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Function and Design Revisited*

David J. Buller

Abstract

Several analyses of biological function — for example, those of Williams, Millikan, and Kitcher — identify an item's function with what natural selection designed it to do. Allen and Bekoff have disagreed, claiming that natural design is a special case of biological function. I argue that Allen and Bekoff's account of natural design is unduly restrictive and that it fails to mark a principled distinction between function and design. I distinguish two approaches to the phenomenon of natural design — the "trait-centered" approach of Allen and Bekoff and the "organism-centered" approach — and defend the latter. When design is understood according to the organism-centered approach, biological function and design are co-instantiated phenomena.

1. Introduction

The concept of <u>design</u> has played a central role in several prominent theories of the nature of biological functions. Williams, for example, argues that the demonstration of design is both necessary and sufficient for the demonstration of function (1966, p. 209). Millikan says: "Having a proper function is a matter of having been 'designed to' ... perform a certain

function" (1984, p. 17). And Kitcher echoes: "the function of S is what S is designed to do" (1993, p. 380). None of these authors, however, provides an analysis of design. Williams assumes, instead, that "design is something that can be intuitively comprehended" by analogy with human engineering (Williams 1966, p. 260; see also 1992, p. 40). And given the fact that Kitcher analyzes function in terms of design, while employing many engineering examples to illustrate the latter, he also appears to take design to be "intuitively comprehended." In contrast with both of them, Millikan appears to treat "function" and "design" as synonyms, which are mutually defined by her version of the etiological theory of functions; for she says that the goal of her "theory of proper functions is to define this sense of 'designed to' ... in naturalist, nonnormative, and nonmysterious terms" (1984, p. 17).

In a trio of recent articles, Allen and Bekoff provide an account of design that removes any need for "intuitive comprehension" and makes design a property of traits that can be objectively ascertained through phylogenetic analysis (Allen & Bekoff 1995a, 1995b; Bekoff & Allen 1995). In providing this account, Allen and Bekoff argue that there are non-biological cases of function without design that have biological analogues and that, consequently, function and design are distinct phenomena in the biological case as well. Biological design, or natural design, they contend, is a matter of having a function plus having undergone a history of modification under selection for better performance of that function. This entails not only that the concepts of function and design are not synonymous (contra Millikan), but that they are not even co-extensive, which in turn entails that the concept of design cannot be employed to analyze the notion of biological function (contra Williams and Kitcher).

In the next section, I will argue that Allen and Bekoff's account of natural design is unduly restrictive and that it fails to mark a principled distinction between biological function and natural design. I will diagnose these problems as a byproduct of their non-biological examples, which are crucially disanalogous to biological cases of function, and I will articulate and defend an alternative conception of natural design that avoids these problems. Before developing that alternative conception of design, however, it will be necessary, in section 3, to explore in more detail the conception of biological function to which both Allen and Bekoff and I are committed. Then, in section 4, I will sketch two distinct ways of approaching the phenomenon of natural design — the "trait-centered" approach, characteristic of Allen and Bekoff, and the "organism-centered" approach — and then articulate and defend the latter. With that alternative conception of design in place, I will show that the concepts of biological function and natural design, while not synonymous, are nonetheless co-extensive. In the biological case, I will argue, function and design are intimately related phenomena (as per the theories of Williams and Kitcher). I will then conclude with a discussion of the implications of this conception of design for the concept of adaptation.

2. Biological Function Versus Natural Design?

Allen and Bekoff begin with examples to show that, in the artifactual case, although design is sufficient for function, it is not necessary:

> 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. (1995b, p. 33)

In these artifactual cases, design involves not only having a function, but being <u>modified</u> in some way in order to <u>better</u> perform that function. In short: artifact design = artifact function + modification for better performance of that function.

Since natural selection frequently modifies traits in the direction of greater "perfection" for their functional roles, Allen and Bekoff contend that an analysis of natural design should parallel their analysis of artifact design. Thus, they propose, a trait T is <u>naturally designed</u> for X if and only if:

    i.   X is a biological function of T and

    ii.   T is the result of a process of change of (anatomical or behavioral) structure due to natural selection that has resulted in T being more optimal (or better adapted) for X than ancestral versions of T. (1995b, p. 34)

So, "natural design entails both possession of biological function and a history of progressive structural modification under natural selection for improved performance of that function" (1995b, p. 3).

Allen and Bekoff intend the conception of biological function in clause (i) as a version of

the etiological theory of functions: "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" (1995b, p. 26). Clause

(ii) is thus intended to build on this conception of function in the following way (see 1995b, p.

38; Bekoff & Allen 1995, p. 254): A (current) version T_n of some trait T is <u>naturally designed</u> to

do X if and only if it is the (etiological) function of T_n to do X and

(ii.a)   there is some antecedent version of T, T_{n-1}, such that T_n arose as a

modification of T_{n-1},

(ii.b) T_{n-1} also had the function of doing X, and

(ii.c)   a comparison of T_n with T_{n-1} shows T_n to be more effective than T_{n-1} in

doing X.

To illustrate, consider the example to which Allen and Bekoff themselves apply their

distinction: the progressive modifications to the forelimb structures of land-bound saurians

that resulted in wings (1995a, pp. 615-616). Their idea is that, if we consider the series of these

modifications to forelimbs, we would find a version of the forelimbs that did not allow flight

and a subsequent modification to them that did enable flight. The modified forelimbs thus

functioned to produce flight, but were not designed for flight, since the ancestral version of the

forelimgs did not function to produce flight — that is, condition (ii.b) is not satisfied. However,

when the modified forelimbs were further modified by selection to produc more effective flight,

the secondarily modified forelimbs were also designed for flight; for they arose as a

modification of an earlier form of forelimbs (so condition (ii.a) is satisfied), that earlier form of

forelimbs had the function of producing flight (so condition (ii.b) is satisfied), and a comparison of the later and earlier forms shows the later form to be more effective in the performance of their shared function (so condition (ii.c) is satisfied). Thus, the secondarily modified forelimbs represented natural selection's modifying the forelimbs in the direction of greater optimality for flight, and is for that reason designed for flight.

