

**Adaptive Explanations of Behaviors: Obstacles and Overcomings**

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## **Adaptive Explanations of Behaviors: Obstacles and Overcomings**

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This paper seeks to clarify and modestly defend the use of adaptive explanations – explaining the existence of a trait by reference to putative historical selection pressures – within the evolutionary behavioral sciences. I identify four major areas of concern: (1) the kind of target that behavior is, (2) the explanatory strategy used by adaptive explanations, (3) the forward-looking or model-based approach to adaptive explanations, and (4) the adaptive explanation of human behaviors. After working through each of these areas, I conclude that, adaptive explanation, even via the forward-looking approach, is a viable strategy to explain the behavior of human and non-human animals, but is subject to legitimate difficulties and limitations concerning hypothesized selection pressures, cognitive complexity, and non-genetic systems of inheritance.

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## PREFACE

I would like to begin by thanking all of those – an impressive number of people for a paper with only one author -- who helped me both start and finish my undergraduate thesis. First off, I would like to thank committee members Edouard Machery, and Kevin Zollman for their invaluable suggestions. Further thanks goes out to my friend and peer Josh Hunt, and neighbor and occasional research mentor Dr. Debra Mariano for similarly valuable comments. I would like to especially thank committee member Jeffrey Schwartz and committee member and research adviser Sandra Mitchell who in their many roles as professor, advisor, mentor, and exemplar had a transformative effect on not only this paper, but also my entire undergraduate experience. Dr. Mitchell's ability to be endlessly bombarded with doomed arguments by an over-enthusiastic undergrad and yet remain helpful and encouraging all the way to the completed thesis says more about her than any list of adjectives I could fit in this preface.

Before beginning the thesis proper, I would like to make a few clarifications. As a reader helpfully pointed out to me, “adaptive explanation” is casually thrown around in the philosophy of biology, but it is actually quite a laden word. To head off any confusion, when I say adaptive explanation I am referring to the explanation of the current existence of a biological trait by appeal to the historical effect of natural selection on the genotypes of a

population. This will be discussed in much more detail, but it may be helpful to start with such a platform. However, this entails that those who challenge either the viability or explanatory power of natural selection may object to the meaningfulness of this paper, even if they acknowledge the argumentation. This paper is not for them. Rather, if this were not a mere undergraduate thesis fated to obscurity, I would hope to engage with two distinct groups. For scientists, this paper could serve as a somewhat casual overview, with the interesting feature that it exposes the supporting philosophical skeleton of practices they are likely quite familiar with in the flesh. For philosophers, who are a bit more agnostic on the topic, I have tried to toe the line between preserving their reservations, and defending what I find to be an interesting and fruitful area of biology.

## INTRODUCTION

Adaptive explanation refers to the explanation of a trait by appeal to the putative forces of selection that made it, e.g. the antlers of elk evolved in response to the selection pressure of male-male competition for mates. In the 1930s, with the advent of ethology – the evolutionary study of behavior – the use of adaptive explanations was broadened from morphological to behavioral traits.<sup>1</sup> Despite their current broad use across the evolutionary behavioral sciences, they remain controversial, particularly when applied to human behaviors. Here, I aim to provide clarification and measured defense. This paper is structured as series of objections to the adaptive explanation of behavior, concerning: (1) whether behavior is an appropriate object for science at all, (2) whether the use of functional accounts generally and adaptive accounts specifically is an appropriate way to explain behavior, (3) whether the model-based approach is an appropriate methodology to arrive at adaptive explanations, and (4) whether human behaviors are an appropriate target for adaptive explanations. With each objection, I characterize the kind of challenge it

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<sup>1</sup> This is not to say that evolutionary explanations were not applied to behaviors before the 1930s; see, for instance, Darwin's exposition on birdsong in the *Descent of Man* (1871, pp. 48-65). Darwin also applies adaptive explanations to human behaviors in the *Descent of Man* (1871) and the *Expression of Emotion in Man & Animals* (1872). However, it is the work of Konrad Lorenz and Nico Tinbergen in the 1930s that is seen as providing a formalized and structured evolutionary science of behavior. Prior to them, by and large, behavior was ignored in the face of anatomical and morphological features, studied in fabricated laboratory settings using a psychological framework, or studied by amateur naturalists (Burkhardt, 2005; Lorenz, 1982). Lorenz and Tinbergen facilitated both a formal methodology and the explicit incorporation of evolutionary theory (see Tinbergen, 1963 and Lorenz, 1982 for discussion).



represents and the way the behavioral sciences have responded. (3) and (4) are particularly contentious, and therefore will form the bulk of my analysis.

## **1.0 BEHAVIOR AS A SCIENTIFIC OBJECT**

I begin by briefly sketching one kind of appropriate scientific object. I then discuss behavior with respect to this account, identifying both its unproblematic and problematic features. I conclude by defending the methodological strategies embraced by the evolutionary behavioral sciences as responsive to these challenges, and commensurately holding behavior to be an appropriate scientific object.

### **1.1 APPROPRIATE OBJECTS OF SCIENCE**

Obviously a full theory of what it takes to be an appropriate object for scientific study is well beyond the scope of this (and perhaps any) paper. Therefore, rather than trying to delimit a conceptual space that is occupied by appropriate objects of science and evaluating whether or not behavior fits within that space, I will instead begin with an uncontroversial object of science, and see if behavior shares the features that seem to make that object so scientifically unproblematic. In short, my approach is expansive rather than constrictive.

Let us begin by looking to two systems: (1) a ball being rolled down a hill, and (2) a gazelle being approached by a lion. Before proceeding further, it is worth clarifying why the second system constitutes a behaving system. The most obvious difference is that the

second system is living or biological – ethologists do not see non-living systems as behaving. However, this is insufficient, after all, excepting the shape, a gazelle being rolled down a hill could be analyzed in the same way as the ball, but one would not consider that the behavior of a gazelle. To be behavior, the gazelle’s actions must also be internally mediated, e.g. by neurotransmission, chemical signaling, or muscular activation, as opposed to merely the replication of interactions that occur in non-biological systems (such as gravitational acceleration) in systems that are incidentally biological.

Now lets us compare the systems specifically with respect to being appropriate objects of science. Both systems are physical and observable (i.e. they make no appeals to undetectable or supernatural forces). However, the ball-hill system is also (fairly) non-contingent, accessible to experiment, predictable, and able to be specified with the precision needed for scientific study (individuated).

The ball-hill system operates with the law-like regularity of physics. An identical system can be recreated simply by putting the ball back on top of the hill. I can easily change just one thing involved in the system, e.g. the coefficient of friction, and see a direct and isolatable change in outcome. If I cover the hill in glue and observe the ball rolling more slowly, I do not have to worry about the possibility that maybe the ball was simply rolling more slowly because I was standing too close and making it skittish. And in fact, given the current knowledge of physics, I can predict the results of almost any change I make on the system, from changing the coefficient of friction to increasing gravity. Finally, the system is easily specified and precisely measurable, starting and stopping under exact parameters. I can describe my setup, e.g. I put a 5kg bowling ball on top of a 30-degree grass-covered hill 3 meters in height, and scientists can then observe an identical system. While balls on hills may not be the most exciting, they are extremely cooperative.

A gazelle being approached by a lion is not so tractable. If the gazelle sees the lion it may run, but it may not see the lion, or it may jump in the air (stot) first – this makes the system both more contingent and less predictable. Nor can I intervene on the system by changing many things. Finally, the gazelle’s actions exist as a stream of information. Sure, it may run from the lion, but then it eats some grass, and then it licks itself, etc., until it dies. Which stretch of actions should I describe such that a scientist will be able to identify (approximately) the same stretch in another gazelle? And how should I describe or quantify them?

Given this apparent divergence from the ball-hill system, there are two broad strategies. First, one could study behavior in a way that makes it as much like the ball-hill system (i.e. physics) as possible. Second, one could defend a particular approach to behavior that, while relevantly different from that used by physicists, nonetheless is scientific.<sup>2</sup>

The first strategy is certainly possible. Scientists could approach the actions of the gazelle as applied physiology: this brain region was activated, these neurotransmitters were released, these muscles twitched, etc. In fact many scientists, e.g. physiologists, neurologists, look to exactly these factors. However, to accept only this strategy is problematic. It does not address the fact that behaviors seem to do something for organisms, a sort of apparent goal-directedness, which is a particularly interesting and salient feature of behavior. Moreover, it is this feature of behavior that the evolutionary behavioral sciences and adaptive explanations utilize, e.g. Melo et. al. (2011) who discuss

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<sup>2</sup> See Mitchell, 2009 for a discussion of why the physics-based approach is seen as paradigmatic, and a wide-ranging philosophical defense of the second strategy. I defend it here in a far more limited sense.

wasps stinging spiders in order to lay their eggs in the them, rather than appealing to the mechanism of the sting.

In light of this, I will undertake a defense of the second strategy. Particularly, I will argue that behavior exhibits the same features that make the ball-hill system a good object of science, but either exhibits them to a different (but still sufficient) degree, or exhibits them in a different manner.

## 1.2 BEHAVIOR ON ITS OWN TERMS

I will structure this defense of a behavior level science based on the features of an appropriate scientific object described above: non-contingent, accessible to experiment, predictable, and able to be specified with the precision needed for scientific study (able to be clearly individuated). In the second section I will go into functional approaches in more detail; however, it is important to my defense here that behaviors can be thought of as doing certain things or performing certain functions for organisms.<sup>3</sup>

A brief clarification before proceeding. Philosophers of science have recently argued against a unitary understanding of behavior, defending that the goals towards which

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<sup>3</sup> This statement seems to commit to a Cummins (1975) or causal role understanding of function. In causal role accounts, a function is understood as the role a function plays in the capacity of a containing system. For instance, the function of the concavity of a bowl is to give the bowl the capacity to hold liquids. For those familiar with the literature, this will seem an unusual starting point, as this paper is moving towards adaptive explanations which are historical and therefore *prima facie* better captured by an etiological understanding of function (see Wright, 1973; Millikan, 1984). However, the reason I begin with such an understanding of function is that much work in the evolutionary behavioral sciences appeals to function, but is ahistorical. Take Caro's work on stotting in Gazelles (1986a, 1986b). It is a short-term study, and he uses no historical investigation strategies but nonetheless aims at functional attribution. I hope to address any tension my methodology evokes in the second section.

research is directed influence the framework used to approach and explore behaviors (Longino, 2013; Weber, 2012). For instance, reflex action may be considered a behavior of interest by a neurologist studying motor neurons, but not by a behavioral ecologist studying interaction between behavior and ecology. With this critique in mind, I seek to defend behavior specifically as understood by the ethological tradition or the evolutionary behavioral sciences (including ethology, behavioral ecology, human behavioral ecology, and evolutionary psychology) – the research tradition that most makes use of adaptive explanations.

