

# **Hyperadaptation–Another Missing Term in the Science of Form**

by

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## **Abstract**

In a 1982 paper, Gould and Vrba argue that a conflation of the two components of adaptation of a feature, historical development of the feature and present utility, has caused evolutionists to overlook a missing term in the science of form, which they call 'exaptation'. In the present project, I show that evolutionary biology still contains a confusion in the use of 'adaptation' due to an inappropriate perception of the interaction between the two components of adaptation. Because of the confusion, evolutionists have missed another term in the science of form. Evolutionary theory, specifically the treatment of adaptation, would profit from the introduction of a term referring to features that have a selective history which causes them to appear overly well adapted to their present function. I suggest we refer to these features as *hyperadaptations*, since they appear to be hyperbolized adaptations. By introducing *hyperadaptation* into the conceptual framework of adaptation, we can sharpen our understanding of related concepts (adaptation to function, exaptation, maladaptation, etc.) and remove or reduce some confusion regarding the interplay between analysis of historical pathways and

ascriptions of (current) function in the diagnosis of adaptation. Furthermore, the improved framework should allow evolutionists to more adequately explain biological phenomena.

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## Introduction

It has been fifteen years since Gould and Vrba's (1982) seminal paper on exaptation charged evolutionary biologists with a conflation of terms in the conceptual taxonomy of evolutionary adaptation. They focus on two distinct components of features that determine whether they are adaptations: the historical development of the features and their present utility to their possessors. Gould and Vrba argue that evolutionists wrongfully conflate these two components and, consequently, have missed one type of evolutionary phenomenon which they term 'exaptation'. In this thesis, I intend to show that evolutionary biology still contains a confusion in the use of 'adaptation' due to an inappropriate treatment of the interaction between the two components of adaptation, i.e. history and (present) usefulness.

In chapter 1, I will discuss the current state of *adaptation*<sup>1</sup> within evolutionary biology. I will argue that there are four predominant uses of 'adaptation' which often create confusions when used ambiguously. I suggest that the adaptation (or selective evolution) of a feature to better perform some particular function (hereafter 'adaptation to function') is the most effective use of the term. Thus, evolutionists should focus on adaptation to function in their use of 'adaptation'.

In chapter 2, I will briefly discuss Gould and Vrba's introduction of 'exaptation' in response to empirical anomalies to the theory of adaptation. I will then show that there is another missing term in the conceptual

taxonomy of adaptation, which I call 'hyperadaptation'. Hyperadaptations are features that appear to be overly well adapted to their present function. Our current understanding of adaptation does not distinguish them from adaptations.

In chapter 3, I will present several examples of hyperadaptations. In a detailed case study, I will show how the mammalian corneal endothelium, the posterior tissue layer of the cornea of the eye, is hyperadapted to its function. I will then discuss other cases which appear to be best labeled as hyperadaptations, including the potential for hyperadaptations caused by social evolution.

In the fourth and final chapter, I will discuss the consequences of the introduction of *hyperadaptation* for the conceptual framework of evolutionary adaptation. I will show how the concept will serve as another label with which experimentalists can describe features. Additionally, hyperadaptation can clarify much of the confusion caused by the current inappropriately constrained conceptual framework. Finally, I will discuss ways in which the introduction of hyperadaptation might cure some common problems in evolutionary thinking.

## Notes

<sup>1</sup> As a convention, I will use italics when referring to concepts, single quotes when referring to terms, and normal type when referring to the phenomena.

## Chapter 1

### 'Adaptation' in Evolutionary Biology

There are as many different uses of 'adaptation' in the context of evolution. In a 1957 paper, Richard Lewontin observed:

There is virtual universal disagreement among students of evolution as to the meaning of adaptation (p. 395).

Not only has a unified understanding of the term not become more clear since Lewontin's critical remark forty years ago, *adaptation* may even be more convoluted now than it was then. The problem is not so much that evolutionists disagree on the *meaning* of 'adaptation' but that we are promiscuous with its *use*.

In this chapter, I will attempt to demarcate what I take to be the main uses of 'adaptation' within an evolutionary context. From these, I shall argue that the adaptation of a character, trait, or feature of an organism to some function, i.e. the *end result* of a process by which a character has adapted to the environment in a manner that contributes to the overall fitness of its possessor, is the most profitable use of the term to theoretical biology.<sup>1</sup> I will consider problems with this understanding of *adaptation to function*, including epistemological, methodological, and theoretical objections to such a definition. After establishing a definition of adaptation to function, I will move to a more sophisticated discussion of how attempts to apply adaptation, even in its best guise, to natural phenomena have required a retooling of our theoretical work.



There are at least four different aspects or contexts in which 'adaptation' is used in evolution. Each of these correlates with different aspects of evolutionary theory. I have summarized these four uses of 'adaptation' in Table 1. In the first column, I have listed the four aspects of adaptation most commonly used in evolutionary contexts. Each aspect gives a distinct perspective from which evolutionists refer to adaptation and adaptations. Column two presents a name usually associated with each aspect of adaptation. The last column lists some concepts that relate to the particular uses of 'adaptation' given. These concepts are some of the alternative phenomena, subcategories, and synonyms generally connected with each aspect of adaptation.

**Table 1.** The uses of 'Adaptation' in evolutionary biology.

Aspect of Adaptation	Associated Term	Related Concepts
1. Adaptation as a program	Adaptationism	a. adaptationism b. neutralism c. pluralism
2. Adaptation as a process	Adaptation	a. natural selection b. nonadaptive processes <sup>2</sup> c. artificial selection d. sexual selection
3. Adaptation as a state	Fitness	a. organismic adaptation b. adaptedness
4. Adaptation to function	Function	a. function-form adaptation b. feature adaptedness c. exaptation d. maladaptation

## 1.1 Adaptation as a program

'Adaptation' carries a programmatic use in the so called *adaptationist program*, which is based on a belief in *adaptationism*. Adaptationism is the view that essentially all biological phenomena have evolved as the result of adaptations. Those features that are not adaptations themselves evolved nonadaptively due to constraints caused by the evolution of adaptations. For example, sickle-cell anemia is not an adaptation but is a byproduct of the adaptation for malaria immunity which is caused by the same gene that codes for sickle-cell anemia. Though sickle-cell anemia is not an adaptation, its presence, according to an adaptationist, would be explained by its connection to malaria immunity. Supporters of the adaptationist program generally accept adaptationism and thus base their research programs on adaptationism. They focus attention on adaptations and investigate features and organisms with the belief that their research is only interested in the effects of adaptation.

Gould and Lewontin attack adaptationism in a programmatic sense in their 1978 paper by arguing that most biologists overemphasize the importance of adaptations in evolution. Gould and Lewontin argue that this key tenant of the adaptationist program constrains a true understanding of evolutionary theory. Specifically, they charge that the adaptationist program is built on a narrow-minded view of evolutionary history:

We fault the adaptationist program for its failure to distinguish current utility from reasons for origin; for its unwillingness to consider alternatives to adaptive stories; for its reliance upon

plausibility alone as a criterion for accepting speculative tales; and for its failure to consider adequately such competing themes as random fixation of alleles, production of nonadaptive structures by developmental correlation with selected features, the separability of adaptation and selection, multiple adaptive peaks, and current utility as an epiphenomenon of nonadaptive structures (p. 581).

As this quotation suggests, adaptationists assume that all current features of organisms can be explained by adaptation. Adaptationists carry a dogmatic prejudice against alternative explanations to adaptive stories. Consequently, their approach to evolutionary biology is narrow-minded. Gould and Lewontin suggest a pluralistic research program instead.

While adaptationism, at least in the guise presented by Gould and Lewontin, is presently considered an extreme position, pluralism is a more moderate view that integrates both adaptations and neutral mutation events.<sup>3</sup>

By *pluralism*, I mean specifically the view supported by Gould and his co-authors (Gould 1977; Gould and Lewontin 1978; Gould and Vrba 1982).

While pluralism is not as easily defined as adaptationism, generally those who follow a pluralistic program are evolutionists who reject the extreme view of adaptationism<sup>4</sup> (and neutralism) as alone being too restrictive.

Pluralists usually support a variety of modes of evolutionary change including both adaptations and neutral fixation events in addition to unusual trait histories due to developmental, genetic, and/or environmental constraints.

Adaptation as program is probably the least problematic use of the term 'adaptation'. The main issue is that the adaptationist program has taken on a largely negative meaning due to criticisms like Gould and Lewontin's.

Because of the association between 'adaptationism' and 'adaptation', students of evolution and philosophy of biology may mistake the critique of adaptationism as a critique of the investigation of adaptation. Gould and Lewontin introduce adaptationism only to argue for its rejection both in principle and in practice.<sup>5</sup> More recently, Rose and Lauder (1996) charge that an association between adaptationism as a misguided research program and *adaptation* as a concept has kept evolutionists away from studying adaptation. They contend that adaptation should receive more critical attention; I agree.

## **1.2        Adaptation as a process**

The processes of evolutionary change are widely varied. Still, a standard division between so called adaptive and non-adaptive processes has many benefits. In adaptive processes, a feature is adapting to the environment over generations by some form of selection. The gold standard for selection is Darwinian *natural selection*. Darwin defined the term as the "preservation of favorable variations and the rejection of injurious variations" (1859, p. 80). While it has taken on a more sophisticated meaning, 'natural selection' is generally used in the same context as Darwin originally used it. It is the process by which traits that are beneficial to their possessor increase its likelihood to survive and reproduce in relation to conspecifics that do not have such traits. Over several generations, the proportion of individuals with beneficial traits will likely increase, possibly to fixation,

while the proportion of individuals with detrimental traits will decrease, possibly to extinction (see Endler 1992).

Other processes that fall under the guise of selection are artificial (human) selection and sexual selection. Artificial selection is the process which breeders use to improve their stock. It differs from natural selection in that artificial selection is not exactly a process of environmental adaptation.<sup>6</sup> Natural selection can be viewed as a process of adapting to the environment. Thus, organisms are generally better adapted (as a state; see below) to their environment than their ancestors in the traits where natural selection has occurred.<sup>7</sup>

Sexual selection is an alternative processes to natural selection which is generally considered adaptive. The selective pressure involved in sexual selection is the preferences of potential mates during courtship. Many species appear to have evolved features that enable one gender to better attract the other. For example, the female peacocks give mating preference to males with large, showy tail feathers. The male peacock's tail feathers does not serve any purpose other than to aid in attracting females for mating. What makes sexual selection interesting, as exemplified by the peacock, is that the female preference for showy tail feathers in males does not seem to benefit the reproductive success of the female or her offspring.<sup>8</sup> Thus, sexual selection produces features which are only beneficial in perpetuating their own existence. As with artificial selection, many evolutionists feel that, properly speaking, sexual selection is not a natural selective process. Though

it does not exactly fit the mold of natural selection, its relationship with adaptation as a process is analogous.

In addition to the various forms of selection, biologists have identified many non-adaptive processes by which evolution can occur. The strongest contrast with natural selection is random drift. John Beatty (1992) describes it as follows:

What most of the phenomena so designated [in the category of random drift] have in common is one or another biological form of random or indiscriminate sampling, and consequent sampling error (p. 271).

Random drift accounts for such events as the "bottleneck effect" and the "founder effect".<sup>9</sup> In each of these cases, small population sizes increase the likelihood of evolutionary change due to random events and other constraints of isolation. For example, many Hawaiian *Drosophila* populations exhibit unusual characteristics which suggest bottlenecking or founder populations in their evolutionary history. In these populations, natural selection is overshadowed by other evolutionary factors because of the small population size. In order for selection pressures to have a significant effect, highly fit individuals must survive and reproduce in greater numbers than less fit individuals. When the population size is small, fitness differentials play a reduced role in the propagation of offspring into future generations due to a relatively large amount of sampling error.<sup>10</sup> The sampling error often causes gene variants to *drift* in proportion through the population, as opposed to moving in the direction that their selective value predicts when based on fitness alone. Thus, random drift is called a

'nonadaptive' process. Though variations of random drift are the best understood nonadaptive processes, any process which alters a feature without involving a shaping of the feature due to environmental selection is considered a nonadaptive process.

The significance of adaptation as a process is crucial to the understanding of adaptation as a state and adaptation to function (1.3 and 1.4, respectively). Still, since we rarely see the process of adaptation, many biologists underemphasize it. Largely, the study of evolution involves describing how organisms and their characteristics came to be. Without a refined understanding of the different processes which caused the current states, we have no hope of providing such a description of the biological world. The process of adaptation is commonly called 'adaptation' simpliciter, since we recognize that it is the process that defines an adaptation.<sup>11</sup> Still, our motivation in discussing the process of adaptation is usually due to a desire to understand how things are now.