There are, I think, two problems with this conception of natural design. First, it is unduly restrictive. For it counts a trait as an instance of natural design only if it underwent directional selection, in which selection modified the trait toward greater optimality. But some traits are simply maintained by selection in a population, with active selection against any emerging variants. (Stabilizing selection is one form of such maintenance (see Endler 1986).) Since traits that have been maintained in a population by selection will not have undergone modification in the direction of enhanced performance of function, Allen and Bekoff will not classify them as instances of natural design. But this is problematic. For, if selection has maintained a trait in its initial form, selecting against any variants that arose, that is because the trait was already as optimal as possible and no modification could have made it more optimal (relative, of course, to the relevant constraints on the trait). An account of natural design should allow us to say that such traits are cases of good design, albeit as a result of good luck, regardless of whether they have undergone a history of modification. Not to recognize such traits as instances of natural design is to employ an account of natural design that is too tied to only one way in which selection operates (cf. Reeve & Sherman 1993, p. 7).

Second, Allen and Bekoff's distinction between natural design and mere function (i.e. function without design) is not principled. To see this, begin by considering that Allen and Bekoff take it to be an advantage of their conception of natural design that it accords with the traditional — though by no means universal — biological usage of the concept of adaptation. According to the traditional conception of adaptation, "the external world sets certain 'problems' that organisms need to 'solve'" and adaptation is "the process of evolutionary change by which the organism provides a better and better 'solution' to the 'problem'" (Lewontin 1978, p. 213). A trait is an adaptation, then, if it is a product of this process. Thus, the traditional conception of adaptation, like Allen and Bekoff's conception of natural design, incorporates the criterion of modification by selection for more effective performance of some function (better solution of some problem). This results, Allen and Bekoff believe, in a simple relation between natural design and adaptation: Adaptations, and only adaptations, are products of natural design (1995b, p. 38; see also 1995a, pp. 612-613).

But not all adaptations have arisen through progressively better solutions to relatively stable environmental problems. Many adaptive problems an organism faces are set not by the organism's physical environment, but by other organisms in evolving lineages — particularly parasites, predators, and conspecifics that are competing for the same resources. In such cases, the very problems an organism must solve are themselves undergoing evolution. Consideration of these facts has led to a growing treatment of some adaptations as moves within "evolutionary arms races," rather than as solutions to relatively stable environmental problems (Dawkins 1982, chap. 4; Dawkins 1991, chap. 7; Vermeij 1987, chaps. 1 & 15; Weis, et

al. 1989; Davies & Brooke 1991; Endler 1991; Krebs & Davies 1993, chap. 4; Lotem & Rothstein 1995; Ridley 1996, chap. 22). In an evolutionary arms race, there is progressive modification not only in the solutions to an adaptive problem, but in the adaptive problems themselves. "Improving" solutions are continually matched by ever more "difficult" problems, with evolution in either precipitating the evolution of the other. The result is the "Red Queen effect" (van Valen 1973): Lineages evolve as fast as they can merely to be equally effective as they once were in solving adaptive problems; so there is no cumulative progress in their solutions to adaptive problems. While Allen and Bekoff's distinction between natural design and mere function appears plausible given a more traditional conception of adaptation, when viewed within the context of arms races, which are a significant aspect of evolution, it is not a principled distinction.

To see why, consider the following very simplified sketch of an evolutionary arms race, in which progressively modified forms of a trait parallel progressively modified forms of an adaptive problem. A trait (T_1) evolves under selection in a population as a response to an adaptive problem (P_1); thus, it is the (etiological) function of the trait to solve that problem. Over time, mutation introduces a modified form of the trait (T_2), which provides a more effective solution to the adaptive problem. The modified trait (T_2) thus increases in frequency in the population, eventually replacing the unmodified form. This precipitates evolution of the adaptive problem, with a modified form of the problem (P_2) coming to replace the earlier form (P_1). Although the modified trait didn't evolve as a response to the modified problem, it nonetheless adequately solves it (though not as effectively as it had solved the unmodified form

of the problem); so selection maintains the modified trait in the population and it thus becomes the (etiological) function of that trait to solve the new adaptive problem (P2). Again, over time, mutation further modifies the trait, introducing a new form of the trait (T3), which is more effective than the earlier form in solving the new adaptive problem (P2). This precipitates the evolution of the adaptive problem (into P3), and so on.

Now, given Allen and Bekoff's conception of natural design, is T2, the first modified form of the trait, an instance of natural design? There are several conflicting ways of answering this question, and there is no genuinely non-arbitrary way of choosing among them. Consider just a few main options.

(1)   <u>Yes</u>: T2 is an instance of natural design, since it arose as a modification of T1 with which it shared the function of solving P1, and it performed that function more effectively than T1.

But things are not so simple. For (1) ignores the fact that the adaptive problem itself evolved (from P1 to P2) during the tenure of T2 and T2 also functioned to solve the new form of adaptive problem, which it was not a function of T1 to solve. And there is no reason why the two traits should be compared with respect to their functional effectiveness in solving the earlier adaptive problem (P1) rather than the later (P2). We could, then, opt for a more nuanced answer:

(2)   <u>Yes and no</u>: T2 was designed for P1 for the reasons given in (1), but it was not designed for P2, since condition (ii.b) above is not satisfied (that is, the ancestral

trait from which T_2 arose as modification did not share the function of solving

P_2). This would make it the mere function of T_2 to solve P_2.

(2), however, depends on treating successive adaptive problems in an arms race as genuinely

distinct problems (such that solving P_1 is a different function than solving P_2). But there is

nothing in the nature of things to force this interpretation. We could, instead, view such

successive adaptive problems as different versions of the <u>same</u> problem, which differ only with

respect to degree of difficulty. For suppose the successively modified forms of the trait (the Ts)

are progressively increasing running speeds of cheetahs, and the successively modified forms of

the adaptive problem (the Ps) are progressively increasing running speeds of gazelles. Then,

instead of considering catching gazelles running at <u>n</u> mph a distinct problem from catching

gazelles running at $\underline{k} > \underline{n}$ mph, we could consider both the same problem for cheetahs —

namely, catching gazelles — and the various speeds of gazelles as merely different degrees of

difficulty of that problem. This would allow a comparison of T_2 and T_1 as solutions to the same

problem. But it still leaves open how to compare them with respect to their solutions of that

problem <u>at</u> different degrees of difficulty. Comparing them with respect to their solutions of the

P_1 degree of difficulty will generate a modified version of (1). Comparing them with respect to

P_1, taking into account the fact that T_2 also solved the P_2 degree of difficulty, will generate a

modified version of (2). Finally, comparing T_1's solution of P_1 with T_2's solution of P_2 will

generate

      (3)   <u>No</u>: T_2 is not an instance of natural design, since condition (ii.c) above is not

               satisfied because of the Red Queen effect (that is, T_2 was not more effective at

solving P_2 than T_1 was at solving P_1). Again, this would make it the mere

function of T_2 to solve P_2.

