

FUNCTION, NATURAL DESIGN, AND ANIMAL BEHAVIOR: PHILOSOPHICAL AND ETHOLOGICAL CONSIDERATIONS

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Abstract

This essay is on teleological notions in biology, particularly as they are applied to the study of behavior. Biologists and philosophers interested in the conceptual foundations of biology (biophilosophers) have been greatly concerned about the role of teleological language in evolutionary biology. We discuss the role of biophilosophy for understanding teleology in biology and explain why teleology is controversial in biology. We present an analytical survey of recent literature on teleology in biology, in the form of a classification tree. Much of this literature has focused on the notion of biological function. Currently, accounts that "naturalize" the notion of biological function by reference to natural selection are popular but some authors prefer other accounts, e.g., that functional claims metaphorically refer to psychological purposes and intentions. Few theorists have clearly distinguished the notion of biological function from the notion of natural design, apparently assuming that design can be assimilated to function. We argue that it is worthwhile to treat design separately from function and we consider the utility of this distinction for the study of behavior. We conclude that further work is needed on the methodological principles that allow claims about function and design to be based on comparative studies.

Introduction

1. FUNCTION, DESIGN, AND TELEOLOGY

In this paper we argue that biologists in general, and ethologists in particular, can benefit from adopting an analysis of the concept of *natural design* that distinguishes it from the concept of *biological function*. Examples of the use of *teleological* concepts such as function and design in biology include the following statements:

- A (biological) function of stotting by antelopes is to communicate to predators that they have been detected.
- Carid play bows are (naturally) designed to communicate to conspecifics that what follows is play.

Biologists and philosophers interested in the conceptual foundations of biology (biophilosophers) have been greatly concerned about the role played by teleological statements such as these in evolutionary biology. Consequently there is a substantial literature on biological teleology with contributions from both biologists and philosophers of biology. We believe that common objections to the use of teleology in science can be avoided because both biological function and natural design can be given analyses that are naturalistic, meaning that they do not appeal directly or indirectly to the motives of a conscious designer.

As a philosopher (CA) and an ethologist (MB) we initially brought rather different perspectives to bear on the topics of function and design, but after working through the enormous contemporary literature on biological teleology our views have converged on a number of points. In an earlier paper (Bekoff & Allen 1992) we mentioned two different notions of function, one based on the notion of natural selection (Millikan 1984) and another based on the analysis of interacting parts of complex systems (Cummins 1975). In that paper we left these two different notions in tension with one another. However, we now believe that both notions have a role to play in biology (see also Millikan 1989; Godfrey-Smith 1994). These two notions comprise only a fraction of the different views to be found in the contemporary literature. By classifying the large range of positions we found that we were able to bring our own views into sharper focus. By including a full survey of the views we encountered we hope to have provided a tool that will allow our readers to bring their own views into similar focus. The survey also provides the background for our argument for the pluralistic view we have adopted.

Our earlier work had led us to endorse naturalistic accounts of function. In particular for understanding most but not all functional claims in biology, we prefer an etiological (historical) natural selection account, such that a function of a trait is an effect of the trait that has contributed (in ancestral populations) to the preservation of the trait (in descendant populations) via the differential survival and reproduction of entities with that trait. In contrast, we were initially skeptical about the notion of natural design on the grounds that the idea of design without a designer could at best be a metaphor. We also found that the contemporary literature on teleology is heavily skewed towards discussion of biological function, with relatively little direct attention to natural design. We believe that this is because most authors either accept our initial view about the metaphorical status of statements about design, or they simply assimilate the notion of natural design to the notion of biological function. We have come to believe, however, that neither of these positions is correct. Statements about natural design in the absence of a

designer are neither metaphorical nor equivalent to statements about function. This paper, then, is an extended argument in favor of a naturalistic analysis of the concept of natural design that does not assimilate it to the notion of function. On our view, it is possible for a trait to have a biological function without being designed for that function, and we believe this is an important distinction to make in understanding the evolution of behavioral phenotypes.

In Part One we explain the methodological principles underlying the application of philosophical analysis to help understand the notions of *biological function* and *natural design*. With these methodological principles in hand, in Part Two we discuss why teleological notions are controversial in biology, and argue that ethologists stand to benefit from the greater clarity provided by more careful analysis of these notions. In Part Three we aim to provide this more careful analysis in the form of an extensive survey of the recent literature on biological function. In particular, we try to identify the relationships among the various theories of biological function that have been proposed, and we try to show how these theories relate to empirical concerns in the study of animal behavior. This complete survey of views on function allows us to argue in Part Four for an account of natural design that makes it neither metaphorical nor equivalent to function. In our view natural design entails both possession of biological function and a history of progressive structural modification under natural selection for improved performance of that function. Our view and its application to ethological examples are discussed in full detail below. The advantages of this perspective for ethologists include greater clarity about the methodological requirements for justifying teleological claims, and a useful framework for representing different aspects of the selective history of behavioral phenotypes.

2. DEFINITIONS

Before proceeding to implement the strategy just outlined, it is necessary to say something about definitions of key terms, such as *function*, *design*, and *teleology*, and others that will be introduced in subsequent sections. Some readers may feel dissatisfied with our practice of introducing such terms through examples of their use without providing *explicit* definitions for them at the beginning of the paper. Although we do believe that definitions have a role to play in the practice of science, we believe that much of the emphasis on defining key terms in behavioral biology is misguided. Allen & Bekoff (1993) address this topic in some detail but we summarize the main points here (see also Moore 1993 p.595).

The practice of giving explicit definitions in the behavioral sciences has its roots in the frequently-deserved behaviorist criticisms of 19th century comparative psychology (see especially Watson 1930). One result of the criticism directed at the earlier excesses of comparative psychologists is the tendency among many students of behavior to want to specify precisely what they are talking about before presenting empirical results. The lingering influence of behaviorism is beneficial insofar as definitions may facilitate the design and subsequent interpretation of experiments. Definitions may also facilitate communication between scientists. Such definitions are best regarded as working definitions -i.e. rough guides to the phenomena under investigation- that can be revised in response to empirical discoveries and theoretical endeavors. Scientific rigor does not come via precise a priori specification of the concepts used to pick out the examples, but in precise application of experimental techniques to compare and contrast putative examples with respect to observable characteristics. Working definitions and

other means of specifying the conceptual commitments of a given theoretical apparatus serve as important catalysts to the formulation of empirical questions (Bekoff & Allen 1992). However, such working definitions ultimately do not determine the extensions of the concepts they purport to define.

In this paper our goal is to investigate the boundaries of concepts associated with the terms *biological function* and *natural design*. We think it would be a mistake for us to start by stipulating definitions for those terms because such definitions would distract attention from the variety of analyses of function and design that have been offered in the literature. Stipulative definitions at this point in the paper might incorrectly suggest that these terms should be given univocal senses--there may, for example, be room for more than one notion of function in biological explanation (Millikan 1989; Godfrey-Smith 1994).

With these caveats in place, we will say that we favor a working definition of biological function that identifies the functions of traits as those effects of traits that contributed to the differential survival and reproductive success under natural selection of organisms possessing those traits (although we also allow that there may be room in biology for more than a single notion of function). With respect to *natural design* we favor a much more specific definition in terms of adaptive modification of anatomical or behavioral structure that sometimes, but not always, results from natural selection. For example, on our account one function of dogs' paws is to scratch fleas, but we would not say that the paws are designed for scratching fleas, unless they are specially adapted for this purpose (cf. Gould 1980 on the panda's thumb). Our usage of the terms *effect function*, and *design*, is summarized in Table 1, but we postpone a full discussion of these issues until Part Four.

Part One: Philosophy and Biology

1. BIOPHILOSOPHERS AND BIOPHILOSOPHY

Philosophy of biology is simply the attempt to theorize about the conceptual and methodological foundations of the biological sciences. It is equally the domain of theoretically oriented biologists and biologically oriented philosophers. Unfortunately the phrase "philosopher of biology" tends to connote a philosopher who studies the foundations of biology when it equally applies to biologists who study those foundations. So, at the risk of proliferating neologisms, we will use the term *biophilosopher* to indicate anyone who theorizes about biology in this way. Thus Marc Bekoff (or Ernst Mayr) is as much a biophilosopher as Colin Allen (or Ruth Millikan). *Biophilosophy* is the characteristic activity of biophilosophers.

Analysis of the concepts and methodological foundations of biology is essential for identifying the theoretical commitments required by particular biological theories. This in turn supports the explicit formulation of alternative hypotheses and methods for testing those hypotheses. Biophilosophy is not to everyone's taste, but neither is field or laboratory work, or mathematical or computational modeling. All, however, are essential aspects of a complete science and there is much to be gained from interaction between those with different interests.

2. REFORMERS AND ELUCIDATORS

Among other things, biophilosophers are interested in the proper interpretation of claims made by practicing biologists (just as philosophers of physics are interested in the proper interpretation of physicists' claims about quantum mechanical phenomena). Interpreters may be broadly classified as either *reformers* or *elucidators*. *Reformers* sometimes attribute conceptual confusion and false or meaningless pronouncements to the practicing scientists and use this to argue that biologists should alter (they might say "improve") the practices that result in such claims. *Elucidators* take the statements made by biologists about their work more or less at face value--i.e. as true or appropriate statements. Elucidators regard their task as providing a coherent analysis of these statements.

Because biophilosophical arguments are often a priori in nature, because philosophers often seem more prone to being reformers than elucidators, and because reformers sometimes challenge the authority of biologists to make certain claims, many biologists dismiss biophilosophy. Elucidation is generally more palatable to the practitioners of the science because it does not involve questioning their expertise. The (complicated) truth of the matter is that all intellectual endeavors--including philosophy itself--stand in need of both reform and elucidation. In this paper we try to balance elucidation of teleological notions in biology against occasional reformative comments.

3. BIOPHILOSOPHERS MAKE USEFUL DISTINCTIONS

The literature on biological teleology contains a number of independent distinctions that are useful for organizing ideas about the role and importance of teleological notions in biology. We describe two distinctions here that provide a background for the distinctions covered in the third part of this paper.