### **1.3 Adaptation as a state**

Before developing the use of 'adaptation' that I call 'adaptation as a state', I should say a few words on the process/state distinction regarding adaptation. The process of adaptation was discussed in detail in section 1.2. This discussion focused on *characters adapting over time*. The state of being an adaptation, I believe, requires a further distinction between organismic and trait adaptation, where the former involves the adaptation of the

organism as a whole to its environment<sup>12</sup> and the latter involves the connection between a feature and its function. 'Adaptation as a state' refers to organisms viewed as integrated wholes. In the next section, I present my views on the use of adaptation as the end result of the process of adaptation of a feature of an organism.<sup>13</sup>

Adaptation as a state is quite simply a time-slice (or generation-slice) view of individual organisms, evaluating their relationship to the environment. Though adaptation as a state is not exactly the same as fitness, the two are closely related. Fitness is usually described as the propensity of an individual organism to survive and reproduce in a given environment.<sup>14</sup> This is ideally a quantitative measurement that can be used to predict, with a moderate level of accuracy, the evolutionary development of a population in a stable environment. Adaptation as a state, conversely, is not a quantity but a qualitative depiction of individuals in relation to conspecifics within an environment.<sup>15</sup> Thus, organism *A* can be described as being better adapted than organism *B* to their shared environment without reference to fitness differentials determined quantitatively. Robert Brandon (1978) uses the term 'relative adaptedness' to describe such a difference between organisms, though Brandon seems at times to conflate adaptedness and fitness.

Another related use of adaptation as a state is not a comparison among organisms but a description of one organism's connection with the environment. An organism is said to be well adapted to its environment if it can effectively survive and reproduce in that environment. This use of



adaptation is rather vague. By claiming that an individual is well adapted, we must have some standard by which to measure what it means to be well adapted. This either requires comparison with other organisms or necessitates the possibility that an organism can be perfectly adapted to its environment. Most evolutionists seem to agree that a perfectly adapted organism is too difficult a concept to be useful, since this use of adaptation almost never occurs in published papers.<sup>16</sup>

Though adaptation as a state (organismic adaptation) is important, it seems as though the line between it and fitness is very thin indeed. Other than a recognition that fitness is caused by relative adaptedness, I see no reason why we cannot eliminate the term 'adaptation' from discussions of the state of organisms in favor of 'fitness'. 'Adaptation' and 'fitness' are generally used interchangeably in such contexts. However, while 'fitness' does not have other uses in evolutionary biology, 'adaptation' certainly does. I do not mean to imply that 'adaptation' has no purpose in discussions of fitness—certainly it does—but the confusions created by using the term far outweigh the benefit.

#### **1.4 Adaptation to function**

The relationship between adaptation and function exists at the level of features of organisms. By feature, I mean any characteristic which can be identified as contributing to or detracting from the fitness of its possessor. I also use the terms 'trait' and 'character' to refer to a feature. Note that while

many features may be phenotypic, i.e. overt expressions of a genotype, they need not be identifiable as such. Many traits do not map well on to phenotypes because of their complexities. Though this does pose a problem for the evolution of complex or polyfunctional traits, such a discussion is not important for my argument.

The main aspect of characters in relation to adaptation is seen in terms of their functional roles. Characters are said to have adaptive value when they have a particular function that contributes to the fitness of their possessor. Thus, the heart is adaptive because it has the function of pumping blood through the body which in turn contributes to the fitness of animals with hearts. The heart may also be adaptive because the thumping sound it makes is soothing to infants when in their mother's arms. Contrarily, the stomach is probably not adaptive because it growls since a growling stomach does not seem to contribute to the fitness of its possessor.

The common view of adaptation that I have in mind is analogous to that described above in 1.3, but in the context of individual forms as opposed to organismic fitness. A *form* is the physical and physiological state that allows for features. The connection is not exactly causal, but a particular form is a necessary condition for the expression of some feature. In some cases, a feature may be just the form of the organism, as with opposable digits and height. Other features, such as speediness, whose form is some configuration of the skeleto-musculature, require certain forms (or more precisely restrict

certain forms) but are not necessarily produced by the existence of these forms.<sup>17</sup>

A feature is said to be an adaptation when its form has a certain relationship with the environment that can broadly be construed as a function. That is, when a feature is formed in such a way that its function contributes to the overall fitness of its possessor, the feature is adapted for that function. Bock and von Wahlert (1965) call the cohesion of function and form a *faculty*. By their argument, a faculty is the fundamental unit of evolution. As they write:

The faculty, comprising a form and a function of the feature, is what the feature is capable of doing in the life of the organism and is the unit that bears a relationship to the environment of the organism. The faculty is the unit acted upon by natural selection and the aspect of the feature adapted to the environment (p. 276).

In this important passage, Bock and von Wahlert maintain that the faculty (function-form complex) is the thing upon which natural selection acts. As such, the process of adaptation alters faculties of organisms. The end result (or any time-slice for that matter) of the process is also termed an 'adaptation' since it expresses the relationship between the environment and the faculty as the form of a feature adapted to some function. This is what I call '*adaptation to function*'.

Bock and von Wahlert were certainly on target in introducing 'faculty' to explain what adaptation to function means. However, they seem to use analysis of faculties as a *substitute* for historical analysis and not as a supplement. Bock and von Wahlert disagree, claiming that any feature that

is functional, be it because of selection or accident, should be viewed as an adaptation. They argue that making such distinctions is extremely difficult and generally unnecessary. In my view, Bock and von Wahlert's claim poses several problems for a concise understanding of adaptation.

### **1.5 Problems with adaptation to function**

Bock and von Wahlert's arguments indicate two related attacks on the historical component of adaptation to function (more generally, any conception of adaptation involving a historical requirement). First, they argue that the historical development of features is unnecessary to a comprehensive theory of biological evolution. Second, while they do not espouse it directly, their paper implicitly suggests that the history of features is uninteresting to evolutionary biology. While knowing the history of a trait may often be difficult, I will argue for the remainder of this chapter that our ability to learn and understand the history of evolved features is sufficient to warrant providing a place for it within our theory and our research programs. Furthermore, understanding the history of some traits is necessary to their correct characterization. I will present four objections that are consistent with Bock and von Wahlert's criticisms (though they are not necessarily held by Bock and von Wahlert). In responding to each, I hope to show the possibility, importance, and necessity of understanding the historical development of evolved features. From this, the significance of natural history in the study of adaptation (to function) will become clear.

As I said above, there are four problems with a historical component in our definition of adaptation to function. Bock and von Wahlert raise similar objections by inquiring whether adaptations to function require a process of adaptation. Their answer is no. I will use the abbreviation '*adaptation<sub>B</sub>*' to refer to adaptations to function in Bock and von Wahlert's sense. Any feature whose faculty contributes to the fitness of if its possessor would be an *adaptation<sub>B</sub>*. I will refer to the opposing definition involving a historical component as simply 'adaptations'.

The four problems I will consider coincide with the following questions:

- 1.5.1 Does requiring an adaptive history for adaptations make the definition an empty tautology?
- 1.5.2 How can we know which characters have adaptive histories and which do not?
- 1.5.3 Will such a distinction have any bearing on evolutionary biology's research methodology?
- 1.5.4 Does the distinction have any significance for the theoretical development of evolution?

Each question presents a unique challenge to our understanding of *adaptation* as I have defined it. I will consider them in turn.

#### 1.5.1 *The tautology problem*

The issue of tautologousness was, until recently, a significant problem for fitness. Mills and Beatty's 1979 paper has essentially crushed the last remnants of the charge of tautologousness in fitness. The charge of being a tautology can also be levied on '*adaptation*'. Though the response to such an

objection may be obvious to some readers, especially in light of the arguments of Mills and Beatty, it is still worthwhile to state the argument.

'Adaptation (to function)' is used to determine what it means for a feature to have evolved via Darwinian natural selection (and possibly other forms of selection). Accordingly, adaptation is generally defined as follows:

a trait is an adaptation if and only if 1) it currently contributes to the fitness of its possessor (is adapted) and 2) its presence is due to a historical process of selection resulting in its current state.<sup>18</sup>

So, to the question, "Why do we call *this* trait an adaptation?" we answer "Because it has been historically selected for.". When further queried by, "Why was the trait selected?" the answer is often because the trait had a higher adaptive value than its absence. In other words, selection picks adaptive traits. Clearly, our dialogue is turning only left at the corners; it seems as though our definition is a tautology.

The response to this charge is analogous to Mills and Beatty's rejection of the circularity charge regarding fitness. Thus, the answer to the second question (Why was the trait selected?) is not that selection picks adaptive traits. Rather, traits that contribute positively to the fitness of their possessors are more likely (have a higher propensity) to be passed on to future generations. The differential contribution to fitness in relation to conspecifics is not itself an adaptation, but *often causes* changes in the population over generations which develop into adaptations.

### 1.5.2 *The epistemological problem*

The second problem with including a historical component to our understanding of adaptation to function is what I call 'the epistemological problem'. The focus of the problem is on how we can know the adaptive history of particular features. One might argue that since we have very little direct information regarding natural history, speculating about events beyond what little information we have is not justified. While I grant that we certainly have a problem with access to information about natural history, several techniques are available to help experimentalists make educated inferences.

Paleontology and geology have both served integral roles in our understanding of natural history. Geology and the recent development of the theory of continental drift give evolutionary biologists methods of theorizing about environmental conditions at particular times and places, which indicates what conditions existed during the adaptive history of organisms. Similarly, information about natural disasters, such as volcanoes and floods, can often be correlated with evolutionary changes (frequently due to nonadaptive processes). The dating of geological events in concert with fossil evidence also contributes to our knowledge of natural history. While fossil records are usually sparse and difficult to interpret, several studies have given us good grounds to believe that fossil evidence should be taken seriously (see Kitcher 1982).

In addition to information about "ancient history" determined by paleontological and geological evidence, short term evolutionary changes can also be correlated with both past short term and long term evolutionary changes. Research since Darwin has shown how organisms and populations evolve in both laboratory (pseudo-natural) and natural settings. Consequently, our current understanding of many adaptive and nonadaptive processes is fairly clear. We can extrapolate from these cases to consider natural populations in their adaptive history. For example, consider the "founder effect". By isolating a small group of organisms in a new environment, a few interesting things happen. First, the group will either quickly become extinct or grow rapidly, depending on the fitness of the individuals within the environment and a bit of luck. If the population survives, its gene pool will be very small (since the initial population was small). As such, deleterious features may fixate or beneficial features may be eliminated by random drift. These factors usually present the individuals of the population with a strong selection gradient that is associated with rapid evolutionary change. Over many generations, the population (if it survives) will likely have adapted to its new environment, often by unusual or costly adaptations. So, based upon studies with experimental populations, we can infer that natural populations exhibiting similar occurrences are also likely to have had similar adaptive histories. For example, the finches of the Galapagos Islands that Darwin himself described seem to have evolved from



founder populations. Several features of the different species are analogous to the results of experimental founder populations.

With all the work that has been done on natural and experimental populations like the case of Darwin's finches, I see no reason why we cannot assume that speculations regarding the adaptive histories of populations are justified. As long as we admit that there is a fine line between such speculative inferences and "just-so" stories and do our best not to cross the line, evolutionary biologists should be granted that their observations are no less justified than the observations of the electron microscopist or the nuclear physicist. Furthermore, the need for historical distinctions in the study of adaptation is closely integrated in our best research programs. This is a methodological concern, which is the subject of the next section.

### *1.5.3 The methodological problem*

Bock and von Wahlert present a research program based upon the view that we should treat all functional features of organisms as adaptations<sub>B</sub>. This is clearly an adaptationist program in Gould and Lewontin's sense and, as such, is subject to all the criticism levied by these authors. Still, Bock and von Wahlert's position does present an interesting argument. The argument goes: since our knowledge of the adaptive history of features is severely limited, grounding a research program under such a constraint will create significant and unnecessary confusions in our theoretical developments. However, as I argued in 1.5.2., the availability of historical knowledge regarding adaptations is not as limited as it seems.

Bock (1980, p. 225-6) suggests three ways in which evolutionists determine the history of adaptations: by comparison, correlation, and synthesis of organism with environment. By comparison, he means an analysis of similar features in other species. Correlation is the analysis of similarities and relationships among features in a single organism or species. The synthetic approach utilizes relationships between the organism, the faculty in question, and the environment to determine its adaptive value. Bock rejects the first two methods, supporting the last as the only viable option. My arguments from Sec. 1.5.2 do not distinguish these methods, leaving me open to a counterargument from Bock. I hold that his methodological distinctions are not as clear as he would like and that both comparative and correlative techniques are useful when used *in conjunction* with synthetic analysis. Furthermore, without the first two methods, the synthetic approach does not actually distinguish adaptive histories from nonadaptive histories (though Bock likely does not intend to have such a distinction). The lack of discrimination between adaptive and nonadaptive histories create several other problems for Bock as I have argued in this paper.