The problem is that there are no principled grounds for choosing among these various

ways of comparing the functional effectiveness of successive forms of a trait in an evolutionary

arms race. And, since these different modes of comparison generate different classifications of

the same trait under Allen and Bekoff's distinction (some classifying it as an instance of natural

design and others as an instance of mere function), the absence of principled grounds for

choosing among these modes of comparison entails that Allen and Bekoff's distinction between

function and natural design is not principled.

Allen and Bekoff could respond by stipulating that a trait should be compared with its

ancestral version with respect to that point in time at which there was selection for the former

over the latter. This stipulation would entail option (1) above and would thus resolve the

ambiguity in Allen and Bekoff's criteria for classifying a trait as an instance of natural design.

But, again, things are not so simple. Within the clean lines of the above extremely simplified

model there is _steady_ replacement of an ancestral trait with its modified form and,

consequently, a fairly straightforward sense in which there was a "time at which there was

selection for" the latter over the former. "In the wild," however, there is rarely such steady

replacement of one trait by another, and this poses problems for the hypothetical proposed

solution.

To see why, consider a population of a bird species in which some birds have broad beaks and others have slender ones. In drought conditions, the broad-beaked birds enjoy an advantage, since they are better able to feed on the available dry seeds. In rainy conditions, the slender-beaked birds enjoy an advantage, since they are better able to feed on the insects in tree bark. Now, in general, there is selection for one trait over another in the wild just in case the former is increasing in frequency with respect to the latter. In a reasonably extended drought, then, the broad-beaked birds will increase in frequency, so there is selection for broad beaks over slender ones. But this extended drought may be followed by an extended wet period in which the slender-beaked birds stage a comeback and increase in frequency relative to the broad-beaked birds; so there is then selection for slender beaks over broad ones. Climate being what it is, of course, there will be fluctuations in the frequencies of the two beak types over an extended period of time, and hence reversals in the direction of selection. But, when measured in a long enough time span, there may be a clear direction to the changing frequencies: perhaps rainy conditions are more frequent than droughts in the long term, so that slender-beaked birds show an overall increased frequency over broad-beaked birds in the very long haul.

Now let's modify the above arms race scenario to reflect a process of selection that proceeds by such fits and starts, rather than steadily, and see what becomes of the proposed addition to Allen and Bekoff's definition of "natural design." Suppose that it takes 250 years for a modified trait (T_2) to completely replace its ancestral form (T_1) in the population. Over that 250 year period, we can say that there was selection for T_2 over T_1; consequently, we can compare the two traits with respect to how effectively they performed their shared function of

solving the adaptive problem (P_1) during that 250 year period (as per option (1) above). But there will not have been <u>steady</u> selection for T_2 over T_1 during this entire 250 year period. This long period will show some fluctuations, including short periods in which T_1 actually increased in frequency relative to T_2 due to fluctuations in the conditions under which the two traits function to solve the adaptive problem.

At this point, we confront the same difficulty as before. We could take the entire 250 year period as the "time at which there was selection for" the modified trait over its ancestral version, and then we will classify the modified trait (T_2) as an instance of natural design, since it solved the adaptive problem better than the ancestral version (T_1) did in the long haul. But there is nothing in the nature of things forcing us to measure the relative frequencies of the two traits with respect to the entire period in which one replaced the other. We could just as justifiably focus on a shorter time span. Since the frequencies of the two traits fluctuated during the 250 year period, there will be at least one shorter time span <u>s</u> in which T_1 increased in frequency relative to T_2. What are we to say about T_2 during <u>s</u>? We seem to be faced with the following dilemma in applying Allen and Bekoff's revised criteria. On the one hand, we could insist that <u>s</u> be ignored and that the two versions of the trait should be compared only with respect to those periods in which T_2 is increasing in frequency relative to T_1. But this would be wholly arbitrary. On the other hand, we could take <u>s</u> into account. But then T_2 will not count as an instance of natural design during <u>s</u>, since T_1 will be performing their shared function better than T_2 (so condition (ii.c) will not be satisfied by T_2 during <u>s</u>). Thus, within the longer 250 year period in which T_2 replaces T_1, there will be short time spans in which T_2 is an

instance of natural design by Allen and Bekoff's criteria and other short time spans in which it will not be an instance of natural design, but instead will merely have the function of solving the adaptive problem. And, again, there are no principled grounds for comparing the functional effectiveness of the two version of the trait in one of these time spans rather than another, or in the long time span rather than the shorter ones. But, again, this entails that there is no principled distinction between a trait's being designed for solving an adaptive problem and its merely having the function of solving that problem.

3. A Closer Look at Functions.

The distinction between design and mere function was very clear, however, in Allen and Bekoff's artifactual examples. For instance, although a rock of sufficient mass can function as a paperweight, that rock is not designed to be a paperweight unless it has been modified to "perfect" it for the function of being a paperweight. So how can a distinction that is so clear in the artifactual cases that Allen and Bekoff mention be so unprincipled in the biological case? Because Allen and Bekoff's examples of functional artifacts are strongly disanalogous to functional traits of organisms in lineages undergoing evolution. One might think this disanalogy derives from a difference between artifact function and biological function. There is, indeed, a difference between artifact function and biological function; but the source of the disanalogy lies elsewhere. To see this, however, it is necessary first to be very clear about the conception of biological function to which Allen and Bekoff are committed; for I share their conception, and will employ it in section 4.

In the biological case, Allen and Bekoff claim to hold a fairly standard version of the etiological theory of functions. Up to this point, I have treated this version of the etiological theory as ascribing a function to a trait when it has been selected for producing some effect. But elsewhere I have shown that there has been a systematic, yet undetected, ambiguity in the various formulations of the etiological theory (Buller 1998). It has generally been assumed that the various formulations of the theory share the same fundamental commitment and that they are, consequently, merely stylistic variants of that same essential commitment. But the formulations are, in fact, stylistic variants of two non-equivalent versions of the etiological theory.[1]

One standard formulation of the etiological theory is the following, which I will call the "strong etiological theory":

> A current token of a trait $\underline{T}$ in an organism $\underline{O}$ has the function of producing an effect of type $\underline{E}$ just in case past tokens of $\underline{T}$ contributed to the fitness of $\underline{O's}$ ancestors by producing $\underline{E}$ <u>and</u> were selected for (over alternative items) <u>because of</u> this contribution to the fitness of $\underline{O's}$ ancestors.