LITERAL OR METAPHORICAL: Are the teleological claims made by biologists to be interpreted literally or metaphorically? If, on the one hand, the claims are to be interpreted literally, then it is necessary to provide an account of their truth conditions that can then be used to evaluate the truth or falsity of particular teleological claims. Most such accounts rely on the process of natural selection to provide the relevant truth conditions, but different accounts exploit natural selection in different ways. If, on the other hand, teleological claims in biology are to be interpreted metaphorically, then the basis for comparison needs to be identified. The most common version of this view regards teleological claims in biology as inviting comparison to teleological claims about artifacts that are based on the psychological intentions and purposes of the human beings who design and use them.

ESSENTIAL OR HEURISTIC: Is the use of teleology in biology essential for understanding living phenomena or is it merely a heuristically useful way of organizing information that could be described and explained non-teleologically? Many biophilosophers believe that understanding living organisms requires a pattern of explanation that is fundamentally different from the forms of explanation found in physics and the other natural sciences, and that the use of teleological explanations provides a case in point. For example, despite being critical of much use of the concept of adaptation Williams (1966 p. 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 biology." This is opposed by those who believe 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" (Nagel 1961/1984 p.346). Those who view teleology as inessential to biology often point to the history of physics for justification. Aristotelian physics made free use of teleological notions, but these were eliminated by Galileo. Proponents of the view that physics sets the standard for scientific rigor often believe that teleology in biology is destined to go the same way. Nonetheless, proponents of this view may recognize the heuristic value of teleological notions for organizing thoughts about the complex phenomena associated with living organisms subject to natural selection.

Part Two: The Usage of Teleological Notions

1. TELEOLOGICAL CLAIMS

A large and diverse literature on the appropriateness of biological teleology has accumulated during the second half, and especially the last quarter, of the 20th century. Despite the substantial number of theoretical articles and text book discussions of biological function by biologists and philosophers, it is relatively difficult to find explicit claims about function (e.g. "the function of X is Y") in articles where mainly empirical data are reported. For example, in presenting their work on antennal contacts among ants, Gordon et al. (1993) raise the question "What is the function of encounter patterns in ant colonies?" in the title of their paper. Yet these authors nowhere come out with an explicit claim that the function of antennal contacts is such and such. The closest they get to such an explicit statement is to 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." From this statement it is easy to construct a functional claim about antennal contacts, but the authors exercise notable caution in avoiding making such a claim explicitly.

English provides a variety of ways for making *implicit* functional claims without using the word "function" (Van Parijs 1982). While *explicit* claims about function are relatively rare in the empirical literature, implicit functional claims are not (e.g. Alcock 1993; Drickamer & Vessey 1993). For example, in their discussion of the classic work done by Tinbergen and his colleagues on eggshell removal in black-headed gulls, Drickamer & Vessey (1993, p.23) note that one plausible hypothesis is that "Parents remove white eggshells to protect their young", clearly they could just as well have said that for these birds a function of eggshell removal behavior is protection of offspring. Likewise, Holley (1993 p.21) in his analysis of the bipedal stance that brown hares assume when confronted by red foxes writes: "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." This clearly suggests that on the author's view a function of standing erect by brown hares is to deter pursuit by foxes.

Explicit claims about *design* are even more difficult to find in the empirical literature than claims about *function*. This may also partially account for the greater amount of attention paid to

functions in the theoretical literature. Claims about design may be off-putting because they suggest a strong directional component in the evolution (or development) of a behavioral phenotype (R. Dawkins 1986). Many scientists object to statements of the form "X is designed to accomplish some goal", but they do not seem so opposed to similar statements about function ("the function of X is Y"). However, for example, the idea that play signals may be designed to initiate and to maintain social play has been hinted at for numerous mammals, and the notions that play is developmentally scheduled and that sequences of play are designed in terms of their structure (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) to fulfill certain functions, especially practice, has also been suggested (e.g. Rasa 1973; Bekoff 1977, 1982, 1988, 1989a, b, 1993; Leyhausen 1979; Bekoff & Byers 1981; Fagen 1981; Martin & Caro 1985; Hass & Jenni 1993; Pellis 1993; Watson & Croft 1993). Pellis (1993) notes that the structural features of social play (the behavior patterns that are used, how they are combined, and the body areas to which they are directed) in many murid rodents does not resemble play-fighting, but rather sexual behavior. Further empirical study in animals representing wider taxa is needed to assess Pellis' novel ideas about how the resemblance of play to sexual rather than to aggressive behavior might inform discussions of function and design.

2. CONTROVERSY ABOUT TELEOLOGY

As the large theoretical literature attests, teleological notions are controversial in their application to biology. But as the examples drawn from empirical papers suggest, biologists have found it difficult and even undesirable to eliminate teleological notions from their discussions of biological phenomena. Teleological notions are controversial for a number of reasons. They were associated with pre-Darwinian, creationist views about organisms, and were roundly rejected by many post-Darwinian biologists as either (i) vitalistic, (ii) incompatible with mechanistic explanation, (iii) requiring backwards causation, or (iv) mentalistic (Mayr 1974/1988 p.40). To Mayr's list we would add a fifth category of methodological concerns about the empirical testability of teleological claims. These categories are not fully independent. For instance, if teleology required backwards causation from the future then it would be incompatible with mechanistic explanation which allows only forward-directed causation to occur, and would surely entail methodological difficulties also.

Vitalism and creationism are no longer serious worries for most biologists, but the other categories still provide forceful concerns. In the face of such concerns there is an obvious tension between the seemingly indispensable use of teleological notions and the problems such notions raise. *Put concisely, the challenge is to fit teleology into a naturalistic framework*. In section three of this paper we examine attempts to meet this *naturalistic challenge* for the notion of function, and in section four we focus on the notion of design.

3. TELEOLOGY IN PSYCHOLOGY AND BIOLOGY

Besides biology, psychology is the other major locus of teleology in science. Psychological behaviorists made teleological notions such as purpose, goal, and intention controversial in psychology by calling attention to methodological problems with their application. The revival of the cognitive sciences has made these and related notions respectable again in cognitive

psychology, artificial intelligence, and other cognitive sciences. Cognitive ethologists believe in the usefulness of such notions for understanding the behavior of non-human animals--e.g., for revisiting old data and for informing and motivating new studies--but this remains controversial (Griffin 1981, 1984; Bekoff & Allen 1994). Numerous methodological issues in cognitive ethology remain to be worked out but there is considerable interest in cognitive ethology nonetheless (Griffin 1981, 1984, 1992; Cheney & Seyfarth 1990, 1992; Allen & Hausser 1991, 1993; Ristau 1991; Allen 1992a,b; Bekoff & Allen 1992, 1994; Bekoff & Jamieson 1990a,b; Jamieson & Bekoff 1993).

Mayr's fourth category of concern about biological teleology--that it is mentalistic--derives from the view shared by many that all teleological notions are rooted in psychological notions such as intention and purpose. It is important, however, to be clear about the significance of this for the interpretation of current teleological claims in biology. As Cummins (1975/1984 p.400, fn.19) puts it: "Functional talk may have originated in contexts in which reference to intentions and purposes [of designers and users] loomed large, but reference to intentions and purposes does not figure at all in the sort of functional analysis favored by contemporary natural scientists." If Cummins is right that reference to psychology *does not figure at all* in current biological teleology, then the naturalistic challenge must be met by providing a non-psychological (or non-mentalistic) basis for understanding teleological claims in biology. This is the approach that we favor, but we survey alternative views in part three below.

4. FUNCTION AND ADAPTATION

Only rarely do ethologists or behavioral ecologists give the notion of function the detailed consideration that it deserves (but see Hinde 1975; Wenzel 1992; West-Eberhard 1992). In his classic paper published in 1963, Tinbergen identified four major areas with which ethological studies should be concerned, namely, evolution, causation, adaptation (or function), and development. Most ethologists and behavioral ecologists follow Tinbergen (1951/1989, 1963) in identifying function with adaptation. (See for example Marler & Hamilton 1966; Brown 1975; Elbl-Eibesfeldt 1975; Manning & Dawkins 1992; Alcock 1993; Drickamer & Vessey 1993.) If successful, Tinbergen's identification of adaptation and function would go some way towards addressing the naturalistic challenge, but there remain several issues that need clarification.

One problem with identifying function and adaptation is that not all authors operate with the same notion of adaptation. Some authors seem to use the term "adapted" as a synonym for "designed". Other authors seem to use "adapted" and "selected" interchangeably. We argue in Part Four below that selection, function, and design are distinct notions. Given the variety in usage of these terms, there is considerable potential for confusion. Other issues also require clarification. For example, functional explanations generally appeal either to ways in which *past* social and nonsocial environments supposedly affected performance and selection of various behavioral phenotypes, or to ways in which *current* environments influence performance and selection of phenotypes. (For examples with respect to play see: Berger 1979, 1980; Bekoff & Byers 1981; Fagen 1981; kin recognition/discrimination: Byers & Bekoff 1986; Fletcher & Michener 1987; Blaustein et al. 1991; Hepper 1991; the evolution of sociality and group-living: Wilson 1975; Bertram 1978; Bekoff et al. 1984; Alcock 1993; fish schooling: M. Dawkins 1986; anti-predator vigilance: Curio 1978; Quenette 1990; Bekoff 1993; humor and laughter: Westfeldt

1993.) In their discussions of function or adaptation, ethologists and behavioral ecologists rarely make a clear distinction between past, current or future selection effects on phenotypes (Mitchell & Valone 1990; but see Reeve & Sherman 1993). In Part Three of this paper we discuss this distinction further.

Another issue is that the notion of adaptation itself appears to have teleological connotations because it often involves the idea of a phenotype being optimal, suitable, or satisfying, for some particular purpose or goal (Dennett 1983/1987). It would obviously be unsatisfactory to explicate one teleological notion (function) in terms of another (adaptation), so further analysis of the notion of adaptation is necessary. Sober (1984a, 1993) offers an analysis of adaptation in terms of selection (Sober 1993, p.84): "Characteristic C is an adaptation for doing task T in a population if and only if members of the population now have C because, ancestrally, there was selection for having C and C conferred a fitness advantage because it performed task T." Sober's definition is widely accepted by biologists (but see Reeve & Sherman 1993 for dissent).