Regardless, by neglecting history, we are limited in our ability to distinguish between seemingly distinct phenomena. The male peacock's tail is clearly an adaptation<sub>B</sub>, since it contributes to the fitness of its possessor by enabling the males to attract females in courtship and mating. Without a developed understanding of sexual selection, we have no way of separating this odd case from typical cases of adaptation as in the length of the giraffe's

neck. Our understanding of various adaptive and nonadaptive processes, which rest on a historical component of adaptation to function, seems reasonable enough for their benefit. Pleiotropy, exaptation, canalization, group selection, inbreeding effects, frequency-dependent selection, and catastrophic effects all require particular histories when applied to the study of adaptation. By eliminating the study of history, we eliminate these (and other) categories, collapsing all kinds of beneficial traits into the category of adaptations<sub>B</sub>. It seems obvious to me that a methodology which uses natural history in classifying adaptations better explains biological phenomena than a methodology that does not, particularly if we can know the natural history.

#### *1.5.4 The theoretical problem*

The last objection I have to Bock and von Wahlert's conception of adaptation, the theoretical problem, is a direct result of the methodological problem. The key difference between the two problems is that the methodological problem discusses the methodological distinctions used in research programs whereas the theoretical problem addresses problems with the general theoretical framework of evolution. That is, 1.5.3 speaks to the experimental side of the issue and experimental biologists while 1.5.4 speaks more to the theoretical side and philosophers of biology. The concept of 'adaptation to function' is as central to evolutionary theory as any other. While controversies over units of selection, systematics, and sociobiology have received more attention in recent literature, adaptation is no less important to our theoretical framework. As I have stated above,

evolutionists generally have not questioned the received view of adaptation, with Bock and von Wahlert being exceptions. Still, taking a Bockian view of adaptation (adaptation<sub>b</sub>) severely limits our theoretical framework. Now, one may object that a false diverse theory is not better than a true simplistic theory, but this point misconstrues the focus of Bock and von Wahlert's argument. They do not assert that all adaptations<sub>b</sub> truly have evolved to be adaptations to function. Instead, they argue that regardless of the natural history of adaptations<sub>b</sub>, we should base our theory of evolution on information available through analysis of present states of organisms without reference to the past. So, the many categories of adaptations (and non-adaptations) to functions cannot be ignored because of contrary evidence (or even lack of evidence). Conceptually, the distinction between the (present) adaptive value of a trait and the history by means of which the trait acquired that value could not be handled within such a theory of adaptation. As I have shown, our best evidence suggests that the many different ways in which features can evolve have actually occurred in lineages throughout natural history.

I mentioned above that Bock and von Wahlert imply that the history of adapted features is uninteresting to evolution. I should say a few more words on this subject. Darwin stressed in the *Origin* that our best evidence for evolution by natural selection is the presence of so called "accidents of nature". More recently, Gould (1979) has emphasized the fact that oddities and imperfections in the function of features provides one of our best tools in

understanding evolution. The odd features which both Darwin and Gould discuss are only interesting when considered as the product of a historical process. Without reference to the history, the traits are not accidents or imperfections since an accident requires a benchmark non-accident and an imperfection implies an ideal perfection. The oddities would just be facts of nature to be cataloged and of little interest to evolutionary biology. If Darwin followed Bock and von Wahlert's methodology, he would not have made the distinctions that led to the development of evolution by natural selection at all. Fortunately, Darwin did see the importance of natural history to evolution. I concur that the historical processes which have brought about the adaptations to function of individual characters is both interesting and extremely important to our greater understanding of evolutionary theory.

## **1.6 Conclusion**

In this chapter, I have attempted to do three things: present the four most common uses of 'adaptation' in evolutionary biology, argue that 'adaptation to function' is the most profitable use of 'adaptation', and discount the view of adaptation to function that ignores investigation into the natural history of traits and their possessors. The main focus for my discussion has been on the second goal concerning adaptations to function. I hope that the distinctions I made in the first third of the paper justify my preference for this use of 'adaptation' and that my response to the objections raised in light of Bock and von Wahlert's position preserves the significance

of my argument. If both of these are granted, then the importance of adaptations to function become clear.

My general concern is that the lack of care taken by evolutionists in their use of 'adaptation' has caused most of the confusions discussed above. As I said at the start, the problem is not with our understanding of 'adaptation' but that we are promiscuous with its use. Our promiscuity has led to many avoidable confusions, especially in the context of adaptations to function. By recognizing the problem, we can easily rectify it with the help of the distinctions I have made. The four aspects of adaptation are related in important ways, but we must still be careful to distinguish them so as to avoid difficulties and confusions to our collective understanding of evolutionary biology.

However, even a world where all evolutionists have rid adaptation of Bockism is still not the best of all possible worlds. Though the above distinctions and definitions present the framework for a more adequate evolutionary theory, I present them as a starting ground that we may refine into a more accurate understanding of adaptation. In the next chapter, I will argue that the above notion of adaptation to function needs retooling in light of empirical observations that seem to present counterexamples to my view. I will then explain how these counterexamples can be incorporated into a more sophisticated understanding of adaptation to function.

<sup>1</sup> Note that the emphasis is on the result of the process, not the process itself.

<sup>2</sup> By 'non-adaptive processes', I mean the class of various processes and events which lead to evolutionary change by means other than natural or human (artificial) selection. These may include, but are not limited to, pleiotropy, neutral drift, and the "bottleneck" effect.

<sup>3</sup> See Kimura (1992) for explication of neutral mutation and the neutral theory of molecular evolution.

<sup>4</sup> In place of pluralism, I prefer to use the term 'weak adaptationism' with adaptationist programs such as those attacked by Gould and Lewontin called 'strong adaptationism'. The term 'pluralism' is a reference to Gould and Lewontin (1978), who write, "We support Darwin's own pluralistic approach to identifying the agents of evolutionary change." Gould's view does seem to rely heavily on both adaptation and neutral fixation. I feel that while a strong adaptationist program is too restrictive, neutral phenotypic change is unlikely to be a predominant force in evolution (though it is certainly a significant factor). Furthermore, neutralism does not provide for a useful method of studying evolutionary change. Therefore, in my view, a weak adaptationism, that is (in Gould and Lewontin's terminology), pluralism with a bias towards adaptationism, is our best bet for understanding "the agents of evolutionary change".

<sup>5</sup> The subtitle of their article is "A Critique of the Adaptationist Programme".

<sup>6</sup> This depends greatly on the context in which we view the selective process. From the perspective of the organism being bred, selection is in response to environmental factors. That is, all constraints posed to the organism are external and thus environmental. In the larger context of natural processes, we recognize that breeding is a directed process with specific goals that likely run contrary to undirected evolution. In this respect, breeding is not a natural selective process.

<sup>7</sup> At least in the cases when the environment has not changed. I realize that in many (if not most) cases, the environment may have changed to a similar degree along with the features upon which selection acts, but this is not important to the purposes of my argument.

<sup>8</sup> The male offspring of a female who mates with a male with showy tail feathers could have a greater chance of themselves having show tails which would contribute to their fitness, though this only perpetuates the situation and does not explain it.

<sup>9</sup> The "bottleneck effect" occurs when a population is severely and indiscriminately reduced in number due to nonselective catastrophes. The "founder effect" is the result of a small subpopulation transposing to a unique environment where they are reproductively isolated from the population at large. In both cases, the small, randomly selected gene pool causes evolutionary changes not associated with adaptation, such as the fixation of deleterious mutations, the elimination of beneficial traits, inbreeding, and rapid evolution. The American cheetah is characterized as a bottlenecked population, and the Galapagos Island finches are a group of founder populations.

<sup>10</sup> Many standard models of natural selection assume an infinite population. Several authors have suggested that even a very large population may alter significantly due to drift (e.g. Ridley, 1993).

<sup>11</sup> It is also sometimes referred to (incorrectly) as natural selection, but as I have hopefully explained in the preceding paragraphs, the process of adaptation and natural selection are not the same thing (though adaptation as a process may be equated with selection).

<sup>12</sup> This is referred to as *relative adaptedness* by Brandon (1978) as I will discuss below.

<sup>13</sup> I use 'adaptation as a state' for organisms and 'adaptation to function' for features because of the problems in determining what it means for a feature to have a current state independent of its function.

<sup>14</sup> See Mills and Beatty (1979).

<sup>15</sup> While individuals in different environments can in *theory* be compared as to their relative adaptedness, such comparisons require some method of standardization between the two environments, which seems to trivialize the complex relationship between an organism and its environment. Hence, interesting comparisons are effectively only between conspecifics.

<sup>16</sup> Richard Burian points out that recent discussions of evolutionary satisficing may be a way to view organismic adaptation qualitatively without reference to conspecific comparisons. Still, we both agree that such a view may reduce to triviality since all organisms are satisfactorily adapted to their environment due to the fact that they are alive. While there is certainly more to be said about this issue, it is beyond the scope of this paper.

<sup>17</sup> We can imagine a situation where an organism has a form that allows for speediness without the individual actually being capable of speediness.

<sup>18</sup> See West-Eberhard (1992) and Brandon (1981).



## Chapter 2

### Further Problems with Adaptation to Function

#### 2.1 Exaptation

In their 1982 paper, "Exaptation—a missing term in the science of form," Gould and Vrba pointed to a confusion resulting from the ascription of 'adaptation' to certain features of organisms. They argue that the two components of the definition of adaptation of a trait<sup>1</sup>—being built by natural selection (the historical component) and contributing to present fitness (the present utility component)—are often wrongly considered to entail one another such that a feature determined to exhibit one component is presumed to exhibit the other. They claim that this problem is exacerbated by the absence of a term that would be capable of describing features whose present function and historical development *differ*.

For example, the authors discuss the evolution of feathers and flight in birds. Feathers are, in most species of birds capable of flight, a necessary condition for flight. That is, feathers contribute to the fitness of flying birds<sup>2</sup> since feathers are *used* for flying. However, many authors have suggested that feathers originally developed for purposes other than flight (Ostrom 1974, 1979; Bakker 1975),<sup>3</sup> such as thermoregulation, camouflage, and predation effectiveness. Gould and Vrba conclude from this evidence that calling feathers an adaptation for flight in birds is inappropriate.

They recommend the term '*exaptation*' to refer cases such as this. A feature should be referred to as an '*exaptation*' when it has been coopted for some use *that is different from its original function*. Gould and Vrba separate this definition into two subclasses:<sup>4</sup> a) characters that have been shaped by natural selection for some function (adaptations) which have subsequently been coopted for their current use; and b) characters whose evolutionary history cannot be ascribed to the direct action of natural selection (nonadaptations) that are coopted for their current use. In each case, the current use of the character is different from its original function, though the general structure of the feature may remain largely unchanged (and often does).

In their last sections, Gould and Vrba argue that an evolutionary theory which includes *exaptation* in its conceptual and taxonomic schemes is superior to a theory lacking such a concept and corresponding term. They suggest that *exaptation* helps solve the problem of preadaptations and diversifies the application of the concept of adaptation by allowing the ascription of secondary adaptation to features (particularly the first sub-class of *exaptations*; see c) below). Also, the authors stress the importance of nonadaptation in a clear understanding of adaptation and its related terms, suggesting that the negative overtones of 'nonadaptive' are wrong, as is the perceived supremacy of adaptation over nonadaptation in evolutionary theory.<sup>5</sup>

Gould and Vrba make an excellent point in their recommended addition to our vocabulary. Not only does 'exaptation' serve a useful terminological purpose to evolutionists, but the conceptual void it fills in our understanding of adaptation gives us a richer view of evolution. On my understanding, the importance of *exaptation* is not due to the treatment of a large number of organismic features as exaptations. Instead, its greatest benefit is that it produces a change in perspective, leading evolutionary biologists toward a better evolutionary theory. Gould and Vrba make a similar point in their introduction, citing Foucault, by asserting that our classification schemes affect how we think.

My present project will utilize the framework of Gould and Vrba. I will argue that there is another missing term in the science of form which has up to now gone unnoticed. More importantly, it is not effectively captured by our current view of adaptation. Additionally, I hope the addendum will alter the way in which evolutionists understand the conceptual framework of adaptation.

