaper that she thought Thomas would make a better Justice now than he would have done 10 years previously.

Clause (ii) is committed *only* to a *comparative* claim about traits. Thus, no statement about overall adaptedness or optimality is implied. Ruse (1993) draws a similar distinction between the notions of "comparative progress" and "absolute progress" (see also the contributions to Nitecki 1988). It would take us too far afield to discuss the notion of evolutionary progress here, but we are sympathetic to Hull (1988, 45) who claims that "biological evolution has not just [one] direction, but lots of them." In other words, there are many bases for comparison, no one of which can be singled out as an absolute standard. Claims about the natural design of wings are assessed by comparing ancestral forms with descendant forms with respect to effectiveness for the function of flying. Such comparisons can be very specific indeed. For example, the glide ratio of eagle wings can be compared to the glide ratio of the wings of eagle ancestors, perhaps the archaeopteryx. If an eagle's wings result in a higher glide ratio than its ancestors' wings and if having a higher glide ratio provides a comparative fitness advantage, then it can be said that the eagle's wings are designed for soaring. Other wings, e.g., those of hummingbirds, may be designed for other aspects of flying, e.g., hovering.

Because natural selection acts on variation within a population it may reasonably be compared to trial and error testing by human designers. Dennett's "Design Stance" approach to complex systems (Dennett 1971,

1983, 1987) also suggests this comparison. We reject, however, that the view that the legitimacy of the notion of natural design rests on direct comparisons to conscious design by psychological agents. Both biological function and natural design can be fully naturalized (without reference to psychological design).

Hypotheses about natural design are, however, more difficult to establish than hypotheses about biological function. Function, on our view, is neutral with respect to the phylogenetic pathway by which a trait acquires a function. Consider again the behavior of a hare confronted by a fox. Holley (1993) argues that this behavior's function is to indicate to the fox that it has been detected. According to the standard line on functions, Holley's hypothesis is justified if it is reasonable to believe that bipedal standing by ancestral hares had this effect on ancestral foxes, and this effect was (partially) responsible for the transmission of this trait from ancestral hares to descendants. A corresponding design claim about bipedal standing would, on our analysis, require showing that this trait is a direct modification of some ancestral trait that was less efficient with respect to its effects on foxes.

These considerations suggest an answer to question (2) above. A trait may have a biological function but not be naturally designed for that function (although it may be a product of natural design for some other function.) But because showing design is more difficult than showing function, examples are likely to be difficult to find. Gould's (1980) discussion of the panda's thumb provides an intuitively plausible example of a non-behavioral trait with a function—stripping bark from bamboo—for which it is apparently not designed given that the thumb apparently shows no special modifications for bark stripping, although the maintenance of this trait can presumably be (at least partially) explained by its contribution to bark stripping. However, the comparative evidence needed to support this claim is not readily available.

Our distinction between *design* and *function* is usefully contrasted with the widely discussed distinction between *adaptation* and *exaptation* introduced by Gould and Vrba (1982). An adaptation, on their view, is a trait that has been shaped by natural selection for some use; their notion of "shaping" appears similar to our clause (ii) above (and, incidentally, captures the element of change missing from Sober's definition). They reserve the term *function* for cases when such shaping has occurred (thus, like Sober, they conflate function and adaptation, although not in the same way as Sober). They introduce the neologism "exaptation" for cases where either a selected trait of an organism is coopted for a new use (e.g., the use of the tongue to modify speech sounds) or where a characteristic that is produced and maintained by mechanisms other than natural selection is coopted for a current use (e.g., the violinist's use of the chin to hold the

instrument). Exapted traits, according to Gould and Vrba merely have effects, they do not have functions. Millikan (1993, 45) notes that "[Gould and Vrba] are aware, of course, that [their] restriction on the term 'function' is stipulative and not just a reflection of general biological usage." Griffiths (1992) applies a version of the standard line on biological function to argue that Gould and Vrba mischaracterize the distinction between function and (mere) effect. He proposes to refer to "unshaped" traits with the right kind of selective history as "exadaptations" rather than adaptations and he proposes to use the term function in both cases. He does not, however, distinguish function from design. Thus our usage differs from both Gould and Vrba's (1982) and Griffiths' (1992) by distinguishing function from design, while it agrees with Griffiths' usage, but not with Gould and Vrba's, on the range of cases to which the notion of function correctly applies. Our view has the added advantage of not proliferating neologisms.