### **1.2.1 Behavior as contingent**

Like other biological features, the existence of a behavior is contingent upon evolutionary history, development, and experience. Moreover, whether or not a behavior is performed is contingent, dependent upon both internal factors and environmental conditions. Finally, even when performed, the manner of expression is contingent, likewise dependent upon both environmental factors (particular environmental demands) and internal factors. All this adds up to meaning that simply observing a behavior does not mean it occurs predictably or is easily generalizable.

To get more traction on this problem, let us imagine that behaviors, instead, operate in a more lawful manner. Upon a lion getting within a certain distance of a gazelle, the gazelle will begin to move away and the lion will pursue. This happens regardless of whether the lion is spotted, the gazelle is hungry, or an experimenter is present – this is simply how gazelles and lions interact in this universe. Scientists can derive the behavior of new a gazelle from this law-like interaction. If something unusual happens, e.g. the lion

turns away, scientists can look at this with respect to the lion-gazelle law to identify a cause, e.g. a Wildebeest intervened. Unfortunately, evolutionary behavioral scientists do not have it so good. There is the possibility of a superficially similar situation being very different, e.g. gazelle A running from approaching lion A, but gazelle B not running from approaching lion B. Moreover, there may be no easy way to identify the cause of the difference – maybe gazelle B did not see the lion, or maybe it had a small stroke.

However, simply the fact that the evolutionary behavioral sciences deal with these contingent objects is not grounds for dismissal – every science must do so to some extent or the other (see Mitchell, 2009). Two specific questions come to the forefront. First, are behaviors necessarily so contingent that they can never be approached scientifically? Second, if not, can one evaluate the extent to which a behavior is contingent?

The answer to this first question seems to be a definite no. This would entail that every behavior is a sort of miracle contingent upon situations so elaborate that they are never relevantly repeated. Certainly some behaviors may fit this. A starling, a bird noted for its abilities of mimicry, may somehow end up copying a once in a lifetime performance by Yo-Yo Ma. This would seem to tell us little about the normal behavior of starlings.<sup>4</sup> However, most animals definitely perform what *prima facie* appears to be the same behavior a sufficient number of times – look to stotting in gazelles, collecting acorns in squirrels, wasps stinging spiders, etc.

In terms of evaluating the contingency of behaviors (i.e. the obscurity of the combination of causes upon which behaviors are dependent), evolutionary behavioral scientists have at least three strategies available to them: fixed-action patterns,

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<sup>4</sup> To clarify, this would tell us little about the behaviors of starlings; however, it would tell us a great deal about the capacity of Starlings. Similarly, even a single instance of tool use or manufacture could be very powerful, even though the information it provides is not about the behavior of a species *per se*.

comparative methodology, and modeling. A fixed action pattern -- easily recognizable and often repeated complexes of actions – picks out a specific behavior from the stream of information that behavior represents (Hinde, 1982, also see Tinbergen, 1942). After having identified such a behavioral unit, a scientist can simply look for it and empirically evaluate how contingent (and ideally also upon what) a behavior is. Comparative analysis helps to identify the relevant factors that are causing something by identifying the commonalities across situations in which a variety of causes are at work, i.e. natural experiments. Behaviors are susceptible to this approach, and looking at behaviors across environments and species (or even across many member of the same species) can lead to meaningful inferences about the contingency of behaviors. Finding similar behaviors across a wide variety of taxa and environments e.g. mobbing, or mating dances, provides evidence they are contingent upon a less obscure set of causes.<sup>5</sup> In contrast, behaviors found only in a small number of members of one species are likely to be extremely contingent. A third option discussed by Trestman (2011) is hypothetical models of behavior to which natural behaving systems can be matched. For example, given an understanding of optimal foraging behavior, one can model how long shorebirds will search for food in a specific patch and when they will move to a new one – which can then be matched to the birds actual behavior demonstrating a functional character to the bird’s behavior (van Gils et. al 2003). I will return to this modeling based approach in much more detail in the third section.

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<sup>5</sup> See Trestman (2011) for a much more thorough analysis of the comparative or “Lorenzian” approach, albeit the context for his analysis is somewhat different than the “dealing with contingency” problem I am tackling here. Also see Neander & Rosenberg (2013), who provide an excellent look at the role of phylogenetic investigation in the analysis of functions – although their account of function is explicitly historical.

### **1.2.2 Accessible to experiment**

Behaving systems are simply not manipulatable to the degree of balls on hills. The biological nature of the components makes everything messier, and it is very hard to intervene on specific components. However, again, this is far from a death sentence. First, behaving systems can still be experimented upon. Second, there are other ways to get the same kind of information that would be provided by experiments (or other relevant kinds of information).

In addition to simply observing, evolutionary behavioral scientists do engage in experiments. Performing experiments involves toeing a very difficult line, as those in the ethological tradition would like to control as many causal factors as possible, but not control so many factors that behaviors performed are not representative of how the organism performs in its natural environment (see Lorenz, 1982, pp. 47-52, 64). This difficulty can be somewhat overcome through possessing a broad understanding of the organism and the behaviors it performs (ibid. pp.52-53). On this background of a general knowledge of the organism, if experimental intervention leads to aberration, the experimenter is far more likely to identify it. Alternatively, experiments can also be performed in the wild. To assess whether the mane of lions impacted mating, West put one of two dummy (plush) lions that differed only in mane length by a female lion (2005). He can evaluate whether this experiment is useful by looking to both whether behavior induced by one dummy differs with respect to behavior induced by the other, and whether behavior induced by the dummies differs qualitatively from behavior that occurs in response to real male lions.



It is also well established that scientists use non-experimental approaches. Scientists in the ethological tradition have a rich observational literature that highlights many correlations between ecology (or situation) and behavior. And again, the comparative and model-based approaches do work here. The comparative method sets up a sort of natural experiment, in which one can attempt to identify relevant causal factors by looking at an array of different situations. In Shear's research on web-building in spiders, he looks at a connection between particular features of the environment and the structure of the web being built (1994). The finding that there is a correlation between web design and ecology independent of the species of spider making the web evidences that web-design is a reaction to the environment.

### **1.2.3 Predictable**

The complexity and large number of unknown factors, e.g. physiological condition, life history, etc., operating in behaving systems injects a certain sense of unpredictability, and make them difficult to deal with in a causal-mechanical sense. To predict what a gazelle will do when confronted by a lion purely by monitoring its physiology would be extremely complicated. However, predictability can be regained through the application of an intentional or functional approach (see especially Dennett, 1989). As Weber illustrates, if we assume that the gazelle has intent, and it spots a lion sneaking up on it, it should want to preserve its life and run, and moreover, as a matter of prediction, the gazelle will likely do just that (2012). Weber refers to this as the predictive value of the intentional stance, and recasts this in functional terms through the idea that the behaviors of an organism should

all cohere towards (functioning to) increasing self-reproduction, for similar approaches also see Griffith, 2009 and Trestman, 2010.

#### **1.2.4 Able to be individuated**

Unlike other physical systems, behavior represents a continuous stream of information and therefore must be able to be individuated into usable units (see Hinde, 1982). Nanay (2010) preliminarily identifies three major ways to individuate biological traits: function, morphology, and homology. I look to them in turn.

For behaviors, function seems to be the most powerful as it allows for both specificity and generalizability. Let us take a specific behaving system, say a zebra. I can ask which behavior functions to evade predators and arrive at the answer of running. This both picks out a particular action, and differentiates running that functions to evade predators from other instances of running.<sup>6</sup> Now take a skunk. I can ask the same question – which behavior functions to evade predators – and arrive at another distinct trait for the skunk: spraying. “Predator evasion” serves as a general category that can be used to pick out specific behaviors in any behaving system that is threatened by predation.

Morphology can be used to individuate behavior in two senses. First, a behavior can correspond to underlying cognitive and neurological architecture. Second, and in a less reductive sense, behaviors can be more or less like morphological features. Some behaviors, while individuable, are extremely plastic and contingent. Take for instance the use of spears to hunt in particular populations of Chimpanzees (Pruetz & Bertaloni, 2007).

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<sup>6</sup> The relationship between functional accounts and trait (or token) individuation is far more complicated than I am able to discuss here. I refer the reader to Nanay, 2010; Neander & Rosenberg, 2013; Trestman, 2011; and Weber, 2012 for a more focused look.

Other behaviors, such as the stinging of scorpions, are an extremely stable and invariable complex of actions. These invariable behaviors, as captured by fixed action patterns, individuate behavior in the same way as morphology. They provide a stable and specific structural description.

As far as I am aware, homology does not serve to individuate behaviors, but I leave open the possibility.<sup>7</sup>

### 1.3 SUMMARY

Behavior, and more specifically behavior as understood by the ethological tradition, does indeed possess features that make it more difficult to approach scientifically. However, there is nothing about behavior that renders it scientifically intractable. I specifically argued that behavior is naturalistic and observable, and, with the right approaches, also manageably contingent, accessible to experiment, predictable, and able to be specified with the precision needed for scientific study (individuated).

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<sup>7</sup> Although, I am uncertain as to how homology can serve to individuate at all. Homology is nothing more than similarity combined with a theory of relatedness. Even if one had very good reason to believe two organisms were phylogenetically related, they would not identify two organs as homologous without some morphological (including genetic or developmental) correspondence. In short, the individuation work of homology seems to be done morphologically. However, I do not yet have enough confidence in this argument to deny the possibility that homology may be used for individuation.