## **2.2 Comments on *exaptation***

A large portion of the previous chapter has been devoted to justifying the necessity of a historical component in the definition of adaptation to function. This point is by no means novel—several authors have stressed that adaptations must be formed by natural selection (Williams 1966, Gould and Lewontin 1979, Burian 1983). Nevertheless, I feel that the history of features

is still underemphasized in the context of adaptation. Moreover, it is important that the two components of adaptation to function (historical development and present utility) do not entail one another and *that we should never assume in individual cases that they do entail one another*, a position also stressed by Gould and Vrba. That is to say, a trait may have been formed by a history of natural selection and not be presently useful, hence not an adaptation (for example, if the environment has sufficiently changed). Likewise, a trait may contribute to the fitness of its possessor without a history of selection for that function and also not be an adaptation.

To put it another way, the historical development of a feature and its present use are *independent criteria* for evaluating its status as an adaptation or nonadaptation. Therefore, we may imagine traits falling into four classes:

- a) Adaptations: traits developed by natural selection for some function that presently contribute to overall fitness according to that function.
- b) Nonadaptations: traits *not* developed by natural selection that presently contribute to fitness.
- c) Secondary Adaptations (exaptations): traits developed by natural selection for some function that presently contribute to overall fitness *in some capacity other than their original function*.
- d) Exaptations from nonadaptations: traits *not* developed by natural selection that presently contribute to overall fitness *in some capacity other than their original utility* (if any).

This grouping follows closely with Gould and Vrba's breakdown in Table 1.

(p. 5) of their paper, which they attribute to Williams (1966). Notice that in all cases, the described traits have some use or function.<sup>6</sup>

However, there is still a problem in the above schema. Gould and Vrba's argument suggests that traits may be used by organisms for purposes

other than their original function. Thus, they separate traits into adaptations/nonadaptations [(a) and b), respectively] and exaptations [(c) and d)]. But, these four classes are not as distinct as they are presented; that is, some traits may lie between adaptations and exaptations. For example, staghorn beetles have horns that seem to serve several purposes, digging and defense among them. Gould and Vrba imply that only one of these is likely an adaptation, with the other being an exaptation. But, two or more of the uses of the same feature could be selected for. Imagine that one use, say digging, was the primary selective factor for the evolution of the horns, even though the use of horns for defense also had some selective advantage (albeit less than that of digging). Presently, the beetles do not often dig with their horns, though they do on occasion, whereas they have become very adept at using their horns for defense. According to the fable, the dominant use of the beetle horns is presently defense, but using horns for digging still contributes to fitness.<sup>7</sup>

As the example suggests, the categorization I have in mind differs from Gould and Vrba's in that I view the four classes as rough groupings lying in a continuous conceptual space. My point is that there are some features which do not fit well into any of the categories listed above. In the beetle example, would we call the use of the beetles' horns for defense an exaptation coopted from the function of digging or do we call it an adaptation? The evidence seems to support either possibility, since defense has always contributed to fitness on the one hand (suggesting it is an adaptation), but after the original

development of the horns, defense has come into prominence unmatched by its previous role (suggesting it is an exaptation). I hold that either case can be justified by our current understanding of adaptation. Also, assuming the example is true, the main reason for wanting to classify the feature of 'defense using horns' as any of the four possibilities (i.e. adaptation, nonadaptation, secondary adaptation exaptation, or nonadaptive exaptation) seems to be theoretical cleanliness. Messy scientific theories are certainly undesirable, but cleanliness should still not supersede accuracy or correctness.

However, abandoning and replacing, or even overhauling, the present conception of adaptation is quite a large project which I cannot hope to do at present (nor am I sufficiently convinced that such a major renovation is called for). What I will do is suggest examples from nature that justify one type of feature, which I call *hyperadaptation*, that is best described as living in the conceptual space between adaptations, exaptations, and nonadaptations. If I am correct in my reasoning, then hyperadaptations not only occur in nature, but the current conception of adaptation prohibits evolutionists from recognizing them.

### **2.3 Hyperadaptation defined**

Before I delve into particular cases, I should describe what I mean by hyperadaptation. To review a bit, I have already established the received view of adaptation as a trait with a history of selection and present utility. Gould and Vrba point out that some features, namely exaptations, may have

a present utility distinct from their historical development, whether it was adaptive or not. A different way of describing the argument for exaptations is that these traits are often mistakenly called adaptations because they change in function (are coopted) during the time after the period in which they were developed. In effect, there is a *time gap* between the formation of the feature and the development of its present function. Secondary adaptation exaptations were developed by a process of natural selection (the primary adaptation), but the feature has since been coopted for another use (the secondary adaptation).<sup>8</sup> Similarly nonadaptive exaptations were once nonadaptive structures before coopting for a different use (and thus becoming exaptations).

Exaptation indicates the potential for the process by which a feature has formed and its current state to be separated by a lag time. That is, the process of formation occurs long before the evolutionary process that caused a feature's current state. During the time after the feature has been formed, it has been coopted for a different use than initially, thus we call it an exaptation. However, during the same time (after the formation of the feature), traits may follow several pathways other than being coopting for another purpose. One such possibility is that drift or some other process may act on a trait such that it continues to develop beyond its functional state. Natural selection often acts on traits in an open-ended manner, where the selective force is simply a pressure to pass beyond some threshold (e.g. acquire enough food, run fast enough, produce enough pollen). By developing

beyond its functional state, I mean that a feature with such a unidirectional selection pressure may function well above the selective threshold without any apparent effect on its possessors.<sup>9</sup> Once beyond the threshold, the selection pressure is removed and features change by random drift or for some other reason. One of the ways in which a feature may evolve is to a more refined, more productive, or better adjusted state than the state achieved due to selection. Therefore, such a feature would adapt to the environment in response to some selection pressure until it has sufficiently adapted to remove the pressure. Then, while no selection pressure is acting on the feature, it continues to evolve in the same direction as its adaptive development. Such a trait would appear overly well adapted; it is an adaptation with a hyperbole, or a *hyperadaptation*.

#### **2.4 The need for 'hyperadaptation'**

The reason why 'hyperadaptation' is needed as a separate term in our taxonomy is the same as the reason for needing 'exaptation'. Because the term is lacking from our vocabulary, cases which it would be appropriate to call hyperadaptations are mislabeled as something else, probably adaptations. The problem is that hyperadaptations *look* like adaptations at first glance. Without probing into the evolutionary history of a feature or other unusual characteristics (see below, Chapter 3), an evolutionary biologist may not distinguish hyperadaptations from adaptations. More strongly: without a place for hyperadaptations in our conceptual framework, scientists are



*constrained* in distinguishing hyperadaptations. After all, empirical investigation will not force an opening in our conceptual taxonomy without some theoretical manipulation—a project rarely undertaken by experimental biologists.

In some respects, the state of evolutionary adaptation is caught in a vicious circle between theory and experiment. Each plays off the other for verification of its findings. Our articulation of evolutionary theory is grounded in observations of nature, yet our experimental results are constrained by our theoretical framework. As long as no one steps out of the circle, theory and experiment may complement each other without any real progress. It is clear that recent philosophy of science has managed to destroy the empiricist maxim that observation is prior to interpretation. Further, as several philosophers have suggested, our conceptual taxonomy is one way in which our observations are necessarily interpreted.<sup>10</sup>

I am not suggesting that my observations are free from interpretation or that I can solve the problem of observation in philosophy of science. I merely introduce an alteration into our conceptual framework of adaptation such that it allows for the possibility of hyperadaptations. By doing this, I feel we will have a better theory of adaptation and allow a more sophisticated way of describing features in regard to adaptation. This project seems to be a timely one, suggesting a not so subtle attempt to close the communication gap between experiment and theory (and also, between experimentalist and theoretician).

## Notes

<sup>1</sup> This is what I refer to as *adaptation to function*. See section 1.4 above.

<sup>2</sup> This claim is on the assumption that flight itself contributes to the fitness of individuals, which I will not argue here, nor will I discuss the existence of feathers on grounded bird species.

<sup>3</sup> Note that there are also arguments, based upon historical evidence, against feathers being originally an adaptation for flight (which also responds to Bock and von Wahlert—see sec 1.5). Most significant is the argument that early birds and proto-bird species had fewer and/or smaller feathers which would not be sufficient for flight. Furthermore, by rejecting the problematic notion of *preadaptation* (as both Gould and Vrba and I do), some feathers cannot be explained as a pre-development stage of birds with more feathers. See Gould and Vrba Sec. V.A) for greater detail on the example and Sec. VI.A) for their arguments against preadaptation.

<sup>4</sup> See Table 1, p. 5 of Gould and Vrba.

<sup>5</sup> This remark is an indirect attack on the adaptationist program, which Gould had previously rejected in his 1979 paper with Richard Lewontin.

<sup>6</sup> One may object that two more classes should be added, namely situations where a trait has no use both with and without a history of selection. While there does not seem to be any problem with adding these classes, I do not find them particularly useful or strictly correct. Generally, something is called a trait (or feature or character) only if it has some ascribable use for its possessor. Otherwise, we simply refer to the thing as a structure or anatomical component. Regardless, the establishment of useless features does not affect my arguments.

<sup>7</sup> We can imagine experiments that would verify the situation. For example, test beetles, both with horns removed and normals, are placed in an predator-free environment, so defense is not a significant selective factor. In this situation, the beetles with horns are able to dominate because of their better ability to dig than conspecifics. However, the difference is slight and often counteracted by drift. Alternatively, test beetles (both with and without horns) placed in an environment where digging is not a factor (e.g. a hard surfaced environment) show a marked separation between horned and dehorned conspecifics due to predation, with horned beetles being less prone to predation than dehorned. From these two experiments, we can conclude (at least tentatively) that the horns of staghorn beetles are used mainly for defense and less so for digging. Note that I am assuming the historical development described in the main body.

<sup>8</sup> Remember, a secondary adaptation is simply the coopting of a trait to another function. The original function of a trait is its primary adaptation. Gould and Vrba seem to imply that secondary adaptation exaptations will lose their primary adaptations. However, I suspect that they do not intend this as a necessary consequence of exaptation. Likely, they see secondary adaptations which have not lost their primary adaptation as less problematic or less controversial. Regardless of what their view implies or their actual intentions, I reject the implication that secondary adaptations need have any effect on primary adaptations. Furthermore, features may be coopted several times, creating tertiary adaptations (secondary exaptations), etc.

<sup>9</sup> I realize that when considering the organism as a unit as opposed to the individual feature, this overactivity may often become a maladaptation or have negative consequences for the organism. However, we cannot assume that an overly well suited feature must cause consequent maladaptations. This attitude reveals a strong adaptationism, as it assumes that adaptations alone regulate the existence of features. Since I reject strong adaptationism, I am unmoved by this objection, though I do admit that it could pose problems in recognizing hyperadaptations.

<sup>10</sup> **Kuhn's *Structure of Scientific Revolutions* (1962) best illustrates this point, though in a broader respect, the suggestion follows back in the tradition of Kant and the gestalt experience.**

## **Chapter 3**

### **Examples of Hyperadaptation**

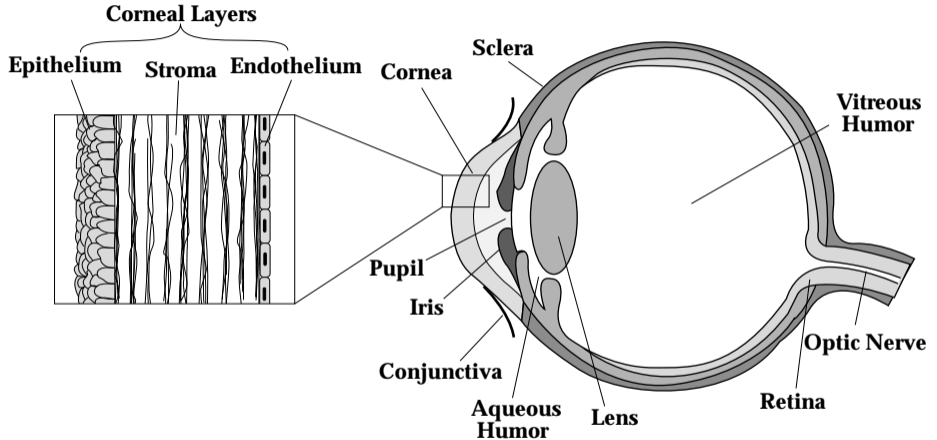
In this chapter, I will discuss some examples of hyperadaptation. I must emphasize that only in the first example, which I will discuss in detail, am I committing myself to calling it a hyperadaptation. Otherwise, I only suggest that the examples are possibly hyperadaptations. Since my detailed knowledge of the appropriate literature is limited to the cornea (which is the subject of the first example), I cannot confidently make assertions regarding other features. Still, I believe that the examples do have some merit and that at least some of the characters discussed can best be described as hyperadaptations.