This formulation is to be found in Millikan (1993, pp. 35-36), in which the parenthetical clause is explicit, and in Neander (1991a, p. 173; 1991b, p. 459) and Godfrey-Smith (1994, p. 359), in which it is not. Regardless of whether the parenthetical clause is explicit, any formulation that appeals to selection in defining the function of a trait is committed not only to the parenthetical clause, but to much stronger conditions as well, as I will show in a moment.

In contrast to the above, the etiological theory is sometimes articulated without appeal to selection for the functional trait, but with an emphasis only on the requirement that the functional trait be a reproduction of items that had the same effect(s) (see, for example, Millikan 1989b, p. 289). This idea is encapsulated in the following, which I will call the "weak etiological theory":

A current token of a trait $\underline{T}$ in an organism $\underline{O}$ has the function of producing an effect of type $\underline{E}$ just in case past tokens of $\underline{T}$ contributed to the fitness of $\underline{O's}$ ancestors by producing $\underline{E}$, and thereby causally contributed to the reproduction of $\underline{Ts}$ in $\underline{O's}$ lineage.

Like the strong etiological theory, the weak etiological theory defines the function of a current token of a trait in terms of the role played by ancestral tokens. Nonetheless, the two theories are not equivalent; for, while the strong etiological theory entails the weak, the converse does not hold.

To see why, consider first the strong etiological theory. By defining the function of a current token of a trait $\underline{T}$ as the production of an effect (in $\underline{O's}$ ancestors) because of which there was selection for past tokens of $\underline{T}$, the strong etiological theory attributes a function to a trait $\underline{T}$ only when the following three conditions are satisfied, each of which is a necessary condition for there being selection for a trait: (1) $\underline{T}$ is hereditary, (2) there has been variation in $\underline{T}$ within a common selective environment (see Brandon 1990), and (3) the bearers of $\underline{T}$ had greater fitness within that common environment than bearers of $\underline{T's}$ variants (at least partly) because of possessing $\underline{T}$. The weak etiological theory, in contrast, does not define the function of a trait in terms of selection for it, and thus does not make it a necessary condition of $\underline{T's}$ having a function

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that there was variation in T. And, since variation is not required, it is also not necessary that

the bearers of T had greater fitness than any other organisms. The weak etiological theory

requires only that T contributed to the fitness of the ancestors of T's current bearers by

producing an effect E and that this, in turn, contributed to the reproduction of Ts. These

conditions are satisfied provided that (1) T is hereditary and (2) T causally contributed to the

fitness of ancestral bearers of the trait. For any trait that satisfies both of these conditions will

have causally contributed to its own reproduction via genetic mechanisms of inheritance and

development.

The weak etiological theory thus attributes functions to traits more liberally than the

strong etiological theory, since it counts as functional any hereditary trait of an organism that

causally contributed to the fitness of that organism's ancestors, regardless of whether there was

selection for that trait. Indeed, in accordance with the above requirements, the strong theory's

function attributions constitute a proper subset of the weak theory's function attributions.

To illustrate the difference between the strong and weak theories, suppose that T is a

hereditary physiological trait that plays a causal role in the process of gamete production, but

that either (a) through genetic happenstance the necessary mutation(s) never occurred in the

population to produce an alternative to T (cf. Kitcher 1993, p. 388), or (b) mutation produced

alternatives to T in the population, but no two of the alternatives occurred within a common

selective environment. In either case, there cannot have been selection for T. But, since ex

hypothesi T does play a causal role in gamete production, T does causally contribute to the

fitness of its bearers. Under these conditions, the strong theory would withhold a function

attribution from T, since there has never been selection for T. But, since T does make a

hereditary contribution to the fitness of its bearers, T does have some effect in virtue of which it

gets reproduced across generations; so the weak theory would attribute a function to T. Thus,

while the strong theory looks for a history of selection for a trait, the weak theory looks only for

a history of a hereditary contribution to fitness.[2]

　　　While not acknowledging the distinction between the strong and weak etiological

theories, Allen and Bekoff clearly seem committed only to the weak etiological theory, as

evidenced by a number of passages. For example, they formulate the etiological theory as

holding that "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" (1995b, p. 26). Here the function of a

trait is not defined in terms of selection for the trait, but rather in terms of the trait's

contribution to the selection of organisms with that trait, where the selection of organisms is a

matter of overall fitness differences among organisms, which may ultimately be due to

differences in other traits. Consequently, this formulation does not require that a functional

trait have a history of variation within a common selective environment, but only that it has a

history of contributing to the fitness of its bearers. "Thus," Allen and Bekoff continue,

> the claim that "a function of a bow in a population of canids is to communicate that
>
> what follows is play" means that the past tendency of bows to communicate that what
>
> follows is play contributed to the reproductive success of ancestors of the present
>
> population. (1995b, p. 26)

In other places as well they formulate the etiological theory in a way that does not require a history of selection for a functional trait, but only a history of contribution to ancestral fitness leading to the reproduction of tokens of the functional trait: "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" (1995b, p. 28). Note here that it is not the differential success of traits that matters, but the differential success of organisms bearing the traits. And, as a final example, in characterizing the "historical notion of function," Allen and Bekoff say, "a trait's function is the specific contribution that ancestral versions of the trait made to individual fitness" (Bekoff, et al. 1995, p. 253).

I have taken pains to clarify these points because it is all too often assumed that the etiological theory requires that a trait have been selected for in order to have a function. But there is a clearly historical — hence etiological — conception of function according to which a trait itself need not have been selected for, but need only have made a contribution to the success of organisms undergoing selection. This is what I have called the "weak etiological theory" and, if we are to take Allen and Bekoff's explicit statements literally (which is what I propose to do), Allen and Bekoff are committed only to the weak etiological theory, not the strong. Since I am also committed to the weak etiological theory (Buller 1998), I am in agreement with Allen and Bekoff about what it is for a trait to have a function. So none of my disagreement with Allen and Bekoff concerning the relation between function and design turns on a difference in our conceptions of biological function.