When studying behavior, trying to provide detailed and convincing information relating function to variations in individual fitness is fraught with difficulties (M. Dawkins 1986), although such attempts can be fruitful (West-Eberhard 1992). Furthermore, as M. Dawkins (1986) points out in her discussion of the adaptive significance of echolocation in bats, one can produce a convincing story without using any information about differential reproductive success whatsoever. Also, Thomas (1993) discusses the aerodynamics of birds' tails and shows how simplistic or univocal functional explanations can be inadequate for explaining how morphology influences behavior patterns such as female choice. In the absence of clear methodological guidelines, functional claims made on such a basis are likely to remain controversial. The importance of an adequate methodology is underscored by criticisms of the empirical testability of adaptationist claims (Gould & Lewontin 1979).

Ethologists and behavioral ecologists need to be clear about what they mean by the term "function" and other teleological terms. So too do neuroethologists (Bekoff 1986; DiDomenico & Eaton 1990; Ferhess 1991; see also Fatz 1992). By providing a thorough investigation of the conceptual issues underlying the variety of views about function and design we hope to provide guidelines for future theoretical and empirical work on function and design.

5. FUNCTION OR FUNCTIONS?

Throughout this paper we are careful to write about *a* function or the functions of a trait to avoid implying that any trait has a unique function. Many authors do not make this distinction, often appearing to imply that a given trait has just one function when multiple functions are likely or possible. For example, Dreiske (1986) states that "It is the function of one's eyes to tell one what *the clock says* [his italics]; it is the function of *the clock* to say what the time is." Likewise, Gordon et al. (1993) ask "What is the function of encounter patterns in ant colonies?" rather than "What are the functions of...?" Dreiske has agreed (personal communication) that he should have described clock-reading as *a* function of eyes. Several of the authors quoted below would probably make similar claims about their own uses of the definite article "the".

A related issue is the question of whether any of a trait's functions can be considered its PRIMARY function. For example, Kitcher (1994 p. in press) claims that "feathers were apparently originally selected in early birds (or their dinosaur ancestors) for their role in thermoregulation; after the development of appropriate musculature (and other adaptations for flight) the primary selective significance of feathers became one of making a causal contribution to efficient flying." A satisfactory notion of primary function would require a specific indication of how one determines that one function is primary over another—for example, how would one determine that the contribution of feathers to flying is more important than their contribution to thermoregulation or to communication? Kitcher provides no indication of how to make such judgements, but presumably one could base them on the relative contribution to overall fitness. However, such relative judgements are extraordinarily difficult to make (Lorenz 1981; M. Dawkins 1986). Nothing we say about function in this paper hinges on the notion of a primary function, so we will avoid making claims that would imply that any function of a trait is the primary function of that trait.

Part Three: Analysis of Views on Teleology in Biology

1. SURVEY STRATEGY: A CLASSIFICATION TREE

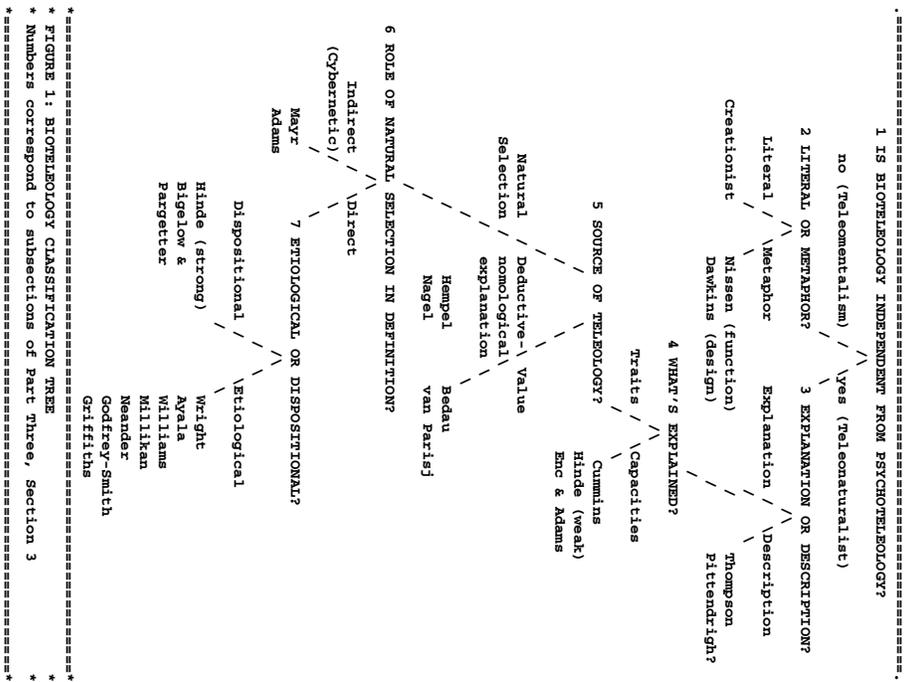
There are many points of contact between the biological and philosophical literatures on biological teleology but there is considerable disunity. For example, Mayr (1988, p.63) complains "I am rather amused to notice that Nagel's [1977] rebuttal of my ideas [Mayr 1974] has been cited with approval in several recent papers in philosophical journals, but not one of these philosophers descended to discuss or even list the paper of the biologist whom Nagel had criticized." We hope that our systematic survey will help to bridge the gap between the biological and philosophical literatures. To our knowledge, this kind of survey has not been done before (but see Mitchell 1994 for a comprehensive historical survey covering some of the same ground).

Our survey is presented in the form of a classification tree (Figure 1). Each node in this tree represents a particular question about the role of teleological notions in biology and each branch in the tree represents a particular response to the corresponding question. We have tried to locate many of the participants in the biophilosophical debate about teleology at a particular leaf in the tree. It is important to note that by focusing on different respects for similarity and difference it would be possible to produce different classification trees for these authors, but we believe ours is a useful organizing tool nonetheless.

The subsections of section 3 below correspond to the nodes in the tree. Each subsection is headed with the question defining that node, contains a brief description of the answers to that question, and is followed by a discussion with references to the relevant literature. It is possible to read the subsections below omitting the discussion of literature but still getting a self-contained description of our classification tree.

2. THE STANDARD LINE ON BIOLOGICAL FUNCTIONS

Although the tree in Figure 1 is intended to classify views on biological teleology much of the literature, hence much of our discussion, focuses on the notion of biological function. We contrast many of the views on function covered below with a view we label "The Standard Line" on functions. *According to the standard line, a trait's function or functions causally explain the*



existence or maintenance of that trait in a given population via the mechanism of natural selection. Three components of the standard line can be usefully separated:

- (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.

Some variant or other of the standard line is held by most but not all biophilosophers. Variants of the standard line differ mostly over how to make the component (2) above 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 & Vrba 1982; we discuss their distinction between adaptation and exaptation below in Part Four section 4). Alternatives to the standard line reject one or more of the components of the standard line.

3. ANALYTICAL SURVEY OF THE LITERATURE

Subsection numbers and titles correspond to the numbers and titles of the nodes in Figure 1. Answers correspond to the labeled branches of the tree.

3.1 IS TELEOLOGY IN BIOLOGY INDEPENDENT OF TELEOLOGY IN PSYCHOLOGY?

NO (TELEOMENTALISM): We classify those who answer the question in this way as *teleomentalists*; meaning that they regard the teleology of psychological intentions, goals, and purposes as the primary model for understanding teleology in biology. Teleomentalists interpret teleological talk literally only when conscious agents are involved. On this view, for example, the claim that a function of a rock on a desk is to act as a paperweight is literally true only if it was placed there because someone consciously intended it to keep the papers in place. Teleomentalists hold that teleological claims in biology should either be literally interpreted because of the involvement of psychological entities in biology or that they should be understood as making only metaphorical claims on the basis of more or less loose comparisons to psychological teleology. This is discussed further in the section 3.2.

YES (TELEONATURALISM): Those who answer the question in this way are labelled *teleonaturalists*; meaning that they seek naturalistic truth conditions for teleological claims in biology that do not refer to the intentions, goals, or purposes of psychological agents. Teleonaturalists are concerned with interpreting teleological claims in biology in a way that avoids the criticisms mentioned by Mayr (Part Two, section 2). Such interpretations are constrained to explain the truth and utility of teleological claims in biology using only vocabulary that is uncontroversial in the rest of biology. In other words, teleonaturalists adopt the strategy reducing teleological statements about biology to equivalent non-mentalist statements using terms

acceptable to the natural sciences. This strategy divides into many different substrategies depending on the answers one gives to various important questions about the role of teleology within biology, including but not limited to: Are such claims explanatory or merely descriptive?; and: if they are explanatory, what are they intended to explain? These and other questions define the nodes on the right hand side of the tree in Figure 1.

Discussion

For present purposes we are contrasting mentalism about biological teleology with naturalism about biological teleology, but this does NOT imply that mental concepts cannot themselves be naturalized. The question of whether it is possible to naturalize the mind can be considered independently of the question of whether biological teleology can be naturalized. In this paper we are concerned with the latter question, although it is worthwhile to note that several contemporary philosophers of mind, especially Millikan (1984, 1993), argue that many psychological concepts, such as thought, belief, and intention, are biological concepts. Millikan's strategy for naturalizing the mind is to provide a naturalized account of biological teleology and then to show how to reduce claims about mental states to biological teleology. Millikan is therefore committed to providing what we are calling a teleonaturalistic (non-mentalist) account of biological teleology otherwise her account would be blatantly circular.

As remarked above, most discussion of teleology in biology focuses on functions, but one might have different opinions about the proper interpretation of different teleological notions. To anticipate a point we will develop more fully in Part Four below, in psychological cases one can think of items with functions that have not been designed to perform those functions--for example a rock on a desk may have the function of keeping papers in place without having been designed for that function. If the notions of function and design can be distinguished for psychological teleology, it is plausible to think the same might be true of biological teleology. So it might be reasonable to take a mentalist line, say, towards the notion of natural design while taking a naturalistic line towards the notion of function.