## **2.0 EXPLAINING BEHAVIORS IN THE EVOLUTIONARY BEHAVIORAL SCIENCES**

I have defended that the targets of adaptive explanation, i.e. behavior, are appropriate targets of scientific inquiry. I will now address whether the techniques used to explain behaviors are appropriate. I do so in three levels, addressing first “functional analysis,” next “selected-for explanation,” and lastly “adaptive explanation.” While functional analysis identifies the role a behavior plays in its containing system, selected-for explanations correspond to the selective (evolutionary) history of trait, and adaptive explanations likewise appeal to selective history, but specifically for genetically mediated natural selection. I conclude with a discussion on how scientists can move from functional analysis to adaptive explanation. To frame this section, I begin with an overview of functional accounts within biology generally, and the evolutionary behavioral sciences specifically.

### **2.1 OVERVIEW**

There are two main understandings of function within the philosophy of science. First is Wright’s (1973) etiological account, of which more biologically specific framings are provided by Millikan (1984, 1989b), Mitchell (1989), and Neander (1991). Second is

Cummin's causal-role account, which is elucidated in a more biologically relevant way by Weber (2012) (also see Bigelow & Pargetter 1987).<sup>8</sup>

Etiological accounts of function aim to explain why a feature (or trait) is there by appeal to the causal process that gave rise to that feature. A bowl has the function of holding because of design. In biological systems, an etiological account will explicitly appeal to the evolutionary history of a trait. For instance, the function of eyelashes would be to keep particulate out of the eye, if (1) there was selection for the capacity to keep particulate out of the eye, and (2) eyelashes arose and are reproduced because of this selection process (see Mitchell 1993). I will refer to this narrower use of the etiological account as a *selected-for function*.

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<sup>8</sup> Another account of function has been recently introduced by Nanay (2010, also see 2013). His account is quite elaborate and is allegedly differentiated from existing accounts by (1) modal force (how "would" a function contribute), (2) a focus on trait tokens rather than trait types, and (3) the use of counterfactuals. He is mistaken about (1) as causal-role can be interpreted as a disposition or propensity to contribute to capacity of a containing system if certain conditions would be met, (Nanay incorrectly identifies dispositional as strictly "future" accounts. Also see Kiritani, 2011 for a defense of modal force in etiological accounts), but this is beside the point.

What matters here is, *if* Nanay were to be correct, would it change my project. The answer seems to be no. Nanay explicitly identifies his account with usefulness – which maps onto the causal-role a trait plays in the capacity of a containing system. Nanay prevents usefulness from collapsing into use through the use of modal force, which is exactly what disposition does for the causal role account. Finally, Nanay prevents his account from simply picking out every way a trait could be useful by contextualizing it with respect to the explanatory project. For instance, one could look to how a trait is useful for increasing survival and reproduction. Causal-role accounts make this same move by specifying the capacity that functions are contributing to, e.g. contributes to the capacity to survive and reproduce. His machinery for identifying function is a little different, but it identifies the same functions as the Cummins-style causal-role account. Or, to put it another way, Nanay's account functions identically to the causal-role account. Therefore I will simply speak of the more established causal-role account with the addendum that what I say about it also applies with Nanay's account. Given this symmetry with the causal-role, it is interesting that Nanay puts forth his account largely as a challenge to the etiological account, which as we will see, aims for a completely different kind of explanation (see Godfrey-Smith 1993; Millikan, 1989a; Mitchell, 1993).

Causal-role accounts of function aim to explain function through the contribution a feature makes to the capacity of a containing system. Eyelashes would have the function of keeping particulate out of the eye, if possessing eyelashes contributed to an organism's capacity to keep particulate out of its eyes. This can be put in more evolutionarily relevant terms by connecting the function of a feature to an organism's inclusive fitness (again see Bigelow & Pargetter, 1987; Weber 2012). For instance, eyelashes have the function to keep particulate out of the eye, if possessing eyelashes contributed to an organism's capacity to keep particulate out of its eyes, and if the capacity to keep particulate out of the eyes contributes to an organism's inclusive fitness. Following Weber, I will refer to this narrower understanding of causal-role function as *biological function*. Significantly, causal-role accounts are time-slice or snap shot evaluations rather than causal-historical, as they can represent the biological functionality a behavior has with respect to a specific set of environmental conditions, either past or present.<sup>9</sup>

As should be clear, these two accounts of function, while often overlapping, have different explanatory projects (also see Godfrey-Smith 1993; Millikan, 1989a; Mitchell, 1993). Moreover, these accounts are appropriate for the explanatory interests of the evolutionary behavioral sciences. Those in the ethological tradition are interested in what a trait does for an organism within its current environment, e.g. how does making a sudden vertical jump before fleeing predators increase the survival of gazelles (Caro, 1986a, 1986b), and therefore must rely on causal-role accounts. Tinbergen refers to this as the study of *survival* (1963, also see Griffiths 2009). However, evolutionary behavioral scientists are also interested in why a behavior exists in light of its selective history. Shear's

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<sup>9</sup> Causal-role accounts are often understood as picking out current function. This is true, but it is true by virtue of them being time-slice and able to pick out function at any specific moment in time. Griffiths makes this clear by discussing the etiological account of function as representing a series of causal-role accounts (1993).

work on the convergent evolution of similar web-design for similar ecologies in spiders is illustrative (1994). This requires the use of etiological accounts (selected-for function), and is discussed by Tinbergen as the study of *evolution* (1963; Griffiths, 2009).

## 2.2 FUNCTIONAL ANALYSIS (AND BIOLOGICAL FUNCTION)

Functional analysis is associated with causal-role function, and very roughly refers to the decomposing of a system into component parts that contribute to a capacity of the containing system (see Cummins 1975). Functional analysis with respect to biological function entails that a system is broken down into all the components that contribute to inclusive fitness. This captures those functions that are relevant to the survival and evolution of a behaving system, i.e. functions of biological interest. I see functional analysis as the first step in the development of an adaptive explanation. I begin here for two reasons – first because biological function likely picks out more behaviors than an etiological account, and second because hypotheses of biological function occur prior to hypotheses of selected-for function (etiological account). After I clarify the use of biological function for functional analysis, I will address these reasons.

We can understand biological function as picking out certain features of a behaving system. Specifically, if we take an organism and ask which behaviors are biologically functional, it should pick out every behavior that has a propensity to increase inclusive fitness with respect to a particular environment, independent of whether there has been selection for that behavior. Usually this environment would be its current environment for reasons of ecological authenticity, but one could apply biological functionality with respect

to any environment.<sup>10</sup> Behaviors picked out by biological function, for which there was not selection for, are understandable as exaptations or the products of broader cognitive mechanisms such as learning. For instance, begging for food in domestic dogs is perhaps biologically functional, but presumably dogs learn to beg rather than having been selected for begging. In fact, every behavior that a dog gets rewarded for with food, e.g. tricks, could perhaps be considered biologically functional depending on context. Given that biological function will pick out all behaviors that increase inclusive fitness whether they are selected for (as long as they are still functional), incidentally useful, or the product of a broader mechanism, it is reasonable to maintain that it picks out more behaviors than the etiological account.

How to engage in functional analysis for biological functionality is a non-trivial problem (see especially Trestman, 2010; Weber, 2012). While I will not go into detail here, the basic strategy as outlined by Weber is as follows. One begins with biological functionality, and then looks to behaviors that contribute to the containing system's biological functionality at a progressively finer granularity. Functional attribution can be checked, by ensuring that each identified function coheres with each other and a total account of the behaving system (Weber, 2005, also see Trestman, 2010). Take an osprey. One starts with biological functionality, of which survival contributes, within survival eating is identified as contributory, within eating catching fish, and within catching fish, looking for fish, diving for fish, and grabbing fish with talons. A scientist can conclude that looking for fish functions for the catching of fish, rather than, say, predator evasion, based on their total understanding of the osprey.

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<sup>10</sup> And scientists often do apply biological functionality with respect to environments other than current ones to gain traction on species that either have undergone environmental shift (e.g. humans or zebra mussels) or will undergo environmental shift (e.g. the introduction of non-local crops).



Hypotheses of biological function are prior to hypotheses of selected-for function due to a circularity concern (see Griffiths, 2009). Essentially, to argue that a behavior exists because it was selected for the ability to do something necessitates that one already has in mind what it was selected for to do. I cannot argue squirrels hide nuts because of a particular selective history, without holding that at least over some period of time, hiding nuts increased the inclusive fitness of the containing system (the squirrel) such that it was selected. However, despite the fact that a scientist must start with a hypothesis of biological function, biological function cannot explain a behavior. I will clarify.

Returning to the difference between etiological accounts and causal-role accounts, not only do they have different aims, but they also have subtly different targets. The etiological account targets physical objects. It seeks to explain why there is a certain structure or action, e.g. why there are eyelashes, and cannot target things that do not exist. In contrast, the causal-role account targets properties or roles. It seeks to explain the role of a behavior with respect to the capacities of its containing system and can engage with counterfactuals, e.g. how being able to breath fire would impact the survival of canaries.<sup>11</sup> Given this, the notion of biological function cannot explain the current physical presence of a behavior within a system, even though it may explain (or arguably describe) the function of a behavior. In a strict sense, accounts of behavior that do nothing more than establish that a behavior, e.g. running from hungry lions, increases inclusive fitness, are explaining a function not a behavior.<sup>12</sup> Scientists must necessarily wed biological functionality to an

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<sup>11</sup> Another way to get at this is through the understanding of etiological accounts as backwards-looking (i.e. tied to actual history) and causal-role accounts as forward-looking (i.e. engaged with potential) (see Bigelow & Pargetter, 1987).

<sup>12</sup> Two caveats. First, simply identifying a biological function is tremendously useful as it lays the groundwork for an etiological explanation or helps to predict future evolutionary trends. Second, many scientists, for better or worse, likely assume an etiological account in the background when they identify a biological function (see Mitchell, 1989).

etiological account (or some other kind of causal process account, e.g. a cognitive mechanism)) in order to explain the behavior as a physical object. Selection-for explanations provide a way for scientists to address this difficulty.