To return, then, to the distinction between artifact functions and biological functions, there is a clear difference between the two. For example, the effect of weighting papers is not an effect of a rock in virtue of which rocks are reproduced (in fact, rocks are simply not reproduced from other rocks at all). Similarly, decorating walls is not an effect of stags' heads in virtue of which stags' heads got reproduced. So there is a sharp difference between biological functions and the functions of Allen and Bekoff's chosen artifacts. Nonetheless, I will now argue that it is not this difference that accounts for the disanalogy between Allen and Bekoff's artifactual examples and the functional traits of organisms. Rather, the source of the disanalogy lies in a difference between the types of <u>item</u> that possess the functions: each example of a functional artifact that Allen and Bekoff cite is radically unlike a functional trait of an organism. And this difference involves a different relation between the phenomena of function and design in the case of organismic traits (but not only organismic traits) than in the artifactual cases. For, I will now argue, every trait that has a function in an organism as per the weak etiological theory (which, I have argued, is how we should interpret Allen and Bekoff's clause (i)) is also designed for its role (contra Allen and Bekoff's clause (ii)).

4. System Design, Constraints, and Component Design

To see this, begin by considering two different paths by which one can approach the phenomenon of natural design, where these are a function of different perspectives on the operation of natural selection. First the two perspectives on selection.

On the one hand, natural selection can be seen as working to create <u>adaptations</u> via accumulated small modifications to traits over evolutionary time. Indeed, historically, one of the central explanatory functions of the theory of evolution by natural selection has been explaining how "organs of extreme perfection" come to be. This trait-centered perspective on natural selection is the perspective of optimization theory, which typically models a trait of an organism in relative isolation from the rest of the organism. Insofar as other traits of the organism enter such models, they appear as historical, developmental, or trade-off constraints on the optimality of the trait under study (see, e.g., Seger & Stubblefield 1996). Given this abstraction of a trait from its organismic context, optimization theory studies how natural selection may have optimized the trait for a particular function by retaining each mutation that moved the trait closer to optimality.

On the other hand, natural selection can be seen as working to create <u>complex organisms</u>, or other living things, which exhibit functional interdependence of parts and overall adaptedness to the environment. This organism-centered perspective on natural selection corresponds to another primary explanatory function of the theory of evolution by natural selection — that of answering the Big Question of the origins of complex living things. Answering the Big Question was one of the major triumphs of Darwin's principle of natural selection over Paley's argument from design, and forcefully articulating and defending this explanation is the principal point of works such as Dawkins' <u>The Blind Watchmaker</u>. As Dawkins puts it:

living things are too improbable and too beautifully "designed" to have come into

existence by chance. How, then, did they come into existence? The answer, Darwin's

answer, is by gradual, step-by-step transformations from simple beginnings, from

primordial entities sufficiently simple to have come into existence by chance. (1986, p.

43)

From this perspective, the theory of evolution by natural selection can be seen as having

"ushered in a new way of thinking about the design of organisms" (Lauder 1996, p. 58;

emphasis added).

Of course, these two perspectives on natural selection are not in the least incompatible.

Indeed, it is one of the strengths of the theory of evolution by natural selection that it explains

the origins of both complex living things and their "organs of extreme perfection." But these

two ways of looking at what it is that natural selection does are avenues to very different

conceptions of natural design. If the phenomenon of natural design is approached from the

trait-centered perspective on natural selection, design will appear in the first instance as a

property of traits, and attempts to articulate the concept of design will take the form of

specifying the conditions under which it is appropriate to say that some trait is "designed for"

some particular role. Given this approach to design, these conditions will be specified in terms

of a particular type of history of natural selection acting directly on a trait, independently of

how that trait fits into the overall structure of the organism possessing it. And this, in fact, is

precisely the approach to design exemplified by Allen and Bekoff's theory. From the organism-

centered perspective, in contrast, design will appear in the first instance as a property of

organisms as wholes (as per the above quoted passages from Dawkins and Lauder). From this vantage point, selection is seen as "choosing" among competing designs in each generation, preserving those designs that exhibit the highest overall adaptedness to the environment (Lauder 1996, p. 60). Traits then appear as "components of design" (Lauder 1996, p. 56), and are considered "designed for" whatever contributions they make to the success of organismal designs under selection. In this case, it will not be necessary for selection to have acted directly on a trait in order for it to be designed for its role, and ipso facto not necessary that the trait underwent modification by selection for its role; it is sufficient simply that it contribute to the overall design of the organism possessing it.

It is important to note that both conceptions of design agree in taking design to be a product of, or created by, the operation of natural selection. So both conceptions of design see natural design only where natural selection has done some work to create it. They differ only with respect to what they emphasize natural selection as acting on — traits or organisms. This, in turn, makes the views differ with respect to how direct a link there must be between the operation of selection and what a trait is designed for. In the trait-centered case, selection must have operated directly on the trait. In the organism-centered case, the link between the design of a trait and the operation of selection can be very indirect: selection must only create overall organismic design and a trait must contribute to that design, independently of whether there was direct selection for the trait's role in that design. Precisely how a trait can be designed by natural selection in this sense is what I will now explain and defend.

To begin, consider again Allen and Bekoff's rock-paperweight example. First, the rock-paperweight is <u>unarticulated</u> — that is, it does not possess an internal articulation into parts that themselves produce effects that are involved in, or required for, the rock's performing its function as a paperweight. Second, the rock-paperweight is <u>unintegrated</u> — that is, it is not itself a component part of a larger paperweight system and, hence, does not produce an effect that plays a causal role within a more inclusive system that is a paperweight (rather, the rock itself is the entire paperweight). Thus, there are no constraints on the rock's function deriving either from processes that it contains or processes in which it is contained. The rock performs its function as a paperweight just by directly "engaging" the world with a single effect, holding down papers, which it produces simply by being placed on top of papers.

In contrast to the rock-paperweight, organismic traits that satisfy the weak etiological theory of functions are <u>articulated,</u> since functional traits are internally complex, decomposable into substructures that themselves make a causal contribution to the production of the functional trait's proper effect. A favorite functional example of philosophers, the heart, clearly illustrates such internal articulation. Such traits are also <u>integrated</u>, since they have functions in virtue of making (or having made in the past) a contribution to fitness via a causal contribution to a component of fitness — to viability, fertility, fecundity, or mating ability. But no trait makes a causal contribution to fitness in isolation from the other traits of the organism possessing it. Rather, and properly speaking, traits are <u>components</u> within complex functionally integrated organismic <u>systems</u>. In all such complex systems (natural or artifactual), a component makes a contribution to features of the entire system in virtue of causal

interactions with the other system components to which it is connected. It is thus the sum of the

actions of this network of connected subsystems that produces the features of the system as a

whole. The heart, again, illustrates such integration; for it makes a contribution to fitness only

in virtue of being properly connected with the rest of the circulatory system, which in turn

makes a contribution to fitness only in virtue of being connected with the rest of an organism's

vital systems (e.g. the respiratory system).