Among biophilosophers, teleomentalism is a minority view (Nissen 1993), although it appears to be somewhat more entrenched among philosophers who do not work in biophilosophy. However, some biophilosophers do seem inclined towards teleomentalist positions. Because teleonaturalism has attracted more attention than teleomentalist approaches to teleology in biology, correspondingly more variations of teleonaturalism have been put forward. This is reflected in the greater number of branches on the right side of Figure 1.

3.2 TELEOMENTALISM: IS THE PRIMARY ROLE OF TELEOLOGICAL CLAIMS IN BIOLOGY LITERAL OR METAPHORICAL?

LITERAL: This is the view that teleological claims about organisms are best understood as literal claims based on either the internal psychology of those organisms or some external source of psychological teleology. Creationists are the most vociferous *external* teleomentalists, taking claims about function and design in nature to be literally true because of the explicit intentions and purposes of a divine being (but see Plantinga 1993 for a more sophisticated defense of this view). Although such views were preeminent before widespread acceptance of Darwin's ideas,

we shall ignore them here (but see R. Dawkins 1986 for an extended refutation of this version of literal teleomechanism). *Internal teleomechanists* take teleological claims to be true only if the organisms themselves have sufficient psychological complexity. When applied to organisms that appear to lack the relevant psychology, internal teleomechanists are inclined to regard teleological claims as literally false.

METAPHORICAL: Metaphorical teleomechanists maintain that teleological claims in biology invite explicit comparison to paradigm psychological cases of function and design. Because metaphors are never precise, this account of teleology in biology accords heuristic value at best to teleological claims. At worst, those who believe teleology in biology to be metaphorical regard it as too imprecise and misleading for scientific purposes.

Discussion

Richard Dawkins (1986) seems to adopt a metaphorical teleomechanist approach to natural design when he subtitled his book "why the evidence of evolution reveals a universe without design", and throughout the book often places scare-quotes around the word "design" and writes about "the illusion of design". According to Dawkins, there isn't really a designer, it just looks as if there is. A teleomechanist about design might agree that there isn't really a designer but maintain that nonetheless claims about design can be given a literal interpretation. Beer (1975 p. 16) approvingly quotes Bowly (1969 p. 125): "In *biology* that consequence which a system appears as though designed to achieve is usually termed the system's "function"". Here the phrase "as though" admits that design or a designer is not really present, although the functions might really be present, indicating that Bowly and, by association, Beer might be metaphorical teleomechanists with respect to design but hold a different view with respect to the notion of function.

Both non-creationist literal teleomechanism and metaphorical teleomechanism seem to suggest that teleology is not essential to biology, because it is either false or of solely heuristic value. Thus the more plausible versions of teleomechanism seem incapable of *elucidating* biological teleology in the sense explained above (Part One, section 2)—i.e. of explaining the truth of teleological claims in biology. In his argument for a literal teleomechanist position, Nissen seems to recognize this point when he says (1993 p. 48): "There remains the problem of accommodating goal-directed behavior of organisms believed not to have the requisite mental life to be the source of the needed intentionality." Nissen's "solution" is to claim that teleological statements about "lower organisms" (p. 48) imply an external source of intentionality where none is present and that this "is the only analysis that explains why teleological language remains controversial in the life sciences" (p. 48). Here, Nissen simply fails to take teleological claims about, for example, the behavior of ants at face value, i.e., as appropriate and true but entailing no connection to psychological intentions. It is our view that certain claims about the functions of ant behavior *are* appropriate and literally true, and that teleomechanism has no hope of explaining this. Thus, for the elucidation of teleological claims in biology, teleomechanism appears to be the only game in town (see also Wimsatt 1972; Bedau 1990).

3.3 TELEONATURALISM: ARE TELEOLOGICAL CLAIMS IN BIOLOGY EXPLANATORY OR MERELY DESCRIPTIVE?

EXPLANATORY: According to this view, teleological claims in biology both describe and explain certain phenomena, although opinions vary about exactly what is explained. According to the standard line about functions, the target of functional explanations in biology is the presence of the trait in a population of organisms. Not all explanatory views of functional claims agree that this is the target. Alternatives are discussed in later sections.

DESCRIPTIVE: The descriptive view of teleological claims in biology is that they apply to observable patterns displayed by biological phenomena independently of whatever (hidden) mechanisms are causally responsible for those patterns and hence independently of any particular explanation of those patterns. The descriptive account is discussed in the remainder of this section.

Discussion

According to the standard line (section 2 above) the use of teleological notions is causal-explanatory. For example, attributing the function of pumping blood (and not making noise) to vertebrate hearts is to say that vertebrates have hearts *because* hearts pump blood (and not because they make noise); likewise, dogs perform play bows *because* play bows serve to communicate that what follows is play (and not because play bows bring the performing animal's abdomen closer to the ground). Thus, the fact that hearts (normally) pump blood is cited to explain the presence of hearts and the fact that play bows (normally) communicate that what follows is play is cited to explain the presence of play bows among canids.

The philosophy of science literature on causal explanation is far too immense to summarize here, but for the sake of specificity it is sufficient to think of a causal condition as a required member of a set of sufficient conditions for the production of a specified effect (Mackie 1965; see Eells 1991 for an alternative probabilistic account of causation). Most biophilosophers identify natural selection as the causal mechanism through which functions operate, but this is by no means the only version of the causal account as indicated in Figure 1 and discussed in subsequent sections.

Thompson (1987) has argued that teleological claims should be regarded as descriptive and not explanatory. Thompson focuses on what he calls the "misappropriation" of Pitendrigh's (1958) term *teleonomy* for explanatory purposes. The use of the term "misappropriation" suggests that Thompson's aims are reformative rather than elucidatory according to our classification scheme (Part One, section 2). Thompson (1987, p.273) defines teleonomy as "the descriptive study of organizational properties of processes and structures without reference to any particular explanatory system." He worries that unless the teleological and adaptive aspects of biological systems can be described independently of natural selection, teleological claims are explanatorily circular, and he argues that several biophilosophers, perhaps including Pitendrigh himself, have failed to avoid this circularity. For the descriptive view of biological teleology to be fully developed it would be necessary to give a naturalistic analysis of the meanings of teleological claims, e.g., of what it would mean to say (in the purely descriptive sense) that a function of vertebrate hearts is to pump blood. Lipton & Thompson (1988b p.238) say that "identifying these properties in

organisms in nature independent of their explainers is not easy but it is surely not impossible. The key is the comparative method." Precisely how a comparative method would support descriptive application of teleological terms is a topic that requires further investigation.

Thompson and Lipton are not alone in worrying about the possible circularity of teleological explanations. For example, Lorenz (1981 p.211) says "To call a function by a name stemming from its teleonomic effect is, in itself, permissible, provided that one remains aware of the danger this name may, as John Dewey pointed out, insidiously raise the false pretension of being an explanation for the function it describes." The paradigm of explanatory circularity is presented by the doctor in Molliere's *The Imaginary Invalid* who explains that a drug puts those who take it to sleep because of its "dormitive virtue" (see also discussion by Lipton & Thompson 1988a). This is a causal explanation--that is, the power of the drug to cause a particular effect is explained by citing a property it possesses. The property in this case is none other than the power to cause the specified effect, hence the circularity. In general, to avoid circularity, causal explanations must provide independent specifications of cause and effect. Thompson expresses his worry about circularity by saying that biologists tend "to use the concept of teleonomy to refer to the properties of things and then later, as part of the same argument, to use it to refer to the causes of things." (1987, p.272) Lipton & Thompson (1988a,b) argue that when carefully applied, explanations in terms of adaptation by natural selection are explanatorily valuable and they are not circular but "recursive". However Thompson and Lipton worry that many biologists are not careful in applying teleological notions and thus fall into the trap of circular explanation.

Our aim here is primarily expository rather than critical, but it is worth pointing out why we think the worry about circularity is overwrought. Something like the standard line about functions--that they explain the presence of traits--is the target for the charge of explanatory circularity. There would be a patent circularity if for a given trait one cited the trait's function to explain *the trait's function*. But, in our example of the heart given above, the standard line is that the heart's function is cited to explain the presence of hearts. On the surface at least, this does not have the patently circular form just mentioned. Now, if hearts were identified only as "organs with the function of pumping blood" the circularity charge might be made to stick. But anatomists identify organs morphologically and then ask whether those organs have any functions. Despite complaints to the contrary, it *is* genuinely informative to be told that a morphologically identifiable organ is present in a class of organisms because, for example, it pumps blood and not because it makes thumping noises. A similar point can be made about the identification of species-typical behaviors in terms of behavioral structure. Such identification can occur prior to investigation of functions of the behaviors thus identified (but see Millikan 1993 for discussion). Thus the charge of circularity does not seem to work against the standard line. For similar reasons the charge also does not work against some of the alternative views of function described below.

3.4 WHAT IS THE TARGET OF EXPLANATION FOR TELEOLOGICAL CLAIMS IN BIOLOGY?

THE PRESENCE OR MAINTENANCE OF TRAITS IN A POPULATION: According to this view, teleological claims about traits of organisms explain the presence (original fixation or maintenance) of those traits in a given population. This is the position adopted by the standard line, but some alternatives to the standard line also adopt the presence of traits as the explanatory target.

THE ROLE OF TRAITS IN COMPLEX SYSTEMS: According to this view, teleological claims about traits of organisms explain the role of that trait in a larger system. With respect to the notion of function, to attribute a function to a trait is to say how that trait contributes to a more complex capacity of an organism. On this view, for example, attributing the functions of providing lift and propulsion to a bird's wings helps to explain how wings contribute to the bird's capacity to fly.

Discussion

The view that teleological claims explain the existence of traits is a part of the standard line that is common among biologists. For example, Ayala (1977 p.498) says "Teleological explanations account for the existence of a certain feature in a system by demonstrating the features contribution to a specific property or state of the system." Many philosophers of science have also accepted this view of the target of teleological explanation and tried to fit it into their preferred accounts of scientific explanation.

During the middle part of the 20th century, the deductive-nomological (or hypothetico-deductive) account of scientific explanation dominated philosophy of science. According to the deductive-nomological account, the proper form of an explanation is a deductive argument where the target of explanation (or *explanandum*) is a logically valid consequence of general statements (causal hypotheses or laws) together with specific statements describing initial conditions. Working within the deductive-nomological account of scientific explanation, Hempel and Nagel shared the agenda of assimilating the explanatory structure biology to that of physics by showing that the structure of teleological explanations in biology was logically no different from the structure of explanations in physics.