### 2.3 SELECTION-FOR EXPLANATION

A selection-for explanation is an etiological account as applied to a behaving system and aims to explain the existence of a behavior. It is the second step in the development of adaptive explanation. I contend that a selection-for explanation is composed of (1) a present or historical biological function, (2) a selection background (see especially Mitchell, 1989), (3) specific selection pressures, and (4) quasi-independence. In practice, scientists concern themselves largely with (1) and (3), with (2) and (4) being assumed.<sup>13</sup> Nonetheless, I discuss all four in turn.

The key move of an etiological explanation is that it makes the function of a behavior the reason for that behavior's existence; within evolving systems this entails that at some point the behavior was selected-for because of its function, hence my use of the term *selection-for explanation*. Specifically a behavior would have been selected for because of its biological function, i.e. contribution to inclusive fitness (also see Griffiths, 1993), and therefore an etiological explanation is necessarily paired with the attribution of present or historical biological function. This does not entail that a behavior is still biologically functional (e.g. evolutionary mismatch, such as moths flying to artificial lighting and being eaten (Fullard et. al., 2000)), or that its current biological functionality matches its

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<sup>13</sup> As will be made clear later in the paper, (2) can be assumed unproblematically, while (4) can often not.

selected-for function (e.g. exaptations<sup>14</sup>, such as the success of the domestic pigeons nesting behaviors in urban environments (Rolando et. al., 1997)).

Selection-for explanations necessarily assume a selection background (see Mitchell, 1989, 1995). While this can be understood at varying levels of specificity, here I would like sketch it out in the broadest possible terms. Namely, an object of interest has a background such that a selection process, e.g. natural selection or cultural selection, could have caused it.<sup>15</sup> This is why the foraging behavior of squirrels is a reasonable target of selection-for explanations, but spell-check in Microsoft Word is not. At this level, it would be extremely unlikely any behavior of interest would not have the appropriate selection background. Note that Mitchell, drawing from Sober, 1984, further identifies selection *of* the target *for* its function as part of the selection background (ibid.). This is correct, and leads to a much richer account. However, scientists use quasi-independence to get at this aspect of a trait's background, and therefore I will stick with the broad understanding of selection background.

Selection-for explanations also invoke the operation of specific selection pressures. As discussed, biological function does not exist as some kind of intrinsic property, but only with respect to particular environments. This applies even to fundamental features such as

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<sup>14</sup> Exaptation is a problematic concept for etiological accounts of function. As Gould & Vrba (1982) originally conceived it, even traits that have had their current function for an extremely long period of time, should be best conceived as exaptations rather than adaptations because their current function does not (fully) explain form. Their primary example is feathers, which likely originally served for thermoregulation, and are now involved in flying. This is problematic because at some point what is being selected-for switches and the continued existence/modification for a trait is based on its new function (also see Allen, 2009). Philosophers of science have attempted to get around this through modern history accounts of function, which look to what a trait has been selected for in recent history, if anything, to attribute etiological function (see, for instance, Godfrey-Smith 1994).

<sup>15</sup> For in-depth discussion of the kinds of populations that can support selective processes see Godfrey-Smith, 2009.

reproduction: having many offspring may be extremely biologically functional in a nutrient-dense jungle, but counterproductive in a nutrient-poor desert, where limited resources must be stretched across these many offspring leading to low survivorship. These environmental features<sup>16</sup> can be understood as selection pressures for which specific behaviors are functional in response (i.e. more functional than other available options). Therefore, when a scientist makes a selection-for explanation, it involves the identification of both a function and, at least implicitly, the corresponding selection pressure.<sup>17</sup> For example, in accounting for the building of bowers (giant decorative nest-like structures) by bowerbirds, Borgia appeals to both fitness gains for the Bowerbird and to selection pressure from female mate choice and visitation (1995).

Quasi-independence (Lewontin, 1978) accounts for the second element Mitchell identifies in the background of etiological explanations, specifically selection *of* the target *for* its function (1989, 1995).<sup>18</sup> Quasi-independence entails a function of a feature within a system has sufficient independence such that it is the function's contribution to fitness that led to the feature evolving (for clarification see Driscoll 2004; Brosnan 2009). Another way to think about this is that the feature must be a heritable evolutionary unit. This is usually applied to genetic features, but cultural features work just as well. For instance, if a cultural anthropologist demonstrated that a belief in Shiva increases fitness, they would have to

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<sup>16</sup> By environmental features I refer not just to the physical environment, but also to inter and intraspecific interactions.

<sup>17</sup> Plasticity can be accounted for unproblematically in this view, as the relevant selection pressures can represent a range of environmental conditions (or even something such as uncertainty itself).

<sup>18</sup> This language makes use of Sober's distinction between selection *for* and selection *of* (1984). To clarify, selection *for* relates to what the selection pressure is acting on and selection *of* relates to what is actually being physically selected. An illustrative example is Belyaev's farm fox experiment. In Belyaev's foxes, selection pressure was only applied to defensiveness around humans, but there was selection of a large number of behavioral and physiological changes such as attention seeking and floppy ears (see Trut, 1999; Trut, Plyusnina, & Oskina 2004).

demonstrate that a belief in Shiva is sufficiently independent from a belief in Hinduism to argue that the fitness gains from a belief in Shiva explain said belief. Otherwise, even if Hinduism plus Shiva is more fit than Hinduism without Shiva, it is Hinduism itself that is doing the evolutionary work.

To review, a selection-for explanation explains a trait just when there is (1) a present or historical biological function, (2) a selection background, (3) specific selection pressures, and (4) quasi-independence.

## **2.4 ADAPTIVE EXPLANATION**

An adaptive explanation is simply a more specific form of the selection-for explanation, and therefore a viable way to explain the existence of a behavior. The difference is that rather than allowing a trait to be mediated through any system of inheritance,<sup>19</sup> an adaptive explanation further specifies that a trait is the product of natural selection mediated through genetic material (see Lewontin, 1978).

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<sup>19</sup> Jablonka & Lamb, 2005 identify at least four: genetic, epigenetic, behavioral (social learning), and symbolic (cultural).

## 2.5 SUMMARY

I have demonstrated that functional accounts give evolutionary behavioral scientists explanatory traction on two questions of interest: first, how does a behavior contribute to survival (or fitness), and second, why does this behavior exist. The first question can be answered by engaging in functional analysis with biological function (causal role), i.e. detailing all behaviors that contribute to an organisms inclusive fitness. The second question requires the incorporation of an etiological account of function, of which I characterize two forms -- selection-for and adaptive explanations. Selection-for explanations explain the existence of behavior through past or present selection pressures, and contain the following: (1) a present or historical biological function, (2) a selection background (3) specific selection pressures, and (4) quasi-independence. Adaptive explanations are selection-for explanations that further contain (5) behavior as a product of genetically mediated natural selection

### **3.0 METHODOLOGY**

Having now defended that the evolutionary behavioral sciences aim towards appropriate explanations of behavior, the next challenge is whether the methodologies used by the evolutionary behavioral sciences allow them to arrive at these explanations. I will focus on adaptive explanations as they are the most philosophically problematic and entail the ability to engage in functional analysis and selection-for explanations. I begin by briefly identifying two broad methodological approaches to arriving at adaptive explanations: backward-looking and the forward-looking or model-based approach. I then relate these strategies to two flavors of explanation within the evolutionary behavior sciences, how-actually (which identifies the actual causal process) and how-possibly (which identifies possible causal processes), arguing that evolutionary behavioral scientists typically aim at how-actually explanation. Finally, I detail the connection between the forward-looking methodology and how-actually adaptive explanations.

#### **3.1 TWO APPROACHES TO ADAPTIVE EXPLANATION**

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evolutionary behavioral sciences allow them to arrive at these explanations. I will focus on adaptive explanations as they are the most philosophically problematic and entail the ability to engage in functional analysis and selection-for explanations. I begin by briefly identifying two broad methodological approaches to arriving at adaptive explanations: backward-looking and the forward-looking, or model-based approach. I then relate these strategies to two flavors of explanation within the evolutionary behavior sciences, how-actually (which identify the actual causal process) and how-possibly (which identify possible causal processes), arguing that evolutionary behavioral scientists typically aim at how-actually explanation. Finally, I detail the connection between the forward-looking methodology and how-actually adaptive explanations.

In the backward-looking approach, one begins with an alleged trait and attempts to indirectly investigate its history, using evidence such as phylogenetic distribution, homology, present day function, and genetics. While this is often difficult for behaviors due to their plasticity and inability to fossilize, it is nonetheless accepted as viable strategy. Due to its uncontroversial nature, in principle if not in practice, I will not discuss it further, but see Brandon, 1990, Lorenz, 1982 pp. 71-103, and Richardson, 2007. Note that a scientist can engage in this kind work without a functional hypothesis... this just will not get them to an adaptive explanation.

In the forward-looking approach one begins with a function, and argues that for a certain behaving system to have a behavior with that function a specific selective history must have happened. Here, models or other forms of inquiry are used to detect the hypothesized function in systems of interest. For instance, Zach, 1979 hypothesized that there was selection pressure for optimal foraging (i.e. energetic efficiency) on the whelk foraging behavior of the Northwestern crow. Upon finding that the Northwestern crow did



indeed behave in accordance with his optimality model, Zach then claimed that the foraging of the Northwestern crow was a behavioral adaptation. I appreciate that the example for the forward-looking approach is not very satisfying, but hopefully concerns will be addressed later in this section.

These approaches are not mutually exclusive and it may be helpful, or even required, to use both. If both strategies are used, one begins with the forward-looking approach to constrain the possibilities, and then switches to the backward-looking approach to evidence a specific hypothesis. The distinction between *how-actually* and *how-possibly* explanations helps to clarify the operation of these two approaches (Dray, 1957; Forber, 2010). I look to that distinction now.

### **3.2 HOW-POSSIBLY AND HOW-ACTUALLY ADAPTIVE EXPLANATION**

*How-actually* explanations, in which the actual causal process is articulated, are distinguished from *how-possibly* explanations, which specify a possible causal process (Dray 1957). Forber further distinguishes between *global* how-possibly accounts, which designate the possible mechanism that could lead to trait, e.g. selection, and *local* how-possibly accounts, which designate the possible specific causal-history, e.g. selection for energetic efficiency acting on whelk foraging behaviors in Northwestern crows (2010; Zach, 1979). Given just their appeal to specific selective history, it is ambiguous whether adaptive explanations should be understood as how-actually explanations or as local how-possibly explanations.