#### **3.1 The mammalian corneal endothelium**

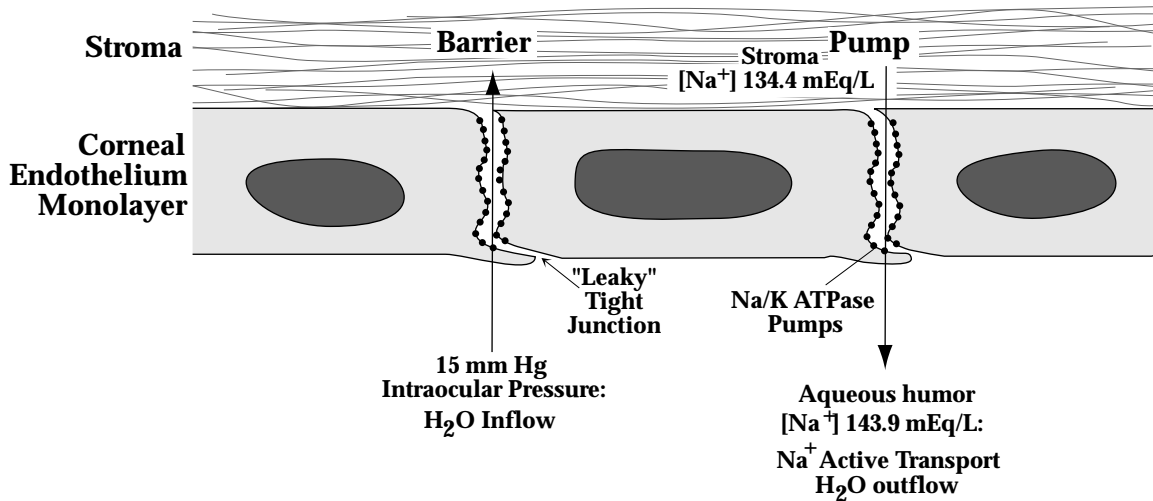
The mammalian corneal endothelium (CE) is a single cell layered tissue that forms the interior surface of the cornea, the clear outer covering of the eye. The function of the cornea generally is to focus light onto the retina. In this sense, corrective lenses can be described as artificial corneas, for they most resemble the cornea and not the lens of the eye, as their namesake suggests. For the cornea, as with any artificial focusing lens, a necessary condition for proper functioning is transparency. This is the role that the CE plays in the eye, i.e., to maintain corneal transparency.

Figure 3.1 presents a diagram of the cornea and CE in relation to the general structure of the eye. The thickest layer of the cornea, which comprises about 90% of its thickness is the stroma, which is composed of a crystalline-like lattice of regularly spaced collagen fibrils of uniform diameter. The highly regular organization of the structure allows almost all light to pass through the cornea, with only a small percentage (less than 2%) of light absorbed by the tissue. However, when the organization of the stroma is altered, light is scattered and does not pass through it. This condition is recognizable because the cornea becomes opaque. The most significant factor affecting the crystalline organization of the stroma is the water content of the tissue. When the water content goes above or below a small threshold (about 78% water by weight), the thickness of the stroma changes, the regularity of the lattice is disrupted, and consequently, the cornea becomes opaque.

Since the epithelial (outer) surface of the cornea is relatively impermeable to water,<sup>1</sup> the CE is the major regulator of stromal thickness. Further, the constitution of the eye globe, with an intraocular pressure of 15 mm Hg, creates a high water gradient in comparison to the surrounding tissues. Thus, a dynamic equilibrium is required to keep the stroma at the appropriate water level. Also, though the CE barrier can reduce the inflow of water into the stroma, the seal is imperfect, requiring an active mechanism to constantly remove water from the stroma to the aqueous humor inside the eye (see Figure 3.2).

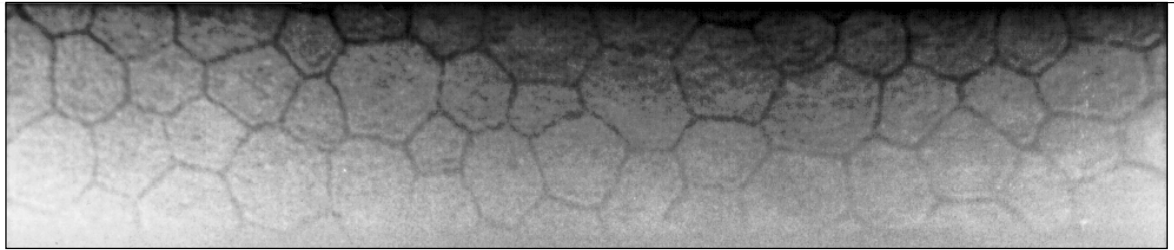


**Figure 3.1.** The anatomy of the cornea and the eye.



leak rate = metabolic pump rate  
 water content of stroma = 78 %  
 corneal thickness maintained

**Figure 3.2. Regulation of stromal water content by the CE. a) The CE forms a partial barrier which allows some water to flow from the aqueous humor into the stroma. b) To counteract the inflow of water, Na/K ATPase enzymes pump sodium ions (Na<sup>+</sup>) into the aqueous humor, with water flowing by osmosis. In a normally functioning CE, the leak rate is equal to the metabolic pump rate. Note that each intracellular junction acts as both a barrier and a metabolic pump.**



**Figure 3.3. Micrograph of the CE surface. The photograph is taken through a specular (light) microscope. The CE cells are seen as a reflection off the dark colored surface of the retina. Notice the regularly sized, hexagonal shape of the cells.**



The functioning of the CE is very closely related to its structure. A micrograph (Figure 3.3) of the CE surface illustrates that it forms a hexagonal mosaic of cells. A cross section illustration (Figure 3.2 above) shows how the cells maintain constant water content in the stroma. To counteract the constant inflow of water, the cells use Na/K ATPase enzymes<sup>2</sup> to pump water out of the stroma. The enzyme proteins are incorporated into the lateral membranes of the endothelial cells. Because of a limitation of both the amount of space available for placing the pump enzymes and the fact that active enzymes function constantly, we can conclude that a certain number of active Na/K ATPase pumps are required to maintain stromal thickness (which is used as a measure of water content). Hence, an organism's corneas must contain at least that number of pump enzymes within their endothelial cells to maintain corneal transparency for proper vision.

While the measurement of active Na/K ATPase proteins is possible (using an inhibitory protein, ouabain), the task is rather arduous. However, since the number of possible enzymes is limited by space on the endothelial cells' surfaces, a measurement of the number of endothelial cells may also be used as an indicator of the tissue's capacity to maintain transparency. In fact, this is the process by which researchers and clinicians measure the functioning of a CE. The result is very telling, as endothelial cells are nonregenerative<sup>3</sup> and serve essentially no function other than the regulation of corneal hydration and water content. Thus, lost cells cannot be regenerated or replaced. Cell numbers are counted by several techniques using

micrographs like the one shown in Figure 3.3. From a small sample of cells (about 50-100), the overall number of cells contained in a cornea may be measured, written in number of cells per square millimeter (# cells/mm<sup>2</sup>). This technique is an indirect, though extremely reliable method of determining a CE's ability to maintain corneal transparency (Yee 1994).

### **3.2 The corneal endothelium and hyperadaptation**

From a clinician's perspective, the corneal endothelium is an ideal structure. Not only does it perform its task excellently (as I shall discuss momentarily), but also its effectiveness in individual cases can easily be determined without compromising the tissue or its possessor organism. Furthermore, the results are readily quantifiable. The vast majority of research on the CE has been carried out on humans; thus, I will concentrate on results, especially numerical values, specific to human corneas.

As stated above, CE effectiveness is best determined by calculating the CE cell number. While participating in studies where CE cell number was calculated, I noticed a rather odd phenomenon that ophthalmologists seem to take for granted. Corneas of humans in their twenties contain approximately 3000 endothelial cells/mm<sup>2</sup>, while the threshold at which corneal edema occurs (the point where a cornea loses its transparency) is only about 500 cells/mm<sup>2</sup>. I found this fact notable because though the cells are nonregenerative, their death rate is very low. One ophthalmology textbook (Glasser 1994) claims that cell number reduces at a rate of approximately 0.5%

per year. Therefore, a human cornea with a normal rate of CE cell death will function appropriately for over 200 years!

I suggest that such an abundance of endothelial cells is a hyperadaptation for maintenance of corneal transparency. There are several reasons why the CE fits the model of a hyperadaptation. As stated in section 2.3 above, a feature is a hyperadaptation if it was at one time an adaptation, but either through a change in environment or nonadaptive changes in the structure is presently overly suited for its function. My argument separates into two parts. First, I will show that its current level of functionality greatly exceeds that which a pretechnological<sup>4</sup> organism requires. Then, I will argue that in light of phylogenetic comparisons, the CE most plausibly evolved to become a hyperadaptation.

### 3.2.1 *The corneal endothelium is more than adequate*

The first requirement for a hyperadaptation is that a trait is overly well suited for its function. As I suggested above, the CE clearly functions well above any physiological or evolutionary necessity. The most significant measure of the strength of the CE is the cell number of the tissue. When the cell number falls below a certain threshold, of about 500 cells/mm<sup>2</sup> in humans, CE decompensation occurs causing the stroma to swell with water and the cornea to become opaque. Note that this value is a threshold and decompensation is typically an "all or none" event, i.e. at 550 or 600 cells/mm<sup>2</sup>, the stroma does not experience any edema. Studies on both humans and other mammals indicate that even over an extremely long life

span, cell number remains well above the threshold. According to one report (Yee, et. al. 1985), cell number of children in their teens (age 10-19) was close to 3400 cells/mm<sup>2</sup> and even adults in their eighties had cell numbers over 2300 cells/mm<sup>2</sup>. This study indicates that not only is cell number extremely high, but normal attrition is comparatively low.

While the above account may be interesting to medicine, three other comments help explain the adaptive significance of the CE. As I mentioned earlier, the cells of the CE are nonregenerative and nondividing after birth. Thus, organisms can never increase their number of endothelial cells, being limited by their birth allowance.<sup>5</sup> This factor is key to my account. Presumably, the inability to proliferate or regenerate is a major link to several other important attributes of CE cells.

In addition to being nonregenerative, CE cells have several unique attributes which makes the high cell number even more impressive. First, the cells themselves comprise a unique type that is not found anywhere else in the body. Also, the CE is relatively isolated from other tissues. On one side lies the stroma, which contains very few cells itself. On the other lies the aqueous humor, which is simply an extracellular solution filling the compartment between the cornea and lens. Because of this isolation, the CE has very little contact with the rest of the body and thus functions effectively independently of exterior factors. The isolation and independence suggest that the function of the CE is limited to maintenance of corneal transparency,

since it does not have enough contact with other cells to play a role in their activity.

Finally, the CE cells have a high stress level. Stromal water content regulation is a dynamic process, requiring the CE cells to constantly pump ions (with water following by osmosis) from the stroma to the aqueous humor. The process expends an enormous amount of energy (Geroski and Edelhauser 1984), which increases the likelihood of errors in cellular mechanisms. Also, since the cornea is directly exposed to sunlight, cancerous mutation through ultraviolet radiation—a known carcinogen—is a constant danger. Last, the delicacy of the cornea, which is exposed to the environment, can cause damage through trauma or environmental stress. Even with all these stress factors, intracellular mechanisms of the CE cells do an excellent job of preventing catastrophes. The cells are extremely efficient at correcting errors in protein synthesis and preventing mechanical errors. Likewise, the cells have very high levels of reduced glutathione, which has been shown to reduce free radicals and oxidized compounds caused by ultraviolet light (Glasser 1994).<sup>6</sup> Both of these mechanisms are not only sufficient to keep individual cells properly functioning for many decades, but their effectiveness far exceeds that of comparable cells throughout the body. Furthermore, clinical problems and diseases of the CE are extremely rare.<sup>7</sup> A type of cancer, Fuch's dystrophy, does occur in humans and some animals, but cases are very rare. Also, the onset of corneal decompensation in Fuch's

dystrophy cases still occurs in humans in their sixties and seventies, well past the life expectancy of pretechnological *Homo sapiens*.

All these factors which show the durability of the corneal endothelium become even more impressive when we consider them in a pretechnological context. By all standard accounts, human life expectancy five thousand years ago was about twenty to thirty years. Assuming that the CE was not significantly different then from how it is now, the durability of the tissue becomes even more striking. The assumption is justified because, as I stated above, the CE is protected from environmental factors by the rest of the cornea, so a harsher environment would not change the functioning of the CE. While other, internal factors, such as nutrition, could conceivably explain why the CE seems hyperadapted, no such cause of CE decompensation is known. If nutrition played a role, then we would find wide cases of corneal decompensation in famine-stricken countries, which we do not. The same would seem to apply to any other explanation that suggests the CE is a byproduct of modern health and hygiene—for every such explanation, we should find counterinstances. Therefore, our best evidence indicates that the CE is not just well suited for its present function of maintaining corneal transparency, but overly well suited for that function.