On Hempel's analysis, part of the analysis of the claim that a trait T has function F in organism O is that the presence of T in O is a SUFFICIENT condition for F to occur in O. For example, part of the analysis of the functional claim about canid play bows is that the trait of producing play bows in dogs is sufficient to communicate to conspecifics that what follows is play. The trouble with Hempel's analysis as an explanation of the presence of the trait is that merely because T is sufficient to produce some effect, we can't infer the presence of T from that effect because other things might also be sufficient to produce the effect (Hull 1974; Cummins 1975). For example, we can't DEDUCE the presence of a play bow from the effect of communicating play intention, because other things--e.g., exaggerated pawing directed at the face, a loose bouncy gait, rapid approaching and withdrawing (including feinting, approaching and rolling over in front of the other animal)--could have produced the same communicatory effect.

Nagel's analysis avoids this logical problem by construing functional claims as involving claims about necessary conditions: the presence of T in O is a *necessary* condition for the occurrence of F in O. Although Hinde is not explicitly committed to the deductive-nomological account of scientific explanation, he too seems committed to traits as necessary conditions for their functions when he says (1975 p.5): "when we speak of the function of bird song, we refer to events consequential upon the birds' singing which would not occur if birds did not sing". If the presence of the trait T was indeed necessary for the effect F, then we could infer the presence of T from the occurrence of F. The trouble with necessary condition analyses, as Cummins (1975) apply argues, is that they make false claims (see also Hull 1974): Singing may be just one way by which a bird produces a particular result. Dogs have other means of communicating play intention so the candid play bow is not strictly necessary to communicate that what follows is play.

Cummins' (1975) account of functions is in part a reaction to the defective accounts of Hempel and Nagel. Cummins (1975) argues that Hempel and Nagel were mistaken on two counts. On his view, appeals to the function of some trait T in organism O (1) help explain some biological capacity C of O (not the presence of T in O) and (2) the form of explanation is "analytical" (not in terms of causal conditions). According to Cummins, a functional analysis decomposes a large capacity of a system into various component capacities; he says (1975/1984 p.403): "The biologically significant capacities of an entire organism are explained by analyzing the system into a number of 'systems'--the circulatory system, the digestive system, the nervous system, etc.--each of which has its characteristic capacities. These capacities are in turn analyzed into capacities of component organs and structures." So, for example, attributing the system into function to hearts helps to explain how the organism manages to get oxygen distributed to its cells. Such explanations analyze the capacity of a complex system into capacities of its components and they do not entail or presuppose that the trait or component subsystem is there because it has the function that it does. (For similar discussion about the evolution of color vision in mammals see Jacobs 1993.) Hence analytical explanations are neutral with respect to the causal relevance of the function to the presence of the trait. They are nonetheless explanatory because given a functional analysis one can understand how a larger system can have a certain capacity in virtue of the capacities of its parts. Furthermore, on Cummins' view, functional analyses are strongly interest-relative. So, for example, if one is interested in how the liver contributes to atherosclerosis one might ascribe to it the function of producing cholesterol. Clearly atherosclerosis is not to the selective advantage of an organism, but unlike the standard line Cummins' notion of function is not explicitly tied to natural selection.

Hinde's (1975) notion of the "weak" functional meaning can also be construed as an account similar to Cummins'. On Hinde's view: "A weak meaning answers the question 'what is it good for? By contrast, 'function' in a strong sense attempts to answer the question 'through what consequences does natural selection act to maintain this character?'" (Hinde 1975, pp 5-6) Hinde's strong sense appears to be a version of the standard line: the maintenance of the trait in the organism(s) is causally explained by reference to natural selection. But in his weak sense of function, what is explained is how a certain trait contributes to some further ability of the organism. Hinde's example is that wings contribute to the capacity for flight. This contribution can be understood independently of knowing how (or even whether) flight contributes to survival and reproductive success, and hence to the presence of the trait.

Functional analyses, in Cummins' sense, are important because they provide different levels of abstraction for the explanation of given phenomena. For example, to understand how hearts contribute to the delivery of oxygen to cells it is necessary to know that they pump blood but it is not necessary to know the precise mechanism by which they do so--replacing a biological heart with a functionally equivalent but physiologically different component such as a mechanical heart need not change the overall capacity of the system. Eng & Adams (1992) make a similar point in terms of what they call the "Thesis of Multiple Realizability", namely that different microlevel properties can underlie the same functional properties. Claims made at the functional level have a higher level of generality than claims that focus on microlevel properties (see also Lipton & Thompson 1987). The functional level, according to Eng & Adams, provides a classification scheme for framing hypotheses, but the functional properties are not themselves causal. Eng & Adams say (1992 p.640): "The force of functional explanations is NOT derived from any causal role that teleological properties may possess. Nonetheless, function attributions do have an important explanatory role."

Several commentators (e.g. Millikan 1989; Sober 1993; Godfrey-Smith 1994) have argued for the pluralistic idea that biology should perhaps incorporate two notions of function, one to explain the presence of traits and the other to explain how those traits contribute to the complex capacities of organisms. Others (e.g. Griffiths 1993; Kitcher 1994) have argued that these two apparently distinct notions of function can be unified by regarding the target of explanation as the biological fitness of a whole organism. Tinbergen (1963) may also have accepted a similar unification of the different notions of function (Godfrey-Smith 1994). We favor the pluralistic account for reasons explained further below.

3.5 WHAT IS THE SOURCE OF TELEOLOGY IN BIOLOGY?

NATURAL SELECTION: The causal mechanisms that legitimize the use of teleological notions in biology trace back either directly or indirectly to natural selection. According to the standard line the link to natural selection is direct: definitions of teleological terms explicitly mention natural selection. Cybernetic views of biological teleology hold that teleological terms can be defined cybernetically and that teleology in biology is appropriate insofar as biological systems are cybernetic systems. Such views are discussed in the next subsection.

DEDUCTIVE-NOMOLOGICAL EXPLANATION: Teleological claims in biology are abbreviated ways of giving deductive-nomological explanations of the presence of traits in organisms. Nagel (1961/1984 p.346) directly argued for the conclusion that "the prevalence of teleological explanations in biology does not constitute a pattern of explanation incomparably different from those current in the physical sciences", hence it was important for him not to appeal to the specifically biological mechanism of natural selection. The views of Nagel and Hempel were discussed sufficiently in section 3.4 and will not be covered again below.

VALUE: Value notions (such as what is "good" for an organism or species) underlie all teleological claims in biology. This is discussed immediately below.

Discussion

In their analyses of biological teleology, Bedau (1992) and Van Paris (1982) propose to take seriously the use of the word "good" in questions such as Hinde's "what is it good for?" mentioned above. Bedau asks, "Where's the good in teleology?" and concludes that any satisfactory analysis of teleological claims in biology must recognize that "value plays an essential role in them" (Bedau 1992 p.781). He distinguishes three grades of involvement for value in teleology, ranging from mere production of good effects (level 1) through selection on the basis of effects that are good, but not necessarily *because* they are good (level 2) to the causal role played by conscious anticipation of good effects (level 3). In Bedau's words (1992, p.802): "Many features of organisms perform valuable functions, and so minimally have grade one teleology. Furthermore, the survival-promoting features produced by natural selection happen also to be good-producing features, so grade two teleology in biology is vindicated. On the other hand, grade three teleology in biology does not exist; there are no true full-blooded teleological explanations in biology. Except for the teleology traceable to the mind, the conditions required for grade three explanations are never present in the natural biological world." Van Paris (1982 p.55) suggests a similar stratification in terms of whether or not the agents involved recognize the effects as good effects.

Bedau's reservation of the terms "true" and "full-blooded" for grade three teleology suggest that he believes biological teleology is somehow less than full teleology. At first blush this would appear to commit him to a teleonomatist position rather than teleonaturalism. This issue is clarified by Bedau (1991 p.655): "But naturalists need not be narrow. A broader view of nature, perhaps roughly Aristotelian in outlook, could reckon objective standards of value as part of the natural order. According to this broader form of naturalism ... values would be real ineliminable natural properties, subject to broadly scientific investigation."

We do not have the space here to assess Bedau's theory in detail except to remark that appeals to Aristotle are not likely to allay the fears of biologists impressed by Mayr's worry (ii) above, that such explanations might be inconsistent with mechanistic explanations of the same phenomena. Bedau & Packard (1991) provide a clue to what Bedau (1992) might mean by objective standards of value by stating that an organism's ability to survive and reproduce provides an objective criterion of its welfare. But given this characterization of value, it's not entirely clear how this proposal differs from natural selection to analyze biological teleology (but see Van Paris 1982, chapter 2, for a possible explanation).

3.6 SHOULD TELEOLOGICAL NOTIONS IN BIOLOGY BE ANALYZED DIRECTLY IN TERMS OF NATURAL SELECTION?

DIRECTLY: Teleological notions in biology should be defined directly in terms of natural selection. Variants of this view are discussed in the section 3.7.

INDIRECTLY: Although natural selection may be important, it is only indirectly responsible for the applicability of teleological notions which are directly grounded in their applicability to cybernetic systems. According to cybernetic views either the presence of feed back mechanisms in natural

selection itself, or in the organisms produced by natural selection, makes cybernetic and hence teleological terminology appropriate. These views are discussed immediately below.