Forber additionally argues that how-actually and how-possibly accounts serve fundamentally different methodological roles. How-actually accounts work to provide confirmatory evidence to local hypotheses concerning the target system. In contrast, how-possibly accounts start with some global realm of causal processes operating in biology and work to narrow down the possible causal processes that could be at work in the target system (2010). Based on this understanding, the backwards-looking approach is structured as a how-actually explanation, as one attempts to bring evidence to bear on the specific, local, causal process. On the other hand, the forward-looking approach is structured as a how-possibly explanation, attempting to constrain the possibilities down to the hypothesized selection pressures.

However, in addition to this methodological difference, Forber also argues that how-possibly and how-actually aim at different *kinds* of explanation (this is in contrast to the prevailing opinion, see Forber, 2010 for an overview). He, going back to Dray (1957), maintains that how-possibly explanations are intended to establish a particular process is a possible explanation (often as opposed to an impossible one), while, again, how-actually explanations seek purchase on the real causal process. This distinction certainly holds some of the time. For instance, Darwin's use of thought experiments or "just-so" stories, e.g. his famous one concerning the origin of the eye, were intended to establish the possibility of an evolutionary explanation, to preempt irreducible complexity based "that's impossible" challenges from creationists (see Lennox, 1991). Similarly, at the global level, Forber discusses how the neutral theory of molecular evolution (Kimura, 1968; King & Jukes, 1969) served as a new possible explanation for certain characteristics of molecular evolution. In line with Forber's analysis, both of these are methodologically how-possibly explanations, and both are explicitly directed towards showing how a causal-process

(locally or globally) could be a possibility. However, maintaining that backward-looking and forward-looking approaches to adaptive explanation have different explanatory aims is more problematic.

Imagine that scientists engage in the forward-looking approach simply to put forward the possibility of something. Say, for the sake of argument, when Zach, 1979 constructed an optimality model for foraging in the Northwestern crow, and identified that the Northwestern crow does behave in accordance with that model, he did not want to claim that selection-pressures for optimal foraging strategies led to the Northwestern crows behaviors, but merely put that forward as an possibility. What would this be doing? It could be seen as a launching point for how-actually investigation, but Zach did not proceed to do such investigation. Nor does it have any pragmatic application -- outside of a context such as responding to irreducible complexity arguments -- therefore Zach cannot be using this explanation only instrumentally. In short, the only way to make sense of the forward-looking approach is that even if it is methodologically a how-possibly explanation, it nonetheless usually aims at capturing the real causal process.

To clarify how this may be work, think of *how-possibly* accounts on a continuum of underdetermination. On one end is a completely undetermined account in which there are no theoretical constraints on which causal processes may operating, on the other end is no underdetermination. "No underdetermination" describes a (theoretical) situation in which, if a hypothesis that a behaving system will have a certain functional behavior is shown to be correct, there is only one possible explanation for how that behavior came to be, and therefore the *how-possibly* explanation is constrained down to an *how-actually* explanation. While Forber correctly evaluates this as methodologically distinct from a *how-actually* explanation, the explanatory account provided is identical and known with equal certainty.

Therefore, it appears that approaches which are formally distinguishable into *how-possibly* and *how-actually* explanations, can nonetheless have equivalent purchase on what actually happened.

Outside this idealized situation, the key factor for a forward-looking adaptive explanation is then the likelihood of the assumed selective history matching the actual selective history (also see Forber 2010). If this likelihood is sufficiently high, it becomes reasonable to assume that the assumed state of reality somehow captures the real state of reality. This largely plays through as an inference to the best explanation, whereby one defends an assumed selective history, through holding that it is the *best explanation* of the predictive success of the forward-looking approach (i.e. successfully finding the predicted functional behavior).

### 3.3 MODELS AND ADAPTIVE EXPLANATION

We can now tersely formulate the fundamental methodological challenge to the forward-looking or model-based approach as follows: does the predictive success (again, predictive success entails identifying the hypothesized functional behavior in a target system) of a model establish that the functional behavior also possesses the features that would allow it to be accounted for by an adaptive explanation. To review, these features are (1) a present or historical biological function, (2) a selection background, (3) specific selection pressures, (4) quasi-independence, and (5) product of genetically mediated natural selection.

I look to the model-based approach, specifically optimality models, to respond to this challenge. I do so first, because such models are widely used within the ethological

tradition forming the foundation of behavioral ecology, and second, because their formal structure lends itself to clearer analysis. I will, however, ultimately extend my arguments to forward-looking approaches that are not based on formal modeling. To frame my analysis, I begin with a discussion of the phenotypic gambit, the assumption that underlies all optimality-model based approaches in the evolutionary behavioral sciences.

### **3.3.1 The phenotypic gambit**

Grafen (1984) formalizes the phenotypic gambit as follows:

The phenotypic gambit is to examine the evolutionary basis of a character as if the very simplest genetic system controlled it: as if there were a haploid locus at which each distinct strategy was represented by a distinct allele, as if the payoff rule gave the number of offspring for each allele, and as if enough mutation occurred to allow each strategy the chance to invade.

While Grafen formalized the gambit, it was used implicitly in behavioral ecology well before (e.g. Zach, 1979). The phenotypic gambit exposed, and commensurately opened up for discussion, the assumptions and structure that underlie the use of optimization models and adaptive explanations in behavioral ecology. Understood in the simplest terms, the phenotypic gambit is nothing more than an assumption that allows scientists to offer adaptive explanations for the target of a model, without engaging in an exhaustive investigative process (Grafen, 1984). Pincock (2012), in a recent discussion of idealization in biology, identified “gambit” idealizations in which “we sacrifice truth with

respect to one feature with the aim of accurately representing some other features.” Clearly, all of the above elements listed by Grafen are false, i.e. sacrificed truth, but if a model built on the phenotypic gambit leads to predictive success, then the adaptive explanation provided is taken to be correct.

Since Grafen, the phenotypic gambit has often been paraphrased in somewhat less structured terms: Borgerhoff Mulder’s and Schacht’s definition of, “the claim that how a trait is inherited does not seriously constrain adaptive responses to ecological variation,” is representative (2012). However, what Grafen’s formalization makes clear is that optimality models are nothing more than idealized adaptive explanations. This can be seen clearly by comparing it to the account above. Optimality models definitionally represent present or historical biological functions as they are explicitly constructed to identify the fittest strategy (i.e. the local fitness optimum). They also obviously assume a selection background. The payoff rule entails that model builders are looking at success in response to specific selection pressures. The representation of each strategy as a distinct allele captures quasi-independence (complete independence actually). And finally, everything is expressly identified in genetic terms -- although a non-genetic formulization that would allow other selection-for explanations is quite conceivable.

Godfrey-Smith has introduced an account of modeling in which the explanation used for a simple case, whether real or idealized, is extended to other relevantly similar cases (2006, 2009 p. 6). This helps to clarify how models built on the phenotypic gambit *could* provide how-actually adaptive explanations; the idealization used in the structuring of the model is relevantly similar to the actual target and its selective history. Moreover, as seen, the phenotypic gambit is explicitly designed to be similar to adaptive explanations on the

relevant dimensions. However, this does not fully clarify the operation of phenotypic gambit based models as relevant similarity is merely assumed rather than established.

To explicate this difficulty, I turn again to Zach's (1979) work on the foraging behavior of the Northwestern crow. This bird will search for whelks, and then drop them repeatedly on rocks to get at the meat inside. Zach developed an optimality model showing that, if the foraging behavior is adapted for energetic efficiency, then (among other predictions) Northwestern crows should prefer large whelks to small whelks, and, if no large whelks are available, they should also prefer non-whelk foods to small whelks. Upon empirical investigation, he did indeed find this behavior pattern. From this predictive success, Zach maintained that Northwestern crow foraging is adapted for energetic efficiency. However, he did not independently establish that the characters and history of the behavior he found in the Northwestern crow are relevantly similar to his model with respect to all the features of an adaptive explanation. Rather, relevant similarity is assumed to have been established by *nothing more than* the predictive success of the model.

This provides us with an express challenge: can the predictive success of an optimality model also indicate the target behavior has the features of an adaptive explanation? To address this challenge it will be helpful to break down models into what I refer to as the *predictive domain* and *explanatory domain*.

### **3.3.2 Predictive and explanatory domains**

The phenotypic gambit, as formalized by Grafen and as most broadly construed, can detect optimal behaviors across an incredibly wide range of phenomenon. If applied to any system that could reasonably fit its "as if" stipulations – that is to say, any system that sustains

some kind of selective process<sup>20</sup>, e.g. culture, and could be at some kind of local optimum<sup>21</sup>-- then the phenotypic gambit will allow for the construction of an optimization model, and the commensurate detection of an optimal behavior. For instance, if “Little Jimmy,” an animal loving neighborhood kid, were teaching Northwestern crows to eat whelks optimally, Zach’s model would have detected the behavior just the same. All behaviors that could be detected by an optimality model built on the phenotypic gambit, independent of the underlying causal process, constitute its predictive domain. That the predictive domain of a model can extend so far beyond its normal use should perhaps not be surprising – look to the applicability of game theoretic models across both biology and economics. As the predictive domain is devoid of causal-process content, predictive success alone is insufficient to lay claim to an explanation.

Pincock has argued that in order for models to support claims, we must believe that certain things are true of the world (2012). This entails that if the behavior identified by the optimality model is found in the system of interest (i.e. predictive success), in order for this to lead to an adaptive explanation, one must *already* believe that a particular set of conditions accounted for that success. This is the *explanatory domain*: when the reasons for which a model is believed to be predictively successful, actually are the reasons (or relevantly similar to the reasons) it is predictive successful. Multiple explanatory domains can be contained within a predictive domain. For instance, whether the Northwestern crow’s behavior is genetically inherited or learned, the phenotypic gambit could be applied with similar predictive success, but the behaviors would fall within different explanatory domains. Within this understanding, selection-for explanations constitute some of the

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<sup>21</sup> See Godfrey-Smith (2009) on Darwinian populations for an analysis of the domain in which evolutionary selective processes can apply. Also see Gintis (2007) for detailed discussion of the broad applicability of modeling techniques for behaviors.



behaviors predicted by phenotypic gambit based optimality models, while within selection-for explanation there are narrower explanatory domains such as adaptive explanation or cultural selection.