When a functional item is, like an organismic trait, both internally articulated and

externally integrated, it is nested within a functional <u>hierarchy</u> of subsystems. There are thus

subsystems "below" the functional item in the hierarchy whose effects are causally necessary

for its producing its proper effect — in particular, those subsystems that constitute its internal

articulation. The heart, for example, is internally articulated into the atria and ventricles

(among other things), the contractions of which are causally necessary for the heart's pumping.

In addition, there are (sub)systems "above" the functional item in the hierarchy to whose

proper effects its own proper effect is causally necessary — in particular, those (sub)systems

with which it is externally integrated. The heart's pumping, for example, is causally necessary

for the circulatory system to produce its proper effect of transporting nutrients to the cells of the

body. Being so nested in a system hierarchy, there are <u>constraints</u> on an item's function that

stem both from the subsystems below it and the (sub)systems above it in the hierarchy. That is,

only an item with a highly specific set of properties could occupy a locus in a system hierarchy

in such a way as to effectively interact causally with other system components and thereby

contribute to the overall success of the system. These constraints on a functional item in effect

constitute a set of system "needs" for the locus occupied by that item; and only an item that can satisfy those "needs" will come to occupy that locus. This contrasts sharply with artifacts such as the rock-paperweight; for there are no constraints on the rock-paperweight deriving from subsystems to which it is connected, since it is neither articulated nor integrated. There is thus a strong disanalogy between organismic traits and artifacts such as the rock-paperweight.

But what does this disanalogy have to do with function and natural design? Well, since there are no systemic constraints on the function of the rock-paperweight, it can perform its function of paperweighting just by being placed on top of papers. Design for paperweighting is thus in no way necessary for the rock to perform this function. Even more than this, however, since the rock can perform its paperweighting function in the absence of design for that function, there is <u>no room</u> for design to enter into the rock's function <u>except</u> by way of modification to better perform the function that it already performs in the absence of design. In contrast, the systemic "needs" that a functional item must satisfy in order to occupy a locus within a complex hierarchical system constitute a set of <u>design constraints</u> on that functional item. That is, the design of the system as a whole — its design as a functionally integrated system — requires an item with a highly specific set of properties to occupy a particular locus within that system in such a way as to interact effectively with the other system components. An item that possesses that set of properties, and effectively interacts with other system components so as to satisfy the design constraints on the locus it occupies, is in a strong sense <u>designed for</u> its role within the system. Thus, design enters into the functions of system components in virtue of the requirements placed on those components by the overall design of

the system of which they are parts. And a component can be designed for the locus it occupies

without ever having been modified to better perform the function required of it.

Let me sharpen these points with an artifactual example that <u>is</u> analogous to an

organismic trait and, thus, more appropriate than the artifactual examples offered by Allen and

Bekoff. Consider the prototype of the gasoline-powered internal combustion engine. The

engine as a whole had to be designed to convert chemical energy into mechanical energy with a

certain minimum degree of efficiency. (Analogously, natural selection designs organisms <u>as</u>

<u>wholes</u> to solve the adaptive problems posed by their environments.) The overall design

requirements on the internal combustion engine in turn required a component that would

perform the function of vaporizing gasoline and delivering the resulting gas-air mixture to the

combustion chamber. This design requirement was satisfied by the carburetor, which had to be

constructed in a highly specific way so as to satisfy the design constraints that the system as a

whole placed on the locus the carburetor was to occupy within it. (Analogously, the

environmental problems that natural selection designs organisms to solve place demands on

those parts of organisms that can be involved in solving those problems, and these demands

create "a hierarchy of ever more specific selection pressures" on the subsystems that compose

those parts (Kitcher 1993, p. 390).) Of course, internal combustion engines underwent

tremendous evolution after the prototype, and part of that evolution involved modifications to

the carburetor to make it more efficient in performing its function. But the crucial question is:

Was the carburetor of the prototype — the first version of the carburetor, prior to any

subsequent modification — designed to vaporize gasoline or not? Clearly the answer is "yes."

So it is not true that only modified versions of the first carburetor were designed to vaporize gasoline, while it was merely the function of the first carburetor to do so. The modified versions of the carburetor were merely better designed.

The difference between the rock-paperweight and the carburetor is that the rock-paperweight can perform the function of paperweighting in the absence of design, whereas nothing can perform the function of vaporizing gasoline in an internal combustion engine without satisfying a set of design constraints derived from the overall design of the engine within which that function is performed. Indeed, in general, no component performing a function in a complex system would even be a component of that system if it did not satisfy the design constraints placed on it by the system; components that do not satisfy such design constraints are eliminated (by natural selection in the biological case and human designers in the artifactual case). In other words, integrating within the overall design of the complex system that contains a component is a necessary condition for that component's performing a function in that system, since selection processes (either natural or artificial) weed out components that fail to integrate within overall system design. Thus, being designed for its role within a complex (artifactual or natural) system is a necessary condition of a component's performing a function within that system, since if the component were not designed for its role it would not be there in the system performing that function.

When the focus is thus shifted from Allen and Bekoff's artifactual examples to artifactual examples that actually are analogous to organismic traits, it can be seen that proper design is a necessary condition for component function in a complex system, even if that component has

never undergone modification for its function. And, since traits are properly speaking components of complex organismic systems, proper natural design of a trait is a necessary condition for biological function, and modification for that function is not necessary for design. For the design of components of complex systems (including traits of organisms) is a function of the role those components play within overall system design. Design, as it were, "trickles in" from the system as a whole to the components that contribute to the system's satisfaction of the design requirements that are placed on it as a whole. Thus, in designing organisms as wholes to respond to certain adaptive problems, natural selection thereby designs the conditions that parts of organisms must satisfy in order to help the organism respond to environmental demands; and when a part satisfies those conditions, it is designed for its role within the organism.

It may seem, however, that this goes too far. For the above discussion may appear to make natural design a wholly non-historical phenomenon, thereby divorcing it radically from the phenomenon of function, which is essentially a historical notion according to the weak etiological theory. In particular, it may appear that an item must first be designed for its role within an organismic system and only subsequently be reproduced because of its playing that role. To put this graphically, a trait T that contributes to the fitness of the "first" organism O in a lineage to possess T does not have a function in that organism, since a trait has a function only if it is a reproduction of earlier items that contributed to fitness in the same way. And it may appear that the conception of design I have been urging would count T as being designed for its contribution to the fitness of O, since it may appear that T causally interacts with other

components of O in such a way as to contribute to O's satisfaction of the design requirements placed on O by its selective environment.