Discussion

R. Dawkins (1976) provides convincing reasons against regarding natural selection itself as a cybernetic feed back mechanism. Several authors, however, have suggested applying cybernetic notions to individual organisms (Beckner 1969; Mayr 1974; Boorse 1976; Adams 1979). Mayr (1974) differs from most biophilosophers by focusing on the notion of goal-directedness rather than function as his main teleological concern. He admits that there is heuristic value in, as he puts it, "the teleological *Fragstellung*" (Mayr 1974/1988 p.60). He claims, however, that a system is genuinely goal-directed only when it is controlled by a "program", and he prefers Pittendrigh's label *teleonomic* for such systems. Mayr also claims that the program notion is what Pittendrigh really had in mind when he introduced the term, although he admits that "Pittendrigh's discussion of *teleonomic* rather confused the issue" (Mayr 1974/1988 p.48). Mayr (1988) adds a postscript to the reprinted 1974 article. In the earlier article he had claimed that the proper way to treat the notion of a function needed further research. In the postscript he argues that functions should be understood in terms of the cybernetic notion of a program and he makes a distinction between genetic programs and somatic programs. Genetic programs are those involving the direct control of DNA. Somatic programs are only indirectly controlled by DNA. Mayr says, "All adapted systems of an organism can be considered to be somatic programs. If this were accepted, then one could call the functional activities of adapted systems teleonomic activities." (1988, pp.62-63) Mayr's appeal to programs to explain biological teleology indeed has his whole orientation towards the notion of goal-directedness rather than function, has much in common with the cybernetic and control theory approaches to naturalizing teleology (such as Adams 1979; see Nissen 1993 for discussion).

For Mayr, the notions of adaptation and natural selection are relevant to the production of programs, as indicated by the mention of adaptation in the description of somatic programs quoted just above, and in the summary conclusions of his 1974 paper where he says (1974/1988 p.60): "Programs are in part or entirely the product of natural selection." In that paper, however, he also claims that the notion of program is not specifically biological--it applies just as well to artifacts, e.g., (Mayr 1974/1988 p.49): "A clock is constructed and programmed in such a way as to strike at the full hour." On Mayr's account, it is the programs themselves, not the processes that produced those programs, that are directly responsible for the appropriateness of teleonomy. Sober (personal communication) complains that Mayr's use of the notion of program here is an unexplained metaphor. For example, where is the program in a clock? Sober objects that the idea of a clock being programmed simply amounts to the claim that someone designed it. We agree that Mayr's use of this notion does not conform to the literal sense in which computers may be said to execute programs and that Mayr must therefore explain his use of the notion before his account of biological teleology can be accepted.

3.7 NATURAL SELECTION ACCOUNTS: FORWARD LOOKING OR BACKWARD LOOKING?

FORWARD-LOOKING: Teleological claims in biology should be evaluated with respect to the present or future performance of organisms subject to selection. According to forward-looking, or

dispositional accounts of function, the functions of a given trait are those effects it is disposed to produce that tend to contribute to the present or future maintenance of the trait in a population of organisms. Thus, for example, the claim that "a function of a play bow is to communicate that what follows is play" means that because play bows tend to have the effect of communicating that what follows is play, the trait of performing play bows is being and will be maintained in the population.

BACKWARD-LOOKING: Teleological claims in biology should be evaluated with respect to natural selection history. According to backward-looking, or *etiological*, accounts of function, the functions of a given trait are those effects the trait had in the past that contributed to the selection of organisms with that trait. Thus, for example, the claim that "a function of a play bow in a population of canids is to communicate that what follows is play" means that the past tendency of play bows to communicate that what follows is play contributed to the reproductive success of ancestors of the present population.

Discussion

Forward-looking or *dispositional natural selection* accounts of function use the present tendency or dispositions of an organism's traits to enhance the organism's future success under natural selection to define function. Hirde appears to adopt a dispositional natural selection account when he says (1975 p.4): "the function of all adaptive characters is ultimately the same, namely, contributing to *eventual* reproductive success" (our emphasis) although he does not explicitly consider or reject etiological accounts of function.

In contrast to Hirde, Biegelow & Pargetter (1987) argue for a dispositional natural selection account as an explicit alternative to etiological accounts. They say (1987 p.192): "A character has a function if and only if the character confers propensities which are survival enhancing in the creature's natural habitat". They are motivated to provide this account because they believe that etiological natural selection accounts of function are explanatorily vacuous, for reasons rather similar to those given by Thompson (1987). Namely, they believe that if a function of a trait is defined as whatever effects of the trait contributed to its maintenance in the population under natural selection, then it would be circular to explain the maintenance of the trait in terms of its function (see Eric & Adams 1992, and Mitchell 1993 for criticisms of their argument).

Biegelow & Pargetter also differ from the standard line on what functional explanations are supposed to explain. The standard view is that functional explanations explain the presence of a trait in a set of organisms. Biegelow & Pargetter, however, believe it is not the presence of the trait that is explained, but how that trait contributes to fitness (Mitchell 1993). Mitchell (1993) argues that this misrepresents the explanatory goals of biologists and defends the standard line.

Wright (1973/1984, 1976) proposed a backward-looking analysis of function that has been very influential, especially among philosophers:

- The function of X is Z means
 - (a) X is there because it does Z,
 - (b) Z is a consequence (or result) of X's being there.
- Wright's account is described as *etiological* or *historical* because it defines function in terms of

the causal contribution of X doing Z in the past to the presence of X. Wright makes no explicit reference to natural selection in his definition of function because his definition is intended to give a general account of function applicable to both biological and non-biological cases. Any process of selection will satisfy clause (a) in Wright's definition. Natural selection is a specific example of a selection process that allows the notion of function to be applied to biological cases. The idea of basing a broad notion of function on a general notion of selection can also be found in Wimsatt (1972), who traces it to Mace (1935), and in Millikan (1984) who states (in Millikan 1993) that her ideas about function developed along similar lines to Wright's although she was unaware of his earlier work. Wimsatt (1972) and Millikan (1984) both also treat natural selection the selection process that legitimizes the notion of a biological function.

Wright's definition has been widely criticized as too broad. For example, Boorse (1976) claims that it applies to a small rock nodding up a larger rock in a river in such a way as to prevent the smaller rock from being washed away--holding up the larger rock is then a function of the smaller rock on Wright's definition. Examples such as these have led several philosophers to modify Wright's original idea to include natural selection *explicitly*, thereby avoiding Boorse's counterexamples (e.g., Neander 1991a,b; Godfrey-Smith 1994; Millikan (1984, 1993) had independently developed an account of function that avoids Boorse-type counterexamples. Her definition of "proper function" places very specific conditions on the patterns of reproduction and selection of traits. Biological functions, on her account, are specific examples of proper functions where biological reproduction and natural selection are the relevant mechanisms. Although Millikan's account of proper functions is intended to apply more generally than just to biological functions, the intricate details of her account are so obviously modeled on the biological processes of reproduction and natural selection, that her account is widely characterized as explicitly based on natural selection.

The basic idea behind *etiological natural selection* accounts of biological function is that a function of a trait is an effect of the trait that has contributed (in ancestral populations) to the preservation of the trait (in descendant populations) via the differential survival and reproduction of organisms with that trait. Thus, pumping blood is a function of your heart (and making beating sounds isn't) if blood pumping contributed to differential survival and reproduction of ancestral organisms (but making those sounds did not).

We believe that some version of the etiological natural selection account is probably the best way to elucidate most teleological claims in biology, but the exact details of such an account remain to be worked out. For example, opinions differ on how to handle subtleties such as whether a vestigial organ such as the human appendix has a function if no longer performs or whether it no longer has a function (Griffiths 1992). Some versions of the theory (e.g., Millikan 1984) consider the entire evolutionary history for the purpose of attributing functions. Other versions (e.g., Godfrey-Smith 1994) place more emphasis on the recent history of selection. There are also differences of opinion over exactly how natural selection is to be involved in the definition of function. (See also Papineau 1987; Hall 1990; Neander 1991a,b; Griffiths 1993.) For present purposes we intend to leave such subtleties undecided, although further conceptual work is clearly needed. The important element of the account is that attributing a function to a trait is an abbreviated way of (partially) explaining the persistence of the trait in a given population.

Etiological natural selection accounts of function are versions of the standard line, introduced in section 2 above, that appear to avoid Mayr's criticisms (i)-(iv). Clearly, the explanations in terms of natural selection make no appeal to vital forces or mental control. Natural selection is compatible with mechanistic explanation. And the etiological natural selection account of function avoids the problem of backward causation because the functions of contemporary hearts are explained in terms of the selective advantage that hearts provided to ancestral organisms.

4. ATTRIBUTING FUNCTIONS TO BEHAVIOR: THE ROLE OF EXPERIMENTAL EVIDENCE

If etiological natural selection accounts avoid Mayr's criticisms, how do they fare with respect to our fifth, methodological concern? Here we use a recent article on ant behavior by Gordon et al. (1993) to illustrate some points about possible relationships between experimental data and attributions of function. Our purpose is not to impugn the fine experimental work of Gordon and her colleagues; we could have used many other functional claims in the literature to make the same points (see also Williams 1966, 1992; Lorenz 1981; M. Dawkins 1986; Gray 1988).

Gordon et al. ask "What is the function of encounter patterns in ant colonies?" and set out to answer this question in the laboratory by manipulating nestmate density for three different species of ant. Among their results they discovered that ants change their antennal contact rates in response to the proportion of contacts with conspecific non-nestmates, rather than absolute number of non-nestmate contacts. The correlation between the behavioral response (rate of antennal contacts) and an environmental variable (proportion of conspecific non-nestmates) seems to suggest that a function of antennal contacts has something to do with the presence of non-nestmates. Gordon et al. never directly answer their title question, but they speculate that "An ant that suddenly encounters alien ants may be in danger ... the increase in contact rate, though short-lived, may be sufficient to generate a defensive response to the intruders" (p. 1099). This leads to the plausible suggestion that a function of antennal contacts may be to initiate defensive reactions to intruders, by helping ants "decide whether to engage in contact" (p. 1083).

Do the experimental results justify this conclusion about function? In the general case, does the correlation between behavioral response B and environmental variable E support the claim that B's biological function is connected to E? The answer to the second question is no. Flicking bees across the visual field of a frog will increase its rate of tongue-flicking, but one should not infer from this experimental result that a function of frog tongue flicking is to catch bees.

So what is the difference between inferring function from the response of ants to non-nestmates and inferring function from the response of frogs to bees? The answer to this question centers on background beliefs about species-typical encounter patterns that, in the case of the experimenters, are based on extensive experience with ants (see also Gordon 1992). One is inclined to accept the functional claim involving non-nestmates because of a prior idea that the presence of alien ants is likely to be a source of selection pressure for ants and therefore relevant to evolved function. On the other hand, one assumes that frogs do not normally encounter bees in their natural environments. Hence, one has the prior idea that bees are not likely to have provided selection pressure on frogs and so should not be part of the description of a function of tongue flicks. Frogs probably flick at bees because bees look like flies to them.