The distinction between predictive and explanatory domains can map onto adaptive explanations, whereby predictive success detects biological functionality and the explanatory domain is represented by the other features of an adaptive explanation. Pincock (2012) addresses this through the concept of anchoring. In order to provide an explanation, a model must be anchored to its target system through a particular empirically couched understanding of reality. Specifically, a phenotypic gambit based model is anchored just when the features of a trait that enabled the model to be predictively successful are the same features that would make the trait an adaptation. Therefore, the concern is whether the systems (organisms) to which phenotypic gambit based models are applied are within the explanatory domain for adaptive explanations, i.e. whether the explanations provided are anchored. To get purchase on this concern, I evaluate predictive success with respect to the features of an adaptive explanation for the kind of systems that are usually targeted by behavioral ecologists.

### **3.3.3 Anchoring adaptive explanations**

Again, I have characterized the features of an adaptive explanation as (1) a present or historical biological function, (2) a selection background, (3) specific selection pressures, (4) quasi-independence, and (5) product of genetically mediated natural selection. Let us see how predictive success works to anchor these features. However, it is important to remember that predictive success need not be the end for a putative adaptive explanation,

additional sources of evidence can be brought forward for clarification, confirmation, or contradiction.

(1) Present or Historical Biological Function: Again phenotypic gambit based models are designed specifically to detect biological functionality. Optimality models begin by first identifying what would be the (locally) optimal strategy with respect to fitness, and then searching for that strategy in a target system. Therefore, the behavior being searched is explicitly biological functional – and not just functional, optimal. It is of course possible for a scientist to misidentify what would represent an optimal strategy, but the impressive track record of optimality models indicates that at least this feature is unproblematic (see Grafen, 1984; for further discussion on the methodology behind optimality models see Maynard Smith, 1978; Orzack & Sober, 1994; Parker & Maynard Smith, 1990).

(2) Selection Background: All systems of interest to those in the ethological tradition can at least support adaptive explanations, being biological with genetic systems of inheritance (see Godfrey-Smith, 2009 for discussion of the kinds of populations that support selective processes). There is the technical possibility that a biologically functional behavior arose through a non-selective system, e.g. drift or as a spandrel (see Gould & Lewontin, 1979), but it hard to imagine optimal or even functional behaviors arising simply through chance (see Dawkins, 1983, 1986; Pinker & Bloom 1992).

(3) Specific Selection Pressures: As mentioned earlier, the specific selection pressures hypothesized are a legitimate theoretical concern because there will always be some measure of underdetermination. However, at least three factors can motivate trust

in the hypothesized selection pressures. First, the predictive success of the model helps to evidence the hypothetical selection pressures from which the optimum was derived. Second, many selection pressures are quite intuitable and involve problems that almost all organisms would face – avoiding predators, acquiring sufficient food, etc. (see Maynard Smith, 1978; Machery, 2008; for a somewhat more tempered position see Lewontin, 1978). Third, in the ethological tradition these selective hypotheses are not coming out of nowhere, but based on a broad understanding of the behavior and life of the organism.

There is the additional concern that even if the correct selection pressures for the behavior as it currently functions are identified, different selection pressures have acted on it historically, i.e. the behavior is an exaptation. How serious this concern is depends on how far one cares to look back.<sup>22</sup> Unless a scientist has knowledge of a recent environmental shift, current behavioral function should provide an extremely good guide to what that behavior was selected for in the recent past. Unfortunately, optimality models do not screen against shifts of functions in the distant past. However, this concern may be a little less significant for behaviors as their plasticity makes it unlikely that similarly structured behaviors would be conserved across vast stretches of time performing radically different functions. Regardless, it at least seems reasonable that a scientist could read the recent selective history of a behavior.

(4) Quasi-independence: Depending on the organism, quasi-independence can be a very serious concern. It may be helpful to think of challenges to quasi-independence at two levels. First as a sort of linkage, in which two (or some small number) of

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<sup>22</sup> For discussion on how to understand exaptations versus adaptations with respect to both the recent and distant past see Allens, 2009; Godfrey-Smith, 1994; Gould & Vrba, 1982,.

behaviors are in some way structurally connected, e.g. antagonistic pleiotropy. This is unlikely to be a problem, as optimality should screen against it – that is, in a structurally connected system either nothing will go to optimum and therefore will not be detected, or only one component goes to an optimum and that is the component that supports the adaptive explanations. Second, however, is as subordination to broader cognitive mechanism. Fawcett et. al. (2012) identifies a *behavioral gambit* in which behaviors picked out by optimality models are assumed to be particular evolutionary units rather than merely one instance of broader cognitive mechanism such as a heuristic, or even learning<sup>23</sup>. Specifically the concern is that certain cognitive mechanisms, e.g. learning, can support multiple behaviors at local optima. And, if a behavior is merely part of a broader capacity, it cannot have the evolutionary independence needed to support an adaptive explanation unless that behavior's function is the reason the entire cognitive mechanism was selected.

How problematic this is depends on the organism being targeted. For instance, in organisms with limited cognitive complexity such as insects or amphibians the failure of quasi-independence may not be a concern. However, for other organisms, e.g. great apes, the organism's own cognitive abilities may provide a very compelling counter-hypothesis to selection. For such organisms, it may be advisable for scientists to engage in further study to discriminate cognitive mechanism from selection. Fawcett. et. al. (2012) also recommend that scientists make specific forward-looking hypotheses aimed to detect broader cognitive mechanism, i.e heuristics or behavioral rules of thumb, rather than just specific

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<sup>23</sup> Not necessarily to simplify learning as unitary process, but it should be clear that learning-type mechanisms, even if a little more specific than as conceived by the behaviorists, can nonetheless contain many, many behaviors.

behaviors (also see Gigerenzer & Gaissmeyer, 2011). This is certainly a viable option, and may be important for future research, but lacks the simplicity of phenotypic gambit based models.

(5) Product of Genetically Mediated Natural Selection: Again, how problematic this assumption is depends on the organism being targeted. For many organisms, there is no system of inheritance beyond the genetic one (plus epigenetic and regulatory elements). In these organisms, a selection-for explanation is automatically an adaptive explanation. However, other organisms of interest can also support selective processes through social learning or even culture (see Avital & Jablonka, 2000; Jablonka & Lamb, 2005). In such organism, e.g. birds, it becomes an empirical question whether or not the selection process was mediated through genetics, although it often simply assumed.<sup>24</sup> This assumption, that phenotypic observations tend to be representative of underlying genetics, is referred to as Cheverud's conjecture. While the correlation between genotype and phenotype has been generally well evidenced for morphological traits (Cheverud, 1988; but see Hadfield et. al., 2007), the evidence is not quite so strong for behavioral traits (although see Dochtermann, 2011).

In summary, it appears that predictive success of optimality models can do a pretty good job of anchoring adaptive explanations. For systems of interest, (1) a present or historical

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<sup>24</sup> It is perhaps a fair criticism that scientists simply assume every selection-for explanation is an adaptive explanation in non-human organism due the prominence of natural selection and its paradigm status as the explanation for biological function. How problematic this is may depend on the pragmatic goals toward which research is directed, e.g. it may not be so problematic for research merely intended to satisfy curiosity, but tremendously problematic for research intended to support intervention on behaviors.

biological function, (2) a selection background, and (to a somewhat lesser extent) (3) specific selection pressures are quite well anchored. (4) quasi-independence and (5) product of genetically mediated natural selection are not quite so certain. They are well anchored in less cognitively complex organisms, which tend to support neither broader cognitive mechanisms underlying multiple behaviors nor non-genetic systems of inheritance. However, in more cognitively complex organisms, while adaptive explanations certainly can be valid, it may be helpful to empirically engage with cognition and the mechanism of selection (also see Avital & Jablonka, 2000; Fawcett, et. al. 2012; Jablonka & Lamb, 2005; Owens, 2006).

### **3.3.4 Beyond the phenotypic gambit**

Finally, while optimality models are a particularly salient case of forward-looking adaptive hypotheses, they are by no means the only way to go about it. One of the key advantages of optimality models is that local fitness optima are an incredibly powerful way to detect biological functionality. However, rather than basing the construction of forward-looking hypotheses off of optimality, which results in the construction of mathematical models, one can also construct forward-looking hypotheses from advantageousness. If something is (locally) optimal, then, with respect to the model, it is *as if* no causes other than selection have been acting. However, many adaptive accounts do not rely on a trait functioning optimally, but rather on a trait simply being advantageous, i.e. increasing an organism's ability to survive and/or reproduce (see Sober, 2000 pp. 78 – 83).<sup>25</sup> In a similar manner to

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<sup>25</sup> And, in a way, this is also represents optimality models themselves. Scientists do not expect perfect fit, but merely good enough fit (see Driscoll, 2009; Parker & Maynard Smith, 1990).

the construction of optimality models, one begins with the hypothesizing of selection pressures, and based on the assumption that an organism should respond advantageously (rather than optimally) to these pressures, generates behaviors/properties of behaviors that the organism should have. The eschewing of optimality will often shed the mathematical dimension (although we can certainly imagine more sophisticated models that can allow for constraints and imperfections), but the process is in principal the same.

### **3.4 SUMMARY**

In this section I have argued that evolutionary behavioral scientists aim at how-actually explanations of behaviors through collapsing the possible causal processes down until they have a good chance of having identified the actual cause process. Using the phenotypic gambit as an exemplar of forward-looking hypothesis, I demonstrated that scientists can provide adaptive explanations by applying optimality models to situations such that the reasons for predictive success are very likely to be relevantly similar to the adaptive explanation built into the model. Finally, I argued that for many non-human organisms predictive success is a pretty good justification for an adaptive explanation, although there are remaining concerns over broader cognitive mechanism and non-genetic systems of inheritance in more cognitively advanced organisms. In the next section, I turn to humans.