### 3.2.2 *The evolutionary history of the corneal endothelium*

In order to fully support my contention that the CE is a hyperadaptation, I must give some evidence of its evolutionary history. As with any soft structure that cannot be seen in fossil records, we cannot make any direct claims about the CE's evolutionary past. Still, from phylogenetic comparisons, I will argue that we have reason to believe that the CE was, at one point in time, an adaptation that evolved via natural selection from lower to higher cell numbers.

While little information is available on CE cell number values across phyla, one study by Yee, et. al. (1987) compared the CE of various vertebrate families. Table 3.1 shows the results of cell number comparisons among the tested organisms. As shown in the table, several mammals have similar cell numbers, all of which are above 2200 cells/mm<sup>2</sup>. Birds also seem to have relatively high cell numbers (Goose cell # > 2400 cells/mm<sup>2</sup>). However, when we move to older taxa, namely reptiles, amphibians, and bony fish, the cell numbers are significantly lower. We may infer that earlier species,

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**Table 3.1 Comparison of vertebrate corneal endothelial cell number**

Family	Organism (age)	Cell # (cells/mm <sup>2</sup> )
Mammalia	Human (52 years)	2567
Mammalia	Dog	2545
Mammalia	Rabbit	3160
Mammalia	Rat (34 weeks)	2211
Avia	Goose	2409
Reptilia	Gecko	481
Amphibia	Bullfrog	550
Teleost	Rainbow trout	578
Teleost	Goldfish	431
Elasmobranch	Dogfish shark	2300 <sup>8</sup>

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specifically the common ancestors of reptiles, birds, and mammals, likely had cell numbers similar to modern reptiles, amphibians, and bony fish. While this is only an inference, I believe it is plausible. Evolutionary orthodoxy holds that the vertebrate eye evolved very early in the development of the order, before significant diversification into families. This suggests that the cornea is a very old structure, predating vertebrate diversification.<sup>9</sup>

Therefore, all modern vertebrates (with the possible exception of elasmobranchs) share a common ancestral CE and corresponding typical cell number.

If the previous claim is true, that all vertebrates evolved from a common ancestor, then the difference in average cell number between the higher vertebrates (mammals and birds) and the lower vertebrates (reptiles, amphibians, and bony fish) should have an explanation. Clearly, one of three cases are possible. The common ancestor's cell number was close to that of modern lower vertebrates, was close to that of modern higher vertebrates, or was different from (and presumably between) both modern groups. If either the first or second possibility is true, then the case for hyperadaptation seems plain. Corneal edema occurs around 500 cells/mm<sup>2</sup>. If the ancestral cell number was an adaptation close to the point of edema, then modern higher vertebrates have become hyperadapted due to an increase in average cell number. If the ancestral cell number was very high, close to that of modern mammals and birds, then lower vertebrates must have slowly reduced their cell number over time. In this case, the mammalian CE is still a



hyperadaptation but the origin of the excessive cells predates their differentiation from reptiles, etc. If the final case were true, then cell number for all modern vertebrates must have changed over time. While this is possible, parsimony suggests that we should consider it the least likely of the three.

One might contend that the phylogeny suggests a punctuated evolutionary history separating lower and higher vertebrates.<sup>10</sup> Whether the evolution of the CE was punctuated or gradual, my point still holds—it is still a hyperadaptation. The speed of the evolutionary change of the CE in ancestral vertebrates that diversified into higher and lower groups does not affect the argument. The fact is that the jump in cell number in mammals (or the reduction of cell number in reptiles, etc.) still occurred and is still due to some nonadaptive process. Furthermore, a punctuation event might help explain why the CE is a hyperadaptation. Possibly, the initial, likely gradual, evolution of the CE in vertebrates along some selective pathway shaped early vertebrates' CEs to be adaptations. Afterward, a nonadaptive punctuation event would shape the mammalian CE into its current, hyperadaptive state.

Regardless, comparative vertebrate physiology of the CE indicates that it is hyperadaptive in mammals (and probably also birds). The conclusion rests on two key premises, which I have justified above. First, the CE is an adaptation with a cell number close to 500 cells/mm<sup>2</sup>. Second, the evolutionary origin of the structure predates the diversification of vertebrates into the five orders of mammals, birds, reptiles, amphibians, and fish. From

these two premises, I infer that at one point, all vertebrates' CE were an adaptation to the function of maintaining corneal transparency. Henceforth, some vertebrates, namely mammals and birds, evolved higher cell numbers in their CE, even though the evolution was not an adaptation due to natural selection. Therefore, I label the mammalian corneal endothelium a hyperadaptation for the function of corneal transparency maintenance.

### **3.3 Other examples of hyperadaptation**

There are several other features in various organisms that may be hyperadaptations. While I do not put as much weight on the assertion that they are hyperadaptations, our current understanding of their adaptive histories and present utility do suggest that such a label may be appropriate. I separate the examples into two general classes. First are cases like the corneal endothelium where the feature has been maintained in a relatively constant environment and the cause of the hyperadaptation seems not to be straightforward adaptation to function. In such a case, the state of the feature cannot be explained by natural selection alone. Second are cases where environmental changes coupled with a preservation of some feature make calling that trait a hyperadaptation appropriate. In these cases, although the formation of the feature can be explained in terms of natural selection, the persistence of the feature cannot. I should qualify this distinction by mentioning that it is merely speculative. Since both types of events can lead to a hyperadaptive trait, the specific mechanism by which the examples have

achieved their current state is not important for my argument. I provide the background only to illustrate how the features under consideration could plausibly have evolved. Thus, while I am providing "just so" stories in a sense, the truth of the particular stories does not affect the need to develop the concept of *hyperadaptation*.

### 3.3.1 *Polytene chromosomes*

Several species of insects, the best known of which are species of *Drosophila*, contain tissues where the individual cells hold an enormous amount of genetic material. The cells replicate their DNA hundreds of times without the sister chromatids separating. Thus, when the cells are viewed under a light microscope, the chromosomes appear as thick strands called 'polytene chromosomes'. Although polytene chromosomes serve as a useful research tool to geneticists, they do not seem to serve any function for the organisms that possess them. Obviously, one set of genetic material is necessary for the cells and even several copies might be useful by increasing the cells ability to produce proteins rapidly. However, like the corneal endothelium, the presence of several hundred copies of DNA seems to be well above what any cell, even under the most extreme conditions, might use. Also, we may assume that having several hundred copies must have evolved from having fewer copies (though the specific leaps from one set of genetic material to hundreds is not important).

The excess DNA in polytene chromosomes is well documented as a notable oddity in biology. Many introductory biology and genetics textbooks

mention polytene chromosomes.<sup>11</sup> Still, an explanation as to why a cell might produce them is unavailable. I suggest that selection cannot explain the presence of polytene chromosomes. One and possibly several copies of DNA may be beneficial to an organism and are possibly adaptations, but several hundred are no better than several dozen or just several. Polytene chromosomes are thus most appropriately labeled as hyperadaptations.

### 3.3.2 *Egg cell production in K-selected populations*

Population genetics uses a system to classify reproduction strategies where populations are classified as either *r*-selected or *K*-selected.<sup>12</sup> Individuals that exhibit *r*-selection produce a large number of relatively small offspring where little care is given to progeny by their parents. These individuals tend to be more varied than the offspring of *K*-selected organisms and generally live in environments which support such a method of reproduction: food supplies and other necessities are in high quantities and readily available, overcrowding is not a danger, predation is high, and the environment is patchy and/or erratic. In an environment that has these characteristics, individuals which can quickly produce a large number of offspring are likely to propagate their DNA into future generations. Conversely, individuals are characterized as *K*-selected when they produce a few number of relatively large offspring that are cared for very intently by their parents. These individuals tend to be "finely tuned" to the stable environments in which they live. The populations are maintained close to carrying capacity, the availability of resources (food, nesting sites, etc.) tend to

be the principal limiting factor, and dangers come from competition with conspecifics more than from predation. *K*-selected individuals survive better by following this reproductive strategy because overproduction of progeny can cause everyone to suffer from a lack of necessities and infighting.

Most *K*-selected individuals still share one interesting characteristic with *r*-selected individuals: both types produce an enormous number of germ cells. In *r*-selected organisms, and even in male *K*-selected organisms, this large production of gametes seems useful. Only a small percentage of gametes can ever become zygotes and eventually develop into complete organisms due to the difficulties of fertilization. Further, gametes are fairly "cheap" for an individual to produce. Thus, the more an individual makes, the more likely it will propagate its genes into future generations. However, in *K*-selected organisms, female gametes are expensive to produce and are not needed in any great abundance. Nor do the organisms typically treat them as expendable in the same way which sperm or spores are. For example, humans females generally release one egg cell at a time. This is the epitome of a *K*-selection situation, since humans almost always have one offspring at a time and the babies require a great deal of care relative to organisms such as cockroaches. Also, human eggs go through the first stages of development before birth, when a woman's entire complement of eggs are produced. But, even though humans only release one egg every 28 days or so, the female body produces approximately 200,000 egg cells. Hence, for a woman to release all of her eggs at a normal, constant rate, she would have to live for well over

15,000 years! Obviously this figure is absurd. There is no reason why a *K*-selected individual should produce such a large number of egg cells. One suggested explanation is that these populations have evolved from *r*-selection to *K*-selection and the abundance of egg cells has been retained through the transitional evolution. In other words, a high level of egg cell production was at one time an adaptation for the ancestors of modern *K*-selected populations, but the current level is nonadaptive.

Again, this appears to be a clear case of hyperadaptation. Furthermore, we may interpret the manner of hyperadaptation along either of the above chains of events. It is possible that *K*-selected populations were previously *r*-selected. Thus, a change in the environment caused the switch in reproduction methods while the germ cell production level was retained. Alternatively (though less plausibly), *K*-selected populations may have long been at equilibrium in a stable environment, but for whatever reason, possibly random drift, the production of egg cells has increased well beyond the environmental requirements. In the first instance, the environment changed while the feature remained constant. In the latter case, the opposite occurred. While the first possibility seems more plausible and is better supported by current theories of population genetics, either is possible. My point is that no matter which events actually led to the present situation, the feature should be considered a hyperadaptation.

### 3.4 Social evolutionary hyperadaptations

Several examples of probable hyperadaptations fall under the general category of social evolution. My primary examples of social evolution are in humans and are a consequence of modern human social and technological developments, though not necessarily grounded in genetic changes. Social evolution has significantly changed the way in which humans interact with the environment. Consequently, many adaptive features of early *Homo sapiens* have become hyperadaptive in modern humans due to improved manipulations of the environment. That is, modern society has transformed stable traits of humans once required for survival, making them superfluous or supererogatory. We can survive environmental hardships well beyond those of our ancestors. Medical techniques, balanced nutrition, and defense capabilities (against both predators and environmental conditions), have effectively eliminated several selection pressures formerly encountered by our ancestors from many populations of human beings, particularly those in highly developed countries. However, many features have evolved, presumably as adaptations,<sup>13</sup> which would contribute to the overall fitness of humans before power and control technologies were available and actually did contribute to the fitness of our ancestors.

My point is that as a consequence of modern social and scientific capabilities, humans have, in effect, significantly reduced or even eliminated many of the selection pressures shaping human adaptations. Since the adaptations are genetically based, they should still be present in the current

population. In other words, humans have several adaptations which are beyond necessity, i.e. hyperadaptations. These hyperadaptations are caused by a persistence of features in an environment which does not require their function at the level to which the features was formed as adaptations.

In addition to human social hyperadaptations, we may also consider similar effects occurring in other species. Many plant and animal species have been domesticated for varied uses. Under domestic situations, several environmental factors are controlled by the breeders, farmers, or scientists who supervise the populations. As such, the individuals will likely have adaptations for some environmental conditions which are completely foreign to their domesticated environment. Like hyperadaptations caused by human social evolution, the domesticated organisms are equipped with adaptations which are overly well suited for the function which their possessors require. That is, the domesticates possess hyperadaptations as a consequence of relaxed environmental conditions.

While I am unsure of the importance of hyperadaptations caused by social evolution to evolutionary theory, they at least present a clear example of how a diminution of environmental constraints can cause a feature to become a hyperadaptation. Hyperadaptations caused by social evolution would certainly be significant if they caused genetic changes. Speculatively, I would guess that genetic changes are likely in these cases because of random drift. Remember, hyperadaptations are not constrained by selection pressures in the way that adaptations are; therefore, drift will play a larger role in their



evolution. Whatever the prospective significance of social evolutionary hyperadaptations to evolutionary theory proper, they still may present a positive research tool to sociobiology, which has been dogged by so much controversy over the years.