But the correlation between tongue flicks and bees does not tell us directly about evolved function (for discussion see Shapiro 1992). The mere correlation between an experimentally induced stimulus and a behavioral response is not in itself sufficient to justify a functional claim.

According to our preferred way of understanding the etiological natural selection account of function, a function of a trait is an effect of the trait that has contributed (in ancestral populations) to the preservation of the trait (in descendant populations) via the differential survival and reproduction of entities with that trait. The claim that a certain effect of a trait is a function of that trait is justified by (i) showing that the trait had the effect in question in ancestral populations and (ii) showing that this effect tended to increase the fitness of ancestors with the trait. Both of these require establishing hypotheses about the past, but of course ethnologists must work with present populations. Nonetheless, it is possible to support hypotheses about the past by studying present populations with the help of reasonable assumptions about relevant similarity between present ecological conditions and past ecological conditions. Thus the discovery that an effect of a certain trait increases fitness in present populations can often be used to support corresponding claims about ancestral populations.

It is intuitively plausible to suppose that ants studied by Gordon et al. encounter conspecific non-nestmates under natural conditions, and that such encounters are potentially hazardous. These assumptions were not, however, tested in the experimental situation. Also, one wonders whether encounters with members of other species might also bear on functions of encounter patterns. Gordon et al. cautiously call for further empirical field work, and they really do not make any very strong claims, but rather suggestions, about functions of antennal contacts. While we agree that more field work is needed, in and of itself it may not help us to learn more about function. It is important to stress that questions about function are extremely difficult to answer and that the proper interpretation of further research requires students of behavior to make explicit the background assumptions that drive their attributions of function and choice of methods used to study function (Godfrey-Smith 1994).

5. PLURALISM ABOUT NOTIONS OF FUNCTION

Our survey of the range of views shown in Figure 1 presented these positions as if they were competitors in the space of possible "correct" accounts of the teleological notion of biological function. This approach is represented by Bechtel (1986, p.40) who says: "Having contrasted teleological functional analyses...with...Cummins' form of functional analysis, it remains to show why the teleological conception should be preferred." A number of authors suggest, however, that there may be more than one notion of function employed by biologists corresponding to different explanatory projects. Millikan (1989) refers to an ambiguity in the term "function", and argues that there is room in biology for at least two different notions--Cummins-functions and etiological functions (see also Godfrey-Smith 1994). Rather than seeing ambiguity, Griffiths (1993 p. in press) argues that "The etiological approach to 'proper functions' in biology can be strengthened by relating it to Robert Cummins' general treatment of function ascription." Cummins (1976) expresses the view that causal explanations of the presence of traits have a different structure from analytical explanations of how traits contribute to complex capacities. Given this it is not clear that Griffiths is right that the two notions can be easily combined. This speculation of ours is, however, far from being a rigorous argument that it cannot be done.

Kitcher (1994 p. in press) 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." He believes however, that Cummins-functions and etiological accounts can be unified by the connection between function and design. We will return to Kitcher's view about this connection in Part Four below, after discussing the notion of design.

Although Millikan and Godfrey-Smith endorse the pluralistic view, they believe, and we agree, that some version of the etiological natural selection account of function underlies the majority of functional claims made by ethologists.

Part Four: Distinguishing Design from Function

1. DESIGN

In the debate about biological teleology, relatively little attention has been paid to the notion of natural design. It is common for authors to slide between claims about function and design as if they accept the principle [ND]: 'T is naturally designed for X if and only if X is a biological function of T. For some authors, acceptance of something like ND is explicit. For example, Kitcher (1993 p. in press) writes: "the function of an entity *S* is *designed to do*' and Millikan (1984 p.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." Many other authors write as if they implicitly accept ND (e.g. Williams 1966 p.9). If one adopts the principle ND, then the claim that hearts are a product of natural design means nothing more than that hearts have a biological function.

There is nothing logically wrong with collapsing the notions of design and function in this manner, and it has the advantage that if the notion of biological function is successfully naturalized then so is the notion of natural design. We believe, however, that the conflation of design and function in ND is unfortunate. Cases of psychological design and function allow for certain distinctions to be drawn between design and function. We believe that similar distinctions are potentially useful to the study of behavior. So we advocate rejecting ND while still basing the analysis of natural design on natural selection. This distinguishes our view from that of Olsson (1987 p.549) who claims that "Optimal forging 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.

The methodology here is a little complicated. The teleological notions of function and design as used by evolutionary biologists are technical notions. Although these terms have uses in psychological contexts, we have argued that their uses in biological contexts should be understood in ways that do not make biological teleology derivative of psychological teleology. The strong constraints on analyses of teleological notions in biology are provided by biological and general scientific practice; considerations from psychological usage provide weak constraints at best on biological uses, and at worst they are possible sources of confusion. Nonetheless, with care, considerations about distinctions between the notions of function and design in psychological contexts can be used to help understand possible roles for the notion of natural

design in biology. Distinctions that are made in psychological uses of "function" and "design" can provide models for distinctions that might be useful in biology. Thus, our strategy is to consider ordinary psychological usage and to apply what we learn to help develop a useful account of natural design.

2. TWO SENSES OF DESIGN IN PSYCHOLOGICAL TELEOLOGY

We start by making clear an ambiguity in the psychological use of "design". In paradigmatic applications to human activity, the term "design" has at least two different, but related, senses.

First there is a sense of "design" which corresponds to detailed planning prior to, or contemporaneously with, the execution of a sequence of behaviors which is geared to achieving a specific goal. This is the sense in which, for example, architects design buildings or football coaches design plays. Design in this sense involves making some functional considerations explicit and attempting to shape an object or behavior to implement those functions. The result of such a process is properly called an artifact. The process of design frequently involves trial and error testing of successively modified versions of a given product, whether that product is a physical artifact or something like a particular set play in a football game. We will call this sense of design "goal-driven design". Domesticated animals provide an interesting case where human goal-driven design may be superimposed on natural design (see Daniels & Bekoff 1990, also see Katz 1993, who seems to hold the implausible view that animals belonging to domesticated species are entirely artifacts).

Second there is a sense of "design" which means intentional. A person may, for example, be rude to someone by design, i.e., intentionally. An action may be intentional, despite little thought about the point of the action or its consequences. One may intentionally be rude to a person even if one has not considered what objectives are served by being rude or what the fallout will be. We will call this sense of design "intent-design".

The two senses of "design" are related because goal-driven design paradigmatically entails intent-design. They are, however, also distinct because goal-driven designers typically take care to attempt to anticipate and overcome contingencies which threaten the success of the project, whereas this is not true, in general, of intentional actions which may occur with relatively little forethought. When designers do not anticipate contingencies diligently, it is appropriate to call something poorly designed, meaning it is ill-suited to the task at hand. In contrast, when speaking of an action that was done deliberately, unless one is using "design" in its goal-driven sense it is as meaningless to call the action poorly designed as to call it poorly intended.

Having distinguished the two senses, we will restrict our attention to goal-driven design. When discussing psychological contexts below, unless explicitly noted, "design" is to be read as "goal-driven design".

3. DESIGN AND FUNCTION IN PSYCHOLOGICAL CONTEXTS

In psychological contexts, (a) design determines function, but (b) not everything that has a function is designed. Take (b) first. In *The Dixie Chicken* in College Station and many other

down-home drinking establishments in Texas, stags' heads function as wall decorations. They are clearly not designed for that purpose. (Although the stags' heads were presumably put on the wall intentionally, hence by intent-design.) Likewise, the function of a rock on a desk may be to hold down loose papers, but unless the rock has been modified by, e.g., having a flat base chiselled into it, it is not appropriate to say that this object was designed for the purpose of holding down papers. Thus, having a function does not entail being designed for that function.

Now (a). Where conscious design is involved, if one knows what something is designed for then one knows its (intended) function. This is so even if the item in question is incapable of performing that function. Conscious design determines function so strongly that an entire class of things may have a given function even if none of them is capable of performing that function. Prior to Oville and Wilbur Wright many contraptions were designed for heavier-than-air flight yet none of them succeeded in flying. Even if modern aviation had never, so to speak, gotten off the ground, it is nonetheless true that the function of those remarkable contraptions was to fly, precisely because they were designed (albeit poorly) to fly. Biological functions are disanalogous in an important way. Although individual hearts (e.g., malformed hearts) may fail to pump blood, hearts would not have the function to pump blood unless some of them succeeded. For a thing to possess a biological function, at least some of the members of the class of things that have that function must have successfully performed the function. This is not true in cases of psychological design, where design can determine function--all the members of the class of things designed to have that function might have been unsuccessful in performing it. Some authors (e.g., Wright 1976; Achinstein 1977; Van Parijs 1982) call such cases "deviant" or "marginal". Nevertheless, the difference holds--they *can* arise in cases of psychological teleology, but not in cases of biological teleology.

To summarize, in psychological contexts, (i) a whole class of things designed for F may fail to perform F yet still have F as a function and (ii) something can have a function F although not designed to perform F.

4. NATURAL DESIGN DISTINGUISHED FROM BIOLOGICAL FUNCTION

The preceding distinctions made about design in psychological contexts suggest two corresponding 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? (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.

As we remarked in Part Three of this paper, we believe that the majority of claims made by ethologists about biological function can be understood to presuppose some version of an etiological natural selection account of function--on our account a function of a trait is an effect of the trait that has contributed (in ancestral populations) to the preservation of the trait (in descendant populations) via the differential survival and reproduction of organisms with that trait. For the purposes of this section we will take questions (1) and (2) above to be referring specifically to etiological natural selection accounts of function. To answer the questions,

however, it is still necessary to have an account of natural design.

We propose to analyze natural design as involving two components. We say that *a trait T is naturally designed to do X* means that

- (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.

This account of natural design incorporates the notion of function in clause (i) so it has the straightforward consequence that the answer to question (1) is no, there are no 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; being naturally designed for X always entails having X as a biological function. Component (i) has already been extensively discussed, so the remainder of this section focuses on (ii).