#### 4.0 ADAPTIVE EXPLANATIONS OF HUMAN BEHAVIORS

Applying adaptive explanations to human behavior has been especially contentious (see, for example, Gray, Heaney, & Fairhall, 2003; Kitcher, 1985; Richardson, 2007). Using the features of adaptive explanations identified above, I problematize each feature with respect to human behaviors and then discuss the ways that the human evolutionary behavioral sciences have responded to these difficulties. Of the human evolutionary behavioral sciences – most prominently human behavioral ecology (HBE), evolutionary psychology, and gene-culture coevolution -- the one most concerning with providing adaptive explanations as discussed here is evolutionary psychology, and therefore it will form the focal point of this section. HBE will occasionally be looked to for comparison, but it is explicitly not interested in adaptive explanations as described above (Borgerhoff Mulder & Schacht, 2012).<sup>26</sup>

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<sup>26</sup> This perhaps merits some explanation, as it far from intuitive why evolutionary psychology is a good target for my paper and HBE is not. After all, HBE explicitly uses optimality models and the phenotypic gambit and therefore seems to follow much more naturally. However, HBE is largely not interested in the features of a system that explain why a prediction holds, and therefore is not a good case study for the broader purpose of this paper. For further analysis of why HBE, despite seeming to be simply a continuation of behavioral ecology, should not actually be seen as such, see Driscoll, 2009.



## 4.1 OBSTACLES AND OVERCOMINGS WITH HUMAN BEHAVIORS

In line with the last section, I will simply review the approach of the human evolutionary behavioral sciences, especially evolutionary psychology, in relation to the features of an adaptive explanation. However, rather than trying to argue that the methodology used on non-human animals can simply be switched to humans, I will defend that specific changes have been made which make the human evolutionary behavioral sciences more able to provide adaptive explanations for human behaviors. This should also help to provide traction on relevant similarities and differences between evolutionary psychology and the evolutionary behavioral sciences generally. Before proceeding, it should be mentioned that evolutionary psychology tends not use optimality models, instead making use of predictions from advantageousness based forwarding-looking hypotheses. Again, the five features of an adaptive explanation are (1) a present or historical biological function, (2) a selection background, (3) specific selection pressures, (4) quasi-independence, and (5) product of genetically mediated natural selection.

### 4.1.1 A present or historical biological function

A key aspect of biological function is that the functionality of target traits are linked to environmental context. And while it is controversial the exact way in which humans are removed from the environment(s) in which most of their evolution took place it is uncontroversial that humans have undergone drastic environmental shift. Given this, there is little reason to expect that human behaviors within their current environment will be biologically functional. As discussed in the second section, one can understand biological

function as representing time-slice functions rather than current functions, i.e. targeting whichever period(s)/environment(s) biological function is believed to most track what a behavior was selected for. However, to do this requires an understanding of this hypothetical past environment and its constitutive selection pressures. The specific hypothetical environment (or more accurately, a hypothetical set of selection pressures) to which traits possess evolved functionality is referred to as the environment of evolutionary adaptedness or EEA (Bowlby, 1969; Tooby & Cosmides, 1992).

The human behavioral sciences take two predominant approaches to detecting biological functionality across the recent environmental shift. First, they use archaeological accounts and anthropological work in traditional societies and historical populations. This attempts to reconstruct the real historical environment (or use relevantly similar populations) and therefore pull out biological functionality. It is important that, excepting archeology, research can be conducted on these populations. While this strategy is used throughout the human behavioral sciences, it is especially characteristic of HBE (Borgerhoff Mulder & Schacht, 2012).

In the second approach, scientists use knowledge drawn from archeology and hunter-gatherer studies to construct the environment of evolutionary adaptedness (EEA) (Tooby & Cosmides, 1992). This approach is characteristic of evolutionary psychology. Rather than identifying a specific environment, this procedure can be understood as coalescing a broad array of selection pressures that humans likely faced into a thought experiment that is useful for detecting biological functionality (see Tooby & Cosmides, 2005). Tooby & Cosmides characterize their understanding of the EEA as the challenges that would face a human living in the Pleistocene era (from 1.8 mya to 10,000 ya) (1992). While both the similarity of traditional societies to ancestral population, and the specific

account of the EEA offered by Tooby and Cosmides have been criticized (for discussion see Laland and Brown, 2002, and Marlowe, 2005), this is nonetheless the right kind of approach to detecting biological functions and likely works at least some of the time.

Unlike evolutionary psychology, HBE is still largely based on the use of optimality models. This is partly because the populations human behavioral ecologists tend to study are considered representative of ancestral behaviors. In contrast, evolutionary psychologists also look at behaviors in agricultural and industrial societies and therefore do not possess a population with which to easily test the predictions of optimality models. In line with the discussion at the end of the third section, evolutionary psychologists instead hypothesize potential biological functions based on the EEA, and then use those to generate specific testable predictions within modern societies.

#### **4.1.2 Selection Background**

Again, humans provide the right broad selection background to support adaptive explanations.

#### **4.1.3 Specific selection pressures**

Specific selection pressures represent a particular difficulty for studies on human behaviors, because there is no way to check against current biological functionality. In organisms that have not undergone environmental shift, current biological function provides an important piece of evidence for selected-for biological function. Unfortunately, I see no way completely around this difficulty. Historical and hunter-gatherer societies may

provide some insight, but ultimately evolutionary psychologists will have to trust in the selection pressures used in their account of the EEA. Nonetheless, evolutionary psychologists are still able to rely on predictive success to support hypotheses of selection pressures, and the use of more obvious selection pressures.

#### **4.1.4 Quasi-independence**

Given that cognitive complexity generally problematizes quasi-independence (see the third section), it is unsurprising that this feature is a particularly acute difficulty for adaptive explanations of human behaviors. An individual behavior could always be part of a broader behavioral capacity (cognitive mechanism) underlying many behaviors, and that capacity is the relevant evolutionary unit. In fact, part of the motivation of the original social sciences approach, e.g. the behaviorist approach advocated by Skinner and Watson, was the principle that humans have only a few extremely general cognitive mechanisms (and perhaps only one – learning). While this degree of domain-generality has been soundly critiqued (see especially Tooby & Cosmides, 1992), given the incredible diversity of human behaviors and the associated cognitive complexity, it remains extraordinarily difficult to know just how to parameterize to arrive at evolutionary units.

HBE and evolutionary psychology take very different approaches to the difficulty with individuation. HBE simply does not worry if the target of interest is an evolutionary unit, or merely part of a larger capacity. This represents a key theoretical difference from behavioral ecology and may help to explain why evolutionary psychology has received the brunt of criticism. Evolutionary psychology, in contrast, has much more of an interest in this. The main theoretical move made by evolutionary psychology is to focus on cognitive

mechanisms rather than behaviors themselves (Tooby & Cosmides, 1992). This makes tremendous sense in theory, as it is all but guaranteed that at some level there will be a cognitive mechanism, which is also an evolutionary unit, underlying a biologically functional behavior. However, as there is not direct observational access to cognitive mechanisms, evolutionary psychologists are now placed in the difficult position of having to infer cognitive mechanisms from behaviors. At least two strategies are used to overcome this challenge: decision heuristics and modularity.

For decision heuristics, rather than hypothesizing a biologically functional behavior, one hypothesizes a biologically functional role of thumb or heuristic, e.g. run from bigger organism if they move towards you above a certain speed. If a human (or any organism for that matter) operates under such a heuristic, then certain responses should be expected in certain situations. This is essentially identical to hypothesizing a biologically functional behavior, except for rather than finding the behavior itself one finds a set of behaviors and infers that a particular underlying heuristic (i.e. cognitive mechanism) is operating (for further discussion see Gigerenzer & Gaissmeyer, 2011).

Modularity is somewhat more contentious. Based on findings that possessing just a few domain-general cognitive modules does not actually lead to behavioral flexibility, evolutionary psychologists argued that underlying cognitive mechanisms are not sweeping all-purpose machines, but instead quite narrowly construed modules (see Tooby & Cosmides, 1992, and for clarification see Machery, 2008).<sup>27</sup> In practice, this means that many evolutionary psychologists deal with a specific behavior (or a limited set of behaviors/preferences) and then make a nod in the direction of an underlying cognitive module.

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<sup>27</sup> For further discussion see Tooby & Cosmides, 1992; Barret & Kurzban, 2006; Machery, 2007.

While the debate is ongoing, it appears likely that this approach is appropriate at least some of time (see Machery, 2008; Tooby & Cosmides, 2005). However, there is still a difficulty. Namely, a cognitive mechanism does not have to be particularly general for the behaviors it enables to fail quasi-independence; it only needs to support more than one optimal (or advantageous) behavior. Nonetheless, this is more of a caveat or precaution than a coup de grace.

#### **4.1.5 Product of genetically mediated natural selection**

This feature of adaptive explanation captures the most notorious challenge – there is always culture to allow for an alternative selection-for explanation. Moreover, simply providing a selection-for explanation of human traits is frowned upon; it seen to be of particular import whether a trait is culturally or genetically mediated. There are likely several explanations for this: because many see culture a key to human identity, because of lingering fears of biological determinism, because of a greater demand to get the science right, or perhaps because of real, and potentially relevant, differences in the way one intervenes on a genetically, rather than culturally, mediated trait. Regardless, separating the genetically mediated from the culturally mediated is a major obstacle.