In this chapter, I have argued that all of discussed cases are best described as hyperadaptations. My hope is that I have, at the very least, sufficiently convinced the reader that some traits may plausibly be classified as hyperadaptations. Granting that hyperadaptations do exist, I will show that an acceptance of the label and understanding of its place within our conceptual taxonomy greatly improves our picture of evolutionary theory. It will not only provide a more precise method of describing organisms but will also better our understanding of evolutionary adaptation.

## Notes

<sup>1</sup> Under certain circumstances, epithelial permeability may occur, e.g. when topical drugs are administered through eye drops. However, this permeability is very transient, lasting at most only a few hours. In extreme cases, epithelial permeability may pose minor medical problems, though as I shall explain, this does not affect stromal thickness.

<sup>2</sup> Na/K ATPase is a common transmembrane transport protein. It functions by exchanging sodium ions (Na<sup>+</sup>) from within a cell for potassium (K<sup>+</sup>) ions from the intracellular space. In the process, water passively flows out of the cell by osmosis.

<sup>3</sup> New Zealand White rabbits (a typical research animal) are one notable exception. At least one study suggests that its endothelial cells have some ability to reproduce under extreme circumstances (Stiemke, et. al. 1991).

<sup>4</sup> By pretechnological, I mean individuals not affected by modern medical techniques. Several factors that are a consequence of modern medicine make corneal decompensation more likely, e.g. intraocular surgery and long term contact lens use. However, these factors do not have any effect on the evolutionary history or significance of the CE. Therefore, my argument concerns the state of the tissue without regard for recent medical intervention.

<sup>5</sup> Many cell types of the central nervous system are also nonregenerative and nondividing, explaining why neural damage is so problematic. Also, the correlation suggests that corneal endothelial cells have a similar developmental origin as neural tissue.

<sup>6</sup> To emphasize the danger of ultraviolet light, I should point out that extremely few cells of the corneal epithelium are capable of division. Only a small ring of cells at the periphery of the basal layer of the corneal epithelium actually divide to produce additional epithelial cells. From there, the tissue grows inward and upward to form the epithelium (McDermott 1994). This fact may also be a defense against ultraviolet radiation since mutations are only a significant factor for dividing cells and the only dividing cells of the corneal epithelium are those best protected from ultraviolet light.

<sup>7</sup> This is not entirely true presently in an age of sophisticated medical technology. Corneal transplants are often performed due to endothelial decompensation. The main causes of decompensation are recent medical techniques which involve invasive actions into the eye. Most notably, intraocular lenses implanted in many cataract surgery patients can often lead to endothelial complications. Nevertheless, invasive surgery performed over the last thirty years does not bear upon the argument regarding the evolutionary adaptiveness of the tissue. I will discuss this more below.

<sup>8</sup> I will not discuss the elasmobranchs (cartilaginous fish) because their mechanism for regulating stromal thickness is not controlled by the CE. Their stromas contain *sutural fibers* which traverse the width of the stroma and hold its thickness constant, regardless of external factors. Thus, the development of the elasmobranch endothelium does not enter into this discussion.

<sup>9</sup> I recognize that the CE may have developed by convergent evolution, though I discount this possibility based upon the principle of parsimony.

<sup>10</sup> Punctuated equilibrium is the theory that evolutionary history does not just occur as a smooth, gradual process. Instead, it is an asynchronous, "jumpy" process involving times of rapid evolutionary change and times of relatively little change. Eldridge and Gould (1972) argue that the fossil record supports the presence of punctuation events. Gould (1983) also charges gradualists (those who reject punctuated equilibrium) with holding to an adaptationist program, which both he and I argue against (see Gould and Lewontin 1979 and section 1.1 above).

<sup>11</sup> See, for example, Campbell 1995.

<sup>12</sup> I am describing the extreme cases of *r*- and *K*-selection, yet particular populations of organisms may fall anywhere on a continuum lying between the extremes.

<sup>13</sup> While this may sound like strong adaptationism, I should point out that only some features need to actually be adaptations for my point to hold. Furthermore, since the features I have in mind are very broad survival traits, like foraging and defense capabilities, it seems safe to assume that at least some aspects of the broad traits evolved due to natural selection.

## Chapter 4

### Consequences of Hyperadaptation

*Hyperadaptation* serves several purposes. I will begin by arguing that the addition of hyperadaptation to our taxonomy solves certain problems that exist within evolutionary biology. Afterward, I will discuss some of the implications of a conceptual scheme containing hyperadaptation and its introduction into that scheme.

When determining whether a trait is an adaptation, an evolutionist must look at the history of the trait and its present usefulness. Since history can only be inferred in most cases, a natural reaction is to focus on analysis of the selective advantage of the trait. While this strategy may lead towards adaptationism, it does not necessarily do so and a conscientious scientist should avoid such slides. Nevertheless, this common attitude causes evolutionists to mislabel hyperadaptive features and leave hyperadaptations unrecognized. Let me explain using the example of the corneal endothelium (CE).<sup>1</sup> When confronted with the case of the CE, an evolutionist must explain why the structure appears to be hyperfunctional (i.e. functioning well beyond the expected need for that feature).<sup>2</sup> Two explanations seem plausible (excluding hyperadaptation). One approach is that it is simply an anomalous adaptation that has some unknown factor which explains why it appears to be hyperfunctional even though it really is not so. While this may be true, it seems to be a poor way of explaining such an odd case. Without any evidence

as to why we falsely observe the CE to be hyperfunctional, this explanation does very little explaining. Another, slightly more sophisticated explanation would recognize that the CE is in fact hyperfunctional but argue that it is a transitional feature which will eventually evolve towards an adaptive state. Again, while this may be correct regarding the CE, the explanation cannot be supported by any available evidence. Consequently, the inference that selection will eventually bring the feature to an adaptive state is merely an ungrounded assumption.

The problem with both of these explanations is that they assume the predominant mode of evolution is adaptive evolution, the key tenant of strong adaptationism, which I argued against above.<sup>3</sup> While these explanations are certainly correct in some cases, we have no reason to assume one of them is always the appropriate explanation for cases of hyperfunctionality. However, without the presence of *hyperadaptation* within our taxonomy, cases of hyperfunctionality seem to force an adaptationist explanation. Since no other explanation is plausible, evolutionists must choose from the above two explanations, neither of which is acceptable. The addition of *hyperadaptation* to our conceptual taxonomy provides a third alternative which is consistent with a pluralistic evolutionary research program. Appropriately labeling features as hyperadaptations does not make any assumptions about the prevalence of adaptations since the term remains agnostic regarding what process caused its evolution past the point where selective pressures were significant.

## 4.1 Direct Consequences

The introduction of *hyperadaptation* affects evolutionary theory both directly and indirectly in addition to the changes discussed above. Directly, 'hyperadaptation' acts as yet another descriptive tool that evolutionists can use to explain evolutionary phenomena. Indirectly, the introduction of the concept into our theoretical framework can help to spearhead a move towards better evolutionary thinking, particularly regarding the subject of adaptation.

The addition of *hyperadaptation* to the conceptual taxonomy of evolutionary adaptation has several consequences which can be classified in terms of their impact on experimental and theoretical concerns. The experimental issues address the ascription of terms such as 'hyperadaptation' to particular features of organisms. Both the experimental and the theoretical issues involved are relevant to all aspects of evolutionary theory. I will return to this point in the next section. Presently, I will elaborate on the issues that seem to follow directly from the terminological addition, which I label as the *direct consequences* of the addition of hyperadaptation and further separate into experimental and theoretical implications.

### 4.1.1 *Experimental implications*

An important research activity in evolutionary biology is the recognition, description, and classification of features of organisms. Specific features may be studied for three reasons in evolutionary biology<sup>4</sup>: 1) simply

as a contribution to the basic catalog of biological information, 2) in order to help reconstruct and understand evolutionary histories, or 3) to articulate or test general theoretical claims. The addition of *hyperadaptation* to our conceptual taxonomy obviously provides another category which biologists can use to describe features and their evolutionary histories. If some features are best described as hyperadaptations, then the addition of the term is useful in this respect. Still, hyperadaptation serves a more crucial role in our understanding of evolutionary histories. Since hyperadaptation describes how features have evolved and identifies features that cannot be fully understood by means of evolutionary scenarios based solely on variation plus selection, it provides an important classification category. Furthermore, our understanding of some evolutionary histories (those which involve hyperadaptations) is limited by our understanding of the concept. Therefore, elaboration of the concept of hyperadaptation and exploration of cases in which features are plausible candidates to be hyperadaptations will serve as a means for developing evolutionary theory and as a crucial tool in reconstructing evolutionary histories.

Additionally, the introduction of hyperadaptation will benefit the third research activity in evolutionary biology, i.e. to formulate or test theoretical claims. Clearly, the recognition of hyperadaptation as a biological phenomenon should inform theoretical considerations. I will elaborate this argument below in section 4.1.2.

Not only will the addition allow for hyperadaptations, but the revised classificatory scheme should be clearer than our present one. Presumably, some features that would most appropriately be described as hyperadaptations are presently not labeled as such (since neither the term nor any synonym is yet being used). Therefore, these features are presently labeled incorrectly.<sup>5</sup> With the addition to the list of labels, experimentalists must consider which features previously considered adaptations, exaptations, or whatever should be redescribed as hyperadaptations. While a reevaluation of every case may not be necessary, if hyperadaptations occur with any significant regularity, then a reinvestigation of many traits is warranted.

Also, based upon the reevaluation and reorganization of our classifications of features in cases in which selectionist explanations have been applied to hyperadaptations, experimentalists might see interesting regularities or correlations that were previously hidden. There is no guarantee that this will occur, but the possibility certainly exists. Likewise, by refining the categories currently used, reclassifying previously difficult cases that are best labeled as hyperadaptations, we may reinforce similarities already suggested or believed to exist. For example, traits that are considered adaptations are generally constrained by a small range of environmental variability, i.e. a relatively small change in a relevant environmental factor will cause a trait to lose or greatly reduce its adaptive value (fitness contribution).<sup>6</sup> Traits that are mistakenly labeled as adaptations instead of hyperadaptations will act as exceptions to this rule. By streamlining the

category of adaptations, we can eliminate the exceptions and reinforce the generalization.

All the implications discussed above show how *hyperadaptation* can be used by experimentalists. The addition not only provides another label to ascribe to features but forces a reexamination of presently labeled features. The post-addition classifications may also entail interesting and novel connections that were previously hidden from scrutiny. Assuming hyperadaptations occur in significant numbers, the addition of the term should have a real impact on evolutionary research and our understanding of features.

#### 4.1.2 *Theoretical implications*

In addition to the effects on experimental practice, the introduction of *hyperadaptation* will also result in theoretical changes. In any conceptual framework, the categories involved are usually believed to provide an exhaustive list of possibilities, with a category describing "none of the above" rarely being available. This fact is certainly true in evolution. Whatever categories may be included within the conceptual framework of adaptation<sup>7</sup>—adaptation, exaptation, fixated neutral mutation, maladaptation just to name a few—evolutionists generally work under the assumption that any examined trait must belong in one of them.<sup>8</sup> By introducing *hyperadaptation* I am not just adding a new category to our list but wedging it into a purportedly full classificatory scheme. I have shown that *hyperadaptation* is beneficial to evolutionary theory and its addition indicates that some categories within the



current framework incorrectly label features. The benefit to our theory comes in the practical application of the term to features of organisms, which affects the conceptual framework as a whole.

First, the introduction of *hyperadaptation* recognizes that the categories from which we label features are not absolute entities with strict borders. The best we can hope for in a conceptual taxonomy of evolutionary adaptation<sup>9</sup> is general labels which capture most of the phenomena most of the time. This point is by no means novel, yet it still remains underappreciated in evolutionary biology. I recommended above<sup>10</sup> that the terms in question should be understood as extremes (or maybe just major groupings) on a continuum.<sup>11</sup> Hyperadaptation, since it fits best in the grey area joining adaptation, exaptation, and nonadaptive evolution, emphasizes the need for a *continuum attitude*. Most evolutionists seem to treat the categories as stable, distinct classes. This attitude oversimplifies the complexity of biological phenomena and also leaves little room for the addition of a concept such as *hyperadaptation*. While I do not *deny* that the terms within the conceptual framework of adaptation really do refer to a distinct evolutionary phenomena, I wish to remain *agnostic* on the distinctiveness of the boundaries of these terms in concrete applications. Given this, there is nothing barring the acceptance of vague categories and fuzzy terms. Better put, my agnosticism does not prevent me from employing such categories by a commitment to a strictly defined conceptual framework.