But this appearance is deceptive; for traits that have no history under a selection process are not actually instances of natural design. The reason is the same as the reason they do not have functions under the etiological conception of function (see Neander 1991b, pp. 460-461). Each token trait that has a function in an organism is embedded in a causal nexus where it produces numerous effects, many of which are not produced by other tokens of its (homologous) type. Which of these numerous effects it is the <u>function</u> of that token to produce is a matter of the contribution of the trait <u>qua type</u> to the fitness of organisms possessing tokens of it — that is, a matter of which effect serves to contribute to fitness <u>when averaged over the class</u> of tokens of that type. Such average contributions to fitness can only be assessed transgenerationally, however, since they are determined by the operation of selection on a lineage. So, under the etiological conception, a trait has the function of producing some effect only when a transgenerationally stable relationship between that <u>type of trait</u> and a <u>type of effect</u> emerges through the process of natural selection. In exactly the same way, and for exactly the same reasons, design ascriptions are also grounded in a transgenerationally stable relationship between a <u>type of trait</u> and the <u>types of design constraint</u> the trait satisfies in the relevant organismic systems; and this transgenerationally stable relationship emerges only through the process of natural selection. Thus, a history under selection (of design constraint satisfaction) is just as necessary for a trait's being an instance of natural design as it is for its having an etiological function. (N.B. In both cases, the relevant selective history consists in the

operation of selection on a lineage, not on a trait. Traits have (weak etiological) functions and design because of their history of contributing to the success under selection of organisms in a lineage.)

Drawing all these considerations together, it is now possible to formulate succinctly an alternative to Allen and Bekoff's conception of natural design. I will call the following formulation the <u>systemic conception</u>: A token of a trait T in an organism O is <u>naturally designed</u> for X if and only if

(i)   O's ancestor/ancestors faced some adaptive problem P, the solution of which contributed to its/their reproductive success;

(ii)   there was some organismic (sub)system S of O's ancestor/ancestors that solved P;

(iii)   the demands that P placed on S required a causally integrated response from components of S and this, in turn, required a component occupying locus L in S to causally interact with the other components of S by performing task X; and

(iv)   T occupied L in S and successfully did X.

To briefly illustrate an application of the systemic conception of natural design: my kidneys are designed for filtering metabolic wastes from my blood, since (i) my ancestors faced the problem of combating toxicity, which (ii) their urinary systems solved by removing metabolic wastes from the body, which (iii) required a causally integrated response from components of the urinary system (e.g., renal arteries, ureters, bladder) and this, in turn, required a component occupying a position of access both to the blood and an outlet to the bladder to perform the

removal of metabolic wastes from the blood, and (iv) the kidneys occupied this position and successfully removed metabolic wastes from the blood.

The systemic conception of natural design is consequently more inclusive than the conception of design defended by Allen and Bekoff, since it does not make modification a necessary condition of design. But it is thereby coextensive, although not synonymous, with the weak etiological concept of function accepted by both Allen and Bekoff and me. For any trait that satisfies the systemic conception will have contributed to an ancestral solution to an adaptive problem and thereby will have contributed to ancestral reproductive success; such a trait will thus also satisfy the etiological conception of function and be ascribed the function of making that particular contribution to reproductive success (fitness).

5. Conclusion: Adaptation Again. The systemic conception of design thus restores the connection between function and natural design, but it loosens the connection between design and adaptation, when adaptation is conceived as requiring modification by selection for greater effectiveness in functional performance (the traditional conception of adaptation, which Allen and Bekoff accept). As the arms-race argument of section 2 showed, however, there is a systematic ambiguity in the notion of "modification for greater functional effectiveness." And this ambiguity infects the traditional conception of adaptation just as much as it infects Allen and Bekoff's conception of natural design. So an account of adaptation lacking this systematic ambiguity may restore a tighter connection between adaptation and natural design.

There are, at this point, two ways in which a tighter connection could be restored. First, one could adopt something like Sober's definition of "adaptation":

> $\underline{A}$ is an adaptation for task $\underline{T}$ in population $\underline{P}$ if and only if $\underline{A}$ became prevalent in $\underline{P}$ because there was selection for $\underline{A}$, where the selective advantage of $\underline{A}$ was due to the fact that $\underline{A}$ helped perform task $\underline{T}$. (1984, p. 208)

This makes "adaptation" synonymous with "function" (when the latter is understood in accordance with the strong etiological theory), and consequently makes both instances of "natural design" under the systemic conception. The disadvantage of this account of adaptation is that it departs rather widely from the common idea that adaptations involve a history of modification.

Second, one could retain the requirement of modification, but divorce it from the notion of greater effectiveness in the performance of some function. This could be accomplished as follows: An adaptation is a trait that has undergone <u>design improvement</u> under selection. Under the systemic conception of natural design, the notion of design improvement would require only that a trait be modified to more efficiently satisfy the overall design constraints of the organismic system of which it is a part. That is, a modification would be judged to be a design improvement strictly in terms of wholly <u>intrasystemic</u> engineering standards, and not in terms of extrasystemic effectiveness in solving a specific adaptive problem: A modification to a system component that results in <u>more efficient overall system design</u> is a design improvement, regardless of whether it results in greater effectiveness in solving the adaptive problem that it is that component's function to solve. Suppose, for example, that mutation produced a

modification to the leg muscles of cheetahs, which made the muscles more efficient in converting chemical energy into contractile force, resulting not in an increase in contractile force, but only in a decrease in the amount of chemical energy used by the muscles in producing the same contractile force as before the modification. Presumably, the leg muscles of cheetahs have the function of enabling cheetahs to catch prey. But this modification would not result in greater running speed, hence would not result in greater effectiveness with respect to solving the problem of catching prey. Nonetheless, the modification would reduce the energy burned by cheetahs in chasing prey, and thus reduce the frequency at which feeding is necessary. In short, the modification produced an overall more efficient organismic design, even though it did not result in "greater functional effectiveness" with respect to running speed and the catching of prey. If adaptations are understood in this way (as traits that have undergone intrasystemic design improvements), the cheetah's modified muscles would count as an adaptation.