The aspect of (ii) likely to be most controversial is its involvement of the notion of optimality or adaptedness. Gould & Lewontin (1978) criticized adaptationism as Panglossian--i.e. as entailing belief that this is the best of all possible worlds. Dennett (1983/1987) attempts to defend the Panglossian paradigm as involving an idealizing assumption about natural selection--an assumption that is probably not true but that is necessary for making predictions using the theory of natural selection. Byers & Bakoff (1990) worry that arguments for optimality can easily involve logical errors and are bothered that in many cases empirical studies make an adaptationist assumption on the basis of inadequate empirical evidence.

Clause (ii) of our analysis avoids these worries because it stresses *comparative* judgments about traits of organisms, e.g., that the traits of present organisms are better at producing some effect than the corresponding traits of ancestral organisms. For example, it is commonly hypothesized that the lineage from land-bound saurians to birds involved progressive modification of the forelimbs into the more aerodynamically efficient forms of wings found in extant species. Presumably, variations in forelimb anatomy were subject to natural selection for their ability to keep the owners of those forelimbs airborne. On our view, to say that (most) birds' wings are designed for flying is to say that (i) enabling flight is a biological function of (most) birds' wings and (ii) the extant morphological forms of such wings are the result of a process of modification of earlier forms where the overall tendency has been towards better adaptation for flying. 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 archaopteryx. If an eagle's wings result in a higher glide ratio than its ancestors' wings and having a higher glide ratio provides a comparative fitness advantage, then it can be said that the eagle's wings are designed for soaring.

Comparative judgments do not require the Panglossian assumption. This claim is based on a simple point about the logic of comparative statements that, despite its simplicity, is frequently overlooked. To 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. For example,

a Cadillac may be better than a Rolls Royce with respect to converting fuel into distance travelled, but it does not follow that the Cadillac has good, let alone optimal, fuel efficiency. Clause (ii) is committed *only* to a *comparative* claim about traits. Thus, for example, no statement about the overall adeptness or optimality of birds' wings for flying is implied. Ruse (1993) draws a similar distinction between the notions of "comparative progress" and "absolute progress" (see also the contributions to Nilecki 1989). It would take us too far afield to discuss the notion of evolutionary progress here, but we are sympathetic to Hull (1988 p.45) who claims that "biological evolution has not just [one] direction, but lots of them." In other words, there are lots of bases for comparison, no one of which can be singled out as an absolute standard.

The process of modification by natural selection can reasonably be compared to trial and error processes employed in many human design endeavors. This approach is suggested by Dennett's notion of a "Design Stance" that can be applied to any complex system (Dennett 1971, 1983, 1987). Our view, however, is that the use of the term "natural design" can also be justified naturally without falling back to the teleonomatist position that natural design is properly understood in direct comparison to conscious design by psychological agents. Naturalizing the notion of design is, however, more difficult than naturalizing the notion of function. The notion of function is neutral with respect to the phylogenetic pathway by which a trait acquires a function. Consider again bipedal standing by hares. Holley (1993) argues that the function of this behavior is to indicate to predatory foxes that they have been detected. According to the etiological natural selection account, Holley's hypothesis about functions is justified if his data support the claims that bipedal standing by ancestral hares had this effect on ancestral foxes, and that this effect was (partially) responsible for those ancestral hares passing this trait on to their descendants. The functional hypothesis does not require showing that the behavioral trait of bipedal standing is a direct modification of some ancestral trait that was less efficient with respect to its effects on foxes. However, a design claim for bipedal standing would, on our analysis, require such a comparison to be made.

This discussion suggests that the answer to question (2) above should be yes; there may be 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 (although it may be a product of natural design for some other function). However, because showing design is considerably more difficult than showing function, especially for behavioral phenotypes, such 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.

Similar methodological issues are relevant to ethologists studying behaviour patterns such as helping, foraging, and group living (see Jamieson 1986, 1991; Gray 1987; White et al. 1991; Ligon & Stacey 1991; Emlen 1991; Richard-Hanson 1993). Furthermore, the classical account of the development of communicative signals via the ritualization of intention movements (Tinbergen 1952) also provides a useful domain for comparing claims about function and design. Many organisms derive information from the behavior of others and it is common to consider transfer of

information as a defining feature of communication (Allen & Hauser 1993). However, several layers of sophistication can usefully be distinguished. Minimally, the behavior of one organism may simply have the effect of providing information to another organism; for example, the arrival of a migratory bird might allow a human observer to infer that the season is about to change. Unless this effect on human observers provided a selective advantage to ancestors of this bird, then it is not appropriate to call communication about change in season a function of the migratory behavior of the bird. For the transfer of information to be a function of a behavior, the behavior has to have been selected for its communicative effect, leading many biologists to have included selective advantage in their definitions of communication (see for example Eibl-Eibesfeldt 1975; Alcock 1993; Drickamer & Vessey 1993). Behavior patterns such as shivering and piloerection, that may convey information about body temperature, hormone levels, or the likelihood of fight and flight responses, may become transformed via ritualization into differentiated expressive behaviors (Eibl-Eibesfeldt 1975). Both ritualized and unritualized behavioral patterns can function to communicate information--under certain circumstances, however, the process of ritualization may transform unritualized behaviors into signals that are clearer and less ambiguous than their ancestral forms (Eibl-Eibesfeldt 1975). Ritualization is an example of the sort of change required to 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, assuming that such comparisons can be made, it is reasonable to regard some behaviors as having communication as a function without being designed for communication, while regarding some signals as specialized behaviors that are designed for communication.

The next section addresses the methodological difficulties involved in showing that a trait is or is not naturally designed for some function, but before going on to discuss these, it is worth contrasting our views on function and design with Gould & Vrba's (1982) distinction between *adaptation* and *exaptation*. Gould & Vrba apply the term *adaptation* when natural selection has shaped a trait for some use; their notion of "shaping" appears to correspond to our clause (ii) above. They recommend applying the term *function* only when shaping by natural selection is involved, which on our view conflates the notions of function and design. They introduce the term *exaptation* to cover cases where either a selected trait of an organism is coopted for a new use or where a characteristic that is produced and maintained by mechanisms other than natural selection is coopted for a current use. As Gould & Vrba use the terms, traits in such cases merely have effects; they do not have functions. Millikan (1993, p.45) notes that "[Gould & 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) relies on an etiological natural selection account of function and argues that Gould & Vrba mischaracterize the distinction between function and (mere) effect. We agree. If the effects of a trait raised the fitness of ancestral organisms possessing that trait and thus contributed to the inheritance of the trait by descendant organisms, then whether or not the trait is shaped by selection such effects are adapted functions. Griffiths proposes to characterize such cases as "exadaptations" rather than adaptations and he proposes to use the term function in both cases, but like Gould & Vrba he also fails to distinguish function from design. Thus our usage, summarized in Table 1, differs from both Gould & Vrba's (1982) and

Griffiths' (1992) by distinguishing function from design, while it agrees with Griffiths' usage, but not with Gould & Vrba's, on the range of cases to which the notion of function correctly applies.

Place Table 1 here

5. EVIDENCE BASES FOR NATURAL DESIGN

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.

Some, but not most, anatomical traits leave traces in the fossil record. Hence, for example, it is possible to use fossils to build models of archaeopteryx wings and then test these for aerodynamic properties in comparison to the wings of modern birds. Soft tissues fossilize poorly so it can be very difficult to find paleontological evidence to support claims about the design of features of soft tissues. 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. It is also sometimes possible to draw inferences about ancestral forms by comparing species from different taxa. 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.

Inferences with respect to design of behavioral traits are almost exclusively limited to the last kind—namely comparison of different extant species and populations. Inferences to the phylogeny of behavior based on such comparisons are difficult but not impossible. For example, Golani (1992) attempts to identify movement patterns and gradients of movement differences across vertebrate species from different taxonomic groups. By looking at variation from the shared movement patterns of vertebrates Golani hopes to derive what he calls (p.264) "the ground plan of vertebrate behavior". If such a project can be carried out, it might be possible to make comparisons about the relative effectiveness of variations in behavior for specific tasks. It might then be possible to draw further inferences about the evolutionary development of complex behaviors, on which claims about behavioral design could be based. The methodological difficulties are enormous and not well understood. This is a prime area for future interdisciplinary and comparative investigation by biologists and philosophers.

Concluding Remarks

A lengthy conclusion is not necessary for we have attempted to summarize each section along the way. It is obvious that additional comparative and interdisciplinary research is needed, and that it will have to involve detailed description, observation, and experimentation. All of those involved in making claims about function and design need to be clear and explicit about the

conceptual commitments involved. As we (and others) have shown, function and design are complex notions, and while they may lend themselves to being discussed together, they should not be conflated. Comparative work is important but will not provide all the answers (Williams 1992 p.41). Nor will interdisciplinary work of the type exemplified here. Different approaches must be combined.

Readers who are primarily interested in the ethological or behavioral ecological study of function and design should realize that many of the problems that we have raised in this essay were of concern to pioneering ethologists such as Konrad Lorenz and Niko Tinbergen. Wenzel (1992), who addresses function in his discussion of behavioral homology and phylogeny, has boldly claimed that (1992 p.361) "Ethology has made almost no advance with respect to a phylogenetic understanding of behavior since the late 1950s, and most modern ethologists simply do not work toward that goal. To honor the proud heritage of Lorenz and Tinbergen we need only to be brave and begin." Simple or univocal claims about function and design will probably fail for any but the most grossly characterized behavioral phenotypes. Behavioral phenotypes do not fossilize making it difficult to trace their phylogeny; because of this fact we must be open to pluralistic methods.

Finally, although it has been the focus of this paper, teleology is not the whole story in the explanation of behavior. Classical ethologists would agree (Tinbergen 1951/1989; Lorenz 1981). Tinbergen (1951/1989 p.4) wrote: "There has been, and still is, a certain tendency to answer the causal question by merely pointing to the goal, end, or purpose of behaviour, or of any life process period. This tendency is, in my opinion, seriously hampering the progress of ethology." Statements about function and design are just one part of the explanatory picture. We must pay careful attention to the criteria that are used when each of us offers what we think is the best explanation in terms of function or design.

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