Second, assuming evolution predominantly occurs by gradual change (which, in spite of the recent controversies over punctuated equilibria, remains the prevalent view among evolutionists), many traits we currently observe must be in transitional states and not at equilibrium. However, most of the terms we use to describe features assume that they are at equilibrium. Thus, our current conceptual taxonomy makes it difficult to describe transient features. Vague categories should help us better describe these transitional features. The transitional states of features are better described by vague categories due to their "in between" status which can easily fall outside the norm of sharp categories that are designed with an eye towards features in equilibrium.

Third, the introduction of *hyperadaptation* can also help clarify some of the vagueness and imprecision inherent in evolutionary theory. Under the presently accepted framework of evolutionary adaptation, the cases which I would call hyperadaptations do not present a severe problem for evolutionists; their mislabeling does not result in any contradictions or enigmas. Generally, theoretical vagueness in science is a relatively small concern, especially for experimentalists. However, by accepting *hyperadaptation* into the conceptual taxonomy of adaptation, evolutionists will recognize that the categories of adaptation become more precise and even more plausible in a conceptual framework that includes *hyperadaptation* compared to a framework without the concept. Evolutionary theory is chock-full of vague categories and uncertain concepts, primarily due to our

extremely limited understanding of evolutionary events. The extraordinary diversity of evolutionary phenomena explains why we should not expect strictly defined and applied concepts. Nevertheless, we should strive to reduce and, if possible, eliminate the vagueness and uncertainties in our theory whenever possible. *Hyperadaptation* does just that. By adding the category to our structure, we sharpen the related categories by removing many of the unusual cases (which are best called hyperadaptations) that were never well suited for their placement anyway.

This consequence is important because it results in a clearer theory that better explains biological phenomena. We gain a more accurate understanding of how features evolve in relation to their functions. Also, we can investigate why a feature might evolve to be hyperadaptive. While I have not discussed any mechanisms by which features become hyperadaptations in great detail, clearly the process would be of interest to evolutionists. Again, the contribution to our overall understanding of evolution is the result.

## **4.2 Indirect Consequences**

The issues discussed in the previous section addressed the direct consequences of *hyperadaptation* for evolutionary theory. In this section, I will discuss some of the indirect ramifications of the addition of the concept. One contrast between the two is that the previous arguments dealt with the consequences of *hyperadaptation* as a concept on our experimental and

theoretical frameworks. Presently, the discussion will deal more with the effects of the *introduction* of hyperadaptation as opposed to the impact of the concept itself. I will consider how the addition of the concept might change the attitudes of evolutionists and their approach to the field.

In one respect, I view the introduction of hyperadaptation as an illustrative response to some common ills in evolutionary thinking. I discussed above, as part of the direct theoretical consequences, how *hyperadaptation* must make conceptual room for itself in a purportedly exhaustive set of concepts regarding adaptation. The reason for this is simple: as with most scientific theories, all observable phenomena are expected to fit into some presently available category. Philosophers of science may even perceive this as a necessary condition of a comprehensive scientific theory.<sup>12</sup> However, in the case of evolutionary theory I hold that such strictness is inappropriate. The extraordinary complexity of biological phenomena coupled with our relatively small corpus of studied organisms, features, and events indicates that we do not have adequate grounds to believe we have a complete theory of evolution (or even something close to a complete theory). Hyperadaptations, due to their peculiar evolutionary histories, may not exist in great numbers (though their lack of prevalence does not detract from their significance). However, if they do exist, we can expect other similarly peculiar evolutionary events to exist. While the current view of evolutionary theory does not reject the introduction of new evolutionary pathways and related concepts, the strictness with which evolutionists hold on to its conceptual

framework discourages such activity. A less stringent view of our conceptual taxonomy will allow for such additions as *hyperadaptation* and encourage the search for other such cases which surely must exist.

Moreover, a more relaxed conceptual atmosphere will relieve the unnecessary pressure placed upon evolutionists to place odd cases neatly in their conceptual taxonomy. At the beginning of this project, I had only the knowledge of an evolutionary oddity in the corneal endothelium.

Recognition of the need for a terminological (and conceptual) addition came after noticing that other features seem to share a similar evolutionary history and current state. Others who observe an unusual feature that does not fit well into our currently accepted categories should have the opportunity to label the feature as "presently undetermined" or "uniquely evolved".<sup>13</sup>

While loosening the strictness with which evolutionists classify features may seem to be bad science to some, it just shows that we are still developing our theory. With a storehouse of unclassified features, novel similarities and consequent trends may become apparent.

Finally, the addition of hyperadaptation reiterates a common theme both in philosophy of biology and philosophy of science (at least over the past few decades). The relationship between experiment and theory is crucial to the development of a science. Although each contributes to the scientific enterprise in a unique way, scientists and philosophers of science must have a deep appreciation of both experimental and theoretical work to understand science. Philosophers of biology have for many years succeeded in bridging

the gap between theory and experiment. The fine line between the two in evolution has no doubt contributed to this success for philosophers of biology. Nonetheless, a vast majority of biological research seems beyond the conceptual grasp of philosophers and theoretical evolutionists. Modern biology has become an enormous field. Not only do we differentiate between the common subdisciplines of physiology, genetics, molecular biology, cell biology, etc., but also into a host of applied fields with their own subcategories. Medicine, agriculture, health and nutrition, engineering, and forestry all participate actively in biological research. Furthermore, technological advances have also opened up new avenues of research in previously unconsidered territories. Consequently, these fields have developed a huge bank of information regarding biological phenomena which is contiguous with the knowledge garnered by so called *basic science* research. My point is that evolutionary biology has a host of case studies at its proverbial fingertips. *Hyperadaptation* was developed to explain a case that was common knowledge in one branch of medicine.<sup>14</sup> A thorough scouring of the wide spectrum of biological research should yield other cases which would be interesting to biology. Also, since the cases are well known to the corresponding research fields, much of the experimental work will likely be done or at least readily available. Evolutionists just need to make the appropriate connections and start looking.

### 4.3 Conclusion

In their 1982 paper on exaptation, Gould and Vrba state in their conclusion:

We believe a failure of evolutionists to codify such a concept [as exaptation] must record an inarticulated belief in its relative insignificance (p. 13).

This claim suggests that concepts such as exaptation, or at least exaptation itself, may have been ignored by evolutionists *intentionally*, due to a belief that the phenomena described by the concepts lack importance or uniqueness to merit articulation; or *unintentionally*, since the same assumption led them to dismiss certain phenomena or considerations as unimportant. Hence, Gould and Vrba conclude<sup>15</sup> by concerning themselves with showing that exaptations are significant phenomena since that is the proof required to justify the importance of the concept.

Whether they were correct in their conclusion regarding exaptation is not my present concern, yet hyperadaptation is sufficiently similar to exaptation that their comment might be extended to include *hyperadaptation* and related concepts also. However, I believe that *hyperadaptation* (at least) makes a stronger point regarding conceptual change in evolutionary theory. The reason why evolutionists have failed to codify *hyperadaptation* and similar concepts is not because of some inarticulated belief in their empirical insignificance. In this case, it is clear that the relevant phenomena lie beyond the observation of evolutionists due to a constrained conceptual framework that does not include the relevant concepts. Without at least a minimal

conceptual understanding of *hyperadaptation*, evolutionists cannot classify particular phenomena as hyperadaptations.

While I do not deny the significance of Gould and Vrba's comment, I want to emphasize the relative severity of the problem to which hyperadaptation is addressed compared to the exaptation problem, at least as Gould and Vrba frame it in their conclusion. Exaptation, according to the authors, needed articulation because it was a more significant phenomenon than was previously thought. Hyperadaptation (like related ideas) needs explication because *its significance is unknowable without a clear understanding of the concept*.<sup>16</sup>

To illustrate, consider the attitude regarding nonadaptive features prior to Darwin. Before Darwin, the dominant view in biology was that all features were adaptive. This premise, usually grounded in a belief in purposeful benevolent creation, repudiated the possibility of nonadaptive or maladaptive features *a priori*. Darwin rejected the theoretical orthodoxy *a posteriori* by pointing to features that were apparently non-beneficial and offering an account of evolutionary change<sup>17</sup> that explained how non-beneficial traits arise. With Darwin's revised framework available, subsequent evolutionists began to observe many features that appeared, based upon Darwin's revisions, not to be adaptive. Thus, a change in the conceptual framework led to the observation of phenomena that were previously thought to be conceptually impossible.



Correspondingly, the significance of hyperadaptations and similar phenomena cannot be adequately considered until we establish a coherent understanding of their underlying concepts. Nevertheless, even if my examples of hyperadaptations are not correct, if hyperadaptations collectively have little importance, I believe my arguments are not in vain. My point is that conceptual change (and subsequent terminological additions) in evolutionary biology must occur to best account for many features which, like the corneal endothelium, are not adequately explained by our present conceptual framework. I hope that this thesis and the introduction of *hyperadaptation* can serve as an instance of how terminological and conceptual additions can provide for a theory that best accounts for biological phenomena.

## Notes

<sup>1</sup> See Section 3.1 above.

<sup>2</sup> I do not use the term 'hyperadaptation' since it would not be available to the person in my example.

<sup>3</sup> See Section 1.1 above.

<sup>4</sup> I am ignoring other instrumental studies of features, such as in biomedical or bioengineering research, concentrating on research within evolutionary biology proper.

<sup>5</sup> Or at the least they are labeled in a weaker or less coherent manner than they would otherwise be when called hyperadaptations.

<sup>6</sup> At least one objection to this example is the adaptation of being highly tolerant of variable environmental conditions. I consider these adaptations not to affect my argument since they are second order adaptations of the organism, not adaptations of the features I am considering. Some may object that this difference in levels is irrelevant and tolerance serves as a severe counterexample to my claim. However, I feel that cases of tolerance have a special character that can be ignored for the present. Regardless, whether this generalization actually holds for the majority of adaptations is of little importance, as the example is just an illustration. The point is that generalizations *such as this* become more salient with the addition of hyperadaptation to our conceptual framework.

<sup>7</sup> Note that 'adaptation' as the title of a conceptual framework differs from 'adaptation' as a label within that framework. The former describes the corpus of terms which attempt to describe the relationship between a feature, its possessor, and the environment in some appropriate manner. The latter is the category where the relationship is that the feature fits the model of an 'adaptation to function' described in 1.4 above. I suppose some may find it ironic that I began this thesis by attempting to clarify the uses of 'adaptation', yet I am concluding it by further complicating the use of the term.

<sup>8</sup> I will evaluate the validity of this assumption (which I reject) in the next section (4.2) as part of the indirect consequences.

<sup>9</sup> At least so far as our current understanding of evolution suggests.

<sup>10</sup> See Section 2.2.

<sup>11</sup> Even a continuum might be too restrictive of an image since it suggests linearity and even progression, neither of which I intend. The ideal analogy would be to an amorphous, three-dimensional collection of Venn spheres of varying sizes, possibly overlapping but not necessarily conjoined to one another.

<sup>12</sup> By a comprehensive scientific theory, I mean a theory with a complete conceptual framework that adequately accounts for all kinds of phenomena and events in that domain.

<sup>13</sup> A feature whose evolution appears different than any previously described trait will seem "uniquely evolved" regardless of whether it truly did evolve by a means unrelated to other undescribed features.

<sup>14</sup> Ophthalmology with the case of the corneal endothelium.

<sup>15</sup> Their conclusion does seem to be a more conservative interpretation of the problem addressed by *exaptation* than in the main body of their paper. At other points, they seem to indicate that *exaptation* was not recognized for conceptual, not empirical, reasons.

<sup>16</sup> I also believe Gould and Vrba felt somewhat similarly about *exaptation* as they suggest in their introduction discussing the impact of classificatory schemes on thinking.

<sup>17</sup> Specifically, decent with modification, though later and more broadly, natural selection and non-adaptive evolutionary change.

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## **Vita**

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David Rudnick was born and raised in Ft. Lauderdale, Florida where he graduated from Plantation High School. He received his bachelor's degree from Emory University in 1995, majoring in Biology and Philosophy. While at Emory, David actively participated in ocular research, focusing on the effects of preservatives and artificial tears on the corneal epithelium. In 1995 he presented a poster at the Association for Research in Vision and Ophthalmology annual conference. This thesis was submitted in partial fulfillment of the Master of Arts degree in Philosophy at Virginia Polytechnic Institute and State University. While at Virginia Tech, David specialized in philosophy of biology, where the focus of his philosophical interests lie. After graduation, he is continuing his involvement in ocular research.