This account of adaptation thus avoids the systematic ambiguity involved in the notion of "modification for greater functional effectiveness." At the same time it accords very well with the conception of adaptation that is at work in discussions of evolutionary arms races. As Dawkins describes evolutionary arms races, for example, there is "progress in design, but no progress in accomplishment," because an arms race is a process of "equipment improving while its net effectiveness stands still" (1986, p. 186). No account of adaptation that defines improvement in terms of increased effectiveness in solving a specific adaptive problem can apply to these sorts of adaptive change. But the adaptive changes that typify arms races fit very

naturally within an account of adaptations as traits that have undergone intrasystemic design improvement, when this is understood in accordance with the systemic conception of natural design. In sum, then, the current proposal can accept Allen and Bekoff's distinction between merely functional traits and adaptations; it simply shows both to be instances of natural design, while showing adaptations to be special cases of natural design.

When the focus is thus shifted away from Allen and Bekoff's artifactual examples to artifactual examples that are articulated and integrated functional components of complex systems, proper design emerges as closely related to function. And functional traits of organisms are precisely such components of complex functionally integrated systems. Of course, Allen and Bekoff's artifactual examples do show that, if we are concerned to provide an analysis of the concept of <u>function</u> in <u>all</u> its uses (if we are concerned to provide something like a set of necessary and sufficient conditions for the fully general employment of the concept), design is not a necessary condition for function. But the considerations that motivate this conclusion are not relevant to cases of <u>biological</u> function. In the biological case, function and design are inseparable.

NOTES

1. The following four paragraphs are adapted from Buller (1998). See that source for a detailed treatment of the differences between the two versions of the etiological theory.

2. It is sometimes assumed (e.g., by Millikan 1989a) that the notion of a trait's "contribution to fitness" can only be made sense of if the trait has been selected for making that specific contribution. But it is just the opposite: The notion of a trait's being <u>selected for</u> can only be made sense of in terms of its contribution to fitness (see Buller 1998, pp. 510-511; see also Sober 1984, p. 100).

REFERENCES

Allen, C. & M. Bekoff (1995a). "Biological Function, Adaptation, and Natural Design,"

Philosophy of Science 62, 609-622.

Allen, C. & M. Bekoff (1995b). "Function, Natural Design, and Animal Behavior: Philosophical

and Ethological Considerations." In: N. S. Thompson (ed.), Perspectives in Ethology 11:

Behavioral Design, Plenum Press, New York, pp. 1-46.

Bekoff, M. & C. Allen (1995). "Teleology, Function, Design, and the Evolution of Animal

Behavior," Trends in Ecology and Evolution 10, 253-255.

Brandon, R. N. (1990). Adaptation and Environment, Princeton University Press, Princeton.

Buller, D. J. (1998). "Etiological Theories of Function: A Geographical Survey," Biology and

Philosophy 13, 505-527.

Davies, N. B. & M. Brooke (1991). "Coevolution of the Cuckoo and Its Hosts," Scientific

American 264(1), 92-98.

Dawkins, R. (1982). The Extended Phenotype, Oxford University Press, Oxford.

Dawkins, R. (1991). The Blind Watchmaker, Penguin Books, London.

Endler, J. A. (1986). Natural Selection in the Wild, Princeton University Press, Princeton.

Endler, J. A. (1991). "Interactions Between Predators and Prey." In: J. R. Krebs & N. B. Davies (eds.), <u>Behavioural Ecology: An Evolutionary Approach</u>, Blackwell Scientific Publishers, Oxford, pp. 169-196.

Godfrey-Smith, P. (1994). "A Modern History Theory of Functions," <u>Noûs</u> 28, 344-362.

Kitcher, P. (1993). "Function and Design," <u>Midwest Studies in Philosophy</u> 18, 379-397.

Krebs, J. R. & N. B. Davies (1993). <u>An Introduction to Behavioural Ecology</u> (3rd ed.), Blackwell Scientific Publications, Oxford.

Lauder, G. V. (1996). "The Argument from Design." In: M. R. Rose & G. V. Lauder (eds.) <u>Adaptation</u>, Academic Press, San Diego, CA, pp. 55-91.

Lewontin, R. (1978). "Adaptation," <u>Scientific American</u> 239(3), 212-230.

Lotem, A. & S. I. Rothstein (1995). "Cuckoo-Host Coevolution: From Snapshots of an Arms Race to the Documentation of Microevolution," <u>Trends in Ecology and Evolution</u> 10, 436-437.

Millikan, R. G. (1984). <u>Language, Thought, and Other Biological Categories</u>, MIT Press, Cambridge, MA.

Millikan, R. G. (1989a). "An Ambiguity in the Notion 'Function,'" <u>Biology and Philosophy</u> 4, 172-176.

Millikan, R. G. (1989b). "In Defense of Proper Functions," <u>Philosophy of Science</u> 56, 288-302.

Millikan, R. G. (1993). "Propensities, Exaptations, and the Brain." In: <u>White Queen Psychology and Other Essays for Alice</u>, MIT Press, Cambridge, MA, pp. 31-50.

Neander, K. (1991a). "Functions as Selected Effects: The Conceptual Analyst's Defense," <u>Philosophy of Science</u> 58, 168-184.

Neander, K. (1991b). "The Teleological Notion of 'Function,'" <u>Australasian Journal of Philosophy</u> 69, 454-468.

Reeve, Hudson Kern & Paul W. Sherman (1993). Adaptation and the Goals of Evolutionary Research. <u>Quarterly Review of Biology</u> 68(1): 1-32.

Ridley, M. (1996). <u>Evolution</u> (2nd ed.), Blackwell Science, Cambridge, MA.

Seger, J. & J. W. Stubblefield (1996). "Optimization and Adaptation." In: M. R. Rose & G. V. Lauder (eds.) <u>Adaptation</u>, Academic Press, San Diego, CA, pp. 93-123.

Sober, E. (1984). <u>The Nature of Selection</u>, MIT Press, Cambridge, MA.

van Valen, L. (1973). "A New Evolutionary Law," <u>Evolutionary Theory</u> 1, 1-30.

Vermeij, G. J. (1987). <u>Evolution and Escalation: An Ecological History of Life</u>, Princeton University Press, Princeton.

Weis, A. E., K. D. McCrea & W. G. Abrahamson (1989). "Can There Be an Escalating Arms Race Without Coevolution? Implications from a Host-Parasitoid Simulation," <u>Evolutionary Ecology</u> 3, 361-370.

Williams, G. C. (1966). <u>Adaptation and Natural Selection</u>, Princeton University Press, Princeton.

Williams, G. C. (1992). <u>Natural Selection: Domains, Levels, and Challenges</u>, Oxford University

Press, New York.