**7. Design vs. Function: An Ethological Example.** The distinction we have drawn between function and design is useful for understanding issues many issues in evolutionary biology. We will illustrate with an example from ethology; specifically we consider the evolution of communicative behavior. Many authors consider transfer of information to be a defining feature of communication (Allen and Hauser 1993). However it seems implausible to treat all information transfer equally as communication. Using the framework developed here, we distinguish three levels of information transfer.

First, the behavior of many organisms provides information even though it is not a biological function of that behavior to do so. For example, migrating birds may provide the information to humans that winter is coming. Plausibly, this effect of migration is not part of the selectional history that accounts for birds migrating. Thus this is a mere effect, not a function (and hence not something that migration is designed to do). Considerations such as these have led many biologists to include selective advantage in their definitions of communication (see, for example, Eibl-Eibesfeldt 1975; Drickamer and Vessey 1992; Alcock 1993); at the second level, then, are those behaviors that have transfer of information as a function. At the third level are those behaviors that have been modified over evolutionary history to better perform this function.

The classical account of the evolution of communicative signals is given by Tinbergen (1952) who considers them to be "ritualized" versions of "intention movements." An intention movement is understood to be a movement from which it is possible to infer what an organism is likely to do next. Ritualization is a process whereby specific features of such movements become progressively exaggerated. Ritualization of a movement is

considered likely when the benefits to an organism of conveying information about its future behavior exceeds the costs of doing so. For instance, conveying information about an intention to fight may be beneficial if it prevents the fight from occurring. In this way, for example, behavior patterns that convey information about the likelihood of fight and flight responses, such as the raising of hair due to a hormonal change, may become transformed via ritualization into differentiated expressive behaviors, e.g., hackle raising in dogs, that are clearer and less ambiguous than their ancestral forms (Eibl-Eibesfeldt 1975). Ritualization is the sort of change that would satisfy clause (ii) of our definition of natural design. If measures of communicative efficiency can be derived from notions such as clarity and lack of ambiguity, and if these measures can be applied to behaviors in the sequence from unritualized behavior to ritualized behavior, then it will be possible to assess the claim that ritualized behaviors are signals that are designed for communication. The chief methodological difficulty lies in comparing extant forms of a ritualized behavior to ancestral forms. However, if such comparisons can be made, it is reasonable to consider the possibility that some behaviors have a communicative function without being designed for communication, while other signals are specialized behaviors designed for communication.

**8. Methodology and Future Work.** On our account, to show that a trait T is naturally designed for some effect X, in addition to showing that X is a function of T one must also show evidence of structural changes in the phylogeny of T so that T is better suited for X than ancestral versions of T. This additional requirement can be very hard to meet, especially when the trait in question is a behavioral trait.

Relatively few anatomical traits fossilize, but fossils can be used to build models for comparison to descendant forms. For example, a model of archaeopteryx wings could be compared aerodynamically to the wings of modern birds. Paleontological evidence of soft tissue changes are extremely difficult to find. Nonetheless, it is sometimes possible to make inferences about soft tissue from fossils—for example, muscle arrangements can be deduced by noticing apparent attachment points on fossilized bones. Comparisons of contemporary species from different taxa can also sometimes be used to draw inferences about ancestral forms. Thus, for example, one might infer natural design in human lungs by comparing membrane oxygen transfer rates to those in the air sacs of certain extant fishes. Such inferences are necessarily very tenuous because they depend on many assumptions about the similarity of those fishes to the common ancestor of terrestrial vertebrates.

For behavioral traits, inferences about design are almost exclusively limited to the comparison of individuals from different extant species and

populations. Inferences to the phylogeny of behavior based on such comparisons are difficult but not impossible. For example, Golani (1992) proposes a scheme for characterizing movement patterns and gradients of movement differences across vertebrate species from different taxonomic groups. He hopes that examination of variations in shared movement patterns of vertebrates will allow specification of what he calls "the ground plan of vertebrate behavior" (ibid., 264). If such a project is successful, it might be possible to compare the relative effectiveness of variations in behavior for specific tasks. It might then be possible to draw further inferences about the evolution of complex behaviors, on which claims about behavioral design could be based. Many methodological difficulties remain unsolved, making this a prime area for future interdisciplinary, comparative research by biologists and philosophers.

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