HBE and evolutionary psychology again differ similarly with respect to identifying the selective mechanism that led to a trait. Human behavioral ecologists are uninterested in whether a biologically functional trait was the product of genetically or cultural mediated selection (Borgerhoff Mulder & Schacht, 2012). In contrast, evolutionary psychologists aim specifically to identify genetically inherited traits (even if they acknowledge these traits are realized through development (Tooby & Cosmides, 1992)). Evolutionary psychologists

have two major approaches to picking out genetically mediated behaviors. First, they look to “direct” evidence of genetic mediation, specifically cross-cultural and developmental evidence (see Machery, 2008). If a behavior (or cognitive tendency) is present across a range of cultures it is assumed not to be caused by cultural selection, and instead by an underlying genetic commonality.<sup>28</sup> Similarly, if a behavior develops before cultural factors could have formed it, it is understood as genetic (again look to Machery, 2008 for elaboration). The second approach is an appeal to design. Specifically, evolutionary psychologists argue that a behavior’s cognitive architecture (i.e. the mechanism) illustrates complex functional design, with the ancillary assumption that complex functional design can only arise through natural selection (see Tooby & Cosmides, 2005; Pinker & Bloom, 1992; also see Dawkins, 1986).

The appeal to complex functional design again relies upon the mechanism underlying a behavior and is a major difference between evolutionary psychology and other evolutionary behavioral sciences. Evolutionary behavioral scientists studying non-human animals tend not to look to design features of behaviors to make adaptive explanations. This is unsurprising for two reasons. First, in non-human animals, unlike in humans, one can rule out cultural selection as an explanation for an observed behavior simply because most animals do not have culture, making an analysis of cognitive mechanism less necessary. Second, functional design is simultaneously both a functional and a structural feature, and the evolutionary behavioral sciences, as discussed in the first section, tend not to look at the underlying structure components of behaviors. It is the mechanism, not the behavior itself, which is seen to illustrate structural design. However,

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<sup>28</sup> Of course, this evidence is not actually direct, but merely assumed to give very good reason to infer genetic mediation. However, the sufficiency of these criteria is not uncontroversial; see especially Gray, Heaney, & Fairhall, 2003.

design features are a staple element of adaptive explanations in evolutionary biology generally, i.e. adaptive explanations for morphological rather than behavioral characters. For instance, the structural matchup between hummingbird beaks and the length of the corollas of flowers is seen as excellent evidence of co-adaptation (Ewald & Williams, 1982; Fenster, 1991; Temeles & Cress, 2003). In essence, evolutionary psychologists are folding some of the strategies used to make adaptive explanations for morphological features into their approach to behavior.

How sensible it is for evolutionary psychologists to use this account for adaptive explanation swings on two particular points. The first concerns whether complex functional design in cognitive architecture is detectable. The second is whether or not complex functional design is a good indicator of natural selection. I tackle these in turn.

Regarding the first concern, despite their focus on mechanism, evolutionary psychologists are still *looking* at behavior – complex functional design is somehow being inferred. Evolutionary psychologists make this inference through what Machery (2008) refers to as design evidence, in which a cognitive mechanism that would be biologically functional in a past environment is found to be operating in the present.

Design evidence is at its most powerful when cultural selection can be explicitly screened out as a competing hypothesis, i.e. in situations of evolutionary mismatch. An evolutionary mismatch occurs when a trait that was functional in an ancestral environment is deleterious or undesirable in a current environment. The corollary to this is that if an undesirable behavioral trait were being mediated through something more responsive to selection than genes, e.g. culture, it would have been extinguished. The human preference for sugars and fats is the classic example of environmental mismatch. In ancestral environments it would have been biologically functional to prefer (uncommon) energy-



dense foods, now it just makes us unhealthy (Cordain et. al., 2005; Drewnowski & Rock, 1995).

The logic of the evolutionary mismatch approach to complex functional design goes as follows: (1) complex functional design indicates adaptation and commensurately natural selection, (2) natural selection is far slower to respond to environmental shift than cultural selection, (3) therefore the same complex functionally designed cognitive architecture that would have been selected for in the EEA will still be around, (4) therefore, if humans behave in a manner mismatched with their current environment, but aligned with the EEA, it indicates complex functional design, (5) therefore some behavior is an adaptation. Ironically, despite the great difficulty the environmental shift has imposed on the study of human behavior, it may also help to screen out the causal effects of natural selection from the human cultural system of inheritance.<sup>29</sup> Unfortunately though, the use of evolutionary mismatch is somewhat limited, as many biologically functional behaviors and traits may be culturally desirable, or even culturally desirable because they once were biologically functional (e.g. Buss' contention that humans find certain features attractive because of their association with reproductive success (1998)).

The general response to the second concern is that, yes, complex functional design is an excellent indicator of natural selection (again see Dawkins 1983, 1986; Pinker & Bloom, 1992; Tooby & Cosmides, 2005). However, this assumption has recently been challenged specifically for human cognitive architecture. Ward (2011), drawing from Dupre (2001), has argued that human neural plasticity may allow for changed cognitive mechanisms

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<sup>29</sup> This is not to say that culturally selected for traits are necessarily biologically functional or good for us just because cultural selection is more responsive. There are clearly many deleterious cultural traits. However, the difference is that deleterious cultural traits, such as watching Fox News or liking Miley Cyrus, would not have served humans well in ancestral environments.

between current and ancestral populations, as the environments for these populations may contain different developmentally relevant factors which can induce novel functional design in brain development. Ward therefore argues that, if this challenge is correct, evolutionary psychologists can no longer assume that complex functional design indicates natural selection and would have to engage in exhaustive empirical research concerning whether the underlying cognitive mechanism of a behavior was shaped by natural selection or novel developmentally relevant factors.

However, Ward mischaracterizes the kind of challenge this may represent – at least to forward-looking hypotheses. Assuming it is possible that the current human sociocultural environment has led to the development of novel complex and functional cognitive mechanisms, there is no reason to expect they would get confused with biologically functional mechanisms formed by natural selection. The novel cognitive mechanism would simply not be detected by an account of biological functionality with respect to the EEA. Neural plasticity does represent a challenge to the testing of hypotheses in evolutionary psychology, as a *real* cognitive mechanism selected for in the EEA, i.e. a cognitive mechanism hypothesized by an evolutionary psychologist that did actually exist, could have been obliterated or distorted by the current developmental environment. But if a predicted complex functionally designed cognitive mechanism is found in contemporary populations, there is little reason to worry about novel changes in the developmental environment as a competing hypothesis.

## 4.2 SUMMARY

To summarize, there are indeed real obstacles to the use of adaptive explanations for human behavior. However, the human evolutionary behavioral sciences, and especially evolutionary psychology, have relevantly changed from the evolutionary behavioral sciences generally to accommodate these difficulties. This is not to say there are not enduring challenges, particularly related to the understanding of the EEA, the modularity hypothesis and quasi-independence, and establishing that a behavior was genetically mediated through design evidence. Nonetheless, the ability of evolutionary psychology to form adaptive explanations is on similarly sound theoretical footing to the approach used on non-human animals.

## CONCLUSION

In this paper I offered a structured clarification and tempered defense of adaptive explanations of behaviors. Broadly, I sought to balance acknowledgement of the authentic difficulties involved in providing such explanations, with the scientific tactics available to overcome these difficulties. I did so in four general steps. First, I held that behavior is different from other physical systems, but is nonetheless an appropriate object for scientific study. Second, I argued that the explanatory project of the evolutionary behavioral sciences is accountable through functional explanation (e.g. adaptive explanation). Third, I defended the methodology, illustrating how the controversial forward-looking or model-based approach within the evolutionary behavioral sciences can arrive at adaptive explanations. And finally, I looked to adaptive explanations for human behavior, maintaining that despite specific challenges, theoretical and methodological changes allow the human evolutionary behavioral sciences to provide adaptive explanations.

## BIBLIOGRAPHY

- Allen, C. (Winter 2009 Edition), Teleological Notions in Biology, *The Stanford Encyclopedia of Philosophy* Edward N. Zalta (ed.), URL = [<http://plato.stanford.edu/archives/win2009/entries/teleology-biology/>](http://plato.stanford.edu/archives/win2009/entries/teleology-biology/).
- Avital, E., & Jablonka, E. (2000). *Animal traditions: Behavioural inheritance in evolution*. Cambridge University Press.
- Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychological review*, 113(3), 628.
- Bigelow, J., & Pargetter, R. (1987). Functions. *The Journal of Philosophy*, 84(4), 181-196.
- Bleich, V. C. (1999). Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy*, 283-289.
- Borgerhoff Mulder, M., & Schacht, R. (2012). Human behavioural ecology. *eLS*.
- Borgia, G. (1995). Why do bowerbirds build bowers?. *American Scientist*, 83(6), 542-547.
- Bowlby, J. (1969). *Attachment and loss v. 3* (Vol. 1). Random House.
- Brandon, R. N. (1990). *Adaptation and environment* (Vol. 214). Princeton: Princeton University Press.
- Brosnan, K. (2009). Quasi-independence, fitness, and advantageousness. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 40(3), 228-234.
- Burkhardt, R. W. (2005). *Patterns of behavior: Konrad Lorenz, Niko Tinbergen, and the founding of ethology*. University of Chicago Press.
- Buss, D. M. (1998). The psychology of human mate selection: Exploring the complexity of the strategic repertoire. *Handbook of evolutionary psychology: Ideas, issues, and applications*, 405-429.
- Caro, T. M. (1986a). The functions of stotting in Thomson's gazelles: some tests of the predictions. *Animal Behaviour*, 34(3), 663-684.

- Caro, T. M. (1986b). The functions of stotting: a review of the hypotheses. *Animal Behaviour*, 34(3), 649-662.
- Cheverud, J. M. (1988). A comparison of genetic and phenotypic correlations. *Evolution*, 958-968.
- Cordain, L., Eaton, S. B., Sebastian, A., Mann, N., Lindeberg, S., Watkins, B. A., ... & Brand-Miller, J. (2005). Origins and evolution of the Western diet: health implications for the 21st century. *The American journal of clinical nutrition*, 81(2), 341-354.
- Cummins, R. (1975) Functional Analysis, *Journal of Philosophy*, 72, 741-65.
- Darwin, C. R. (1871). *The descent of man*. D. Appleton and Company.
- Darwin, C. R. (1872). *The expression of the emotions in man and animals*. London: John Murray. 1st edition.
- Dawkins, R. (1983). Universal Darwinism. In D. S. Bendal (ed.) *Evolution from Molecules to Men*. New York: Cambridge University Press
- Dawkins, R. (1986). *The blind watchmaker: why the evidence of evolution reveals a universe without design*. New York: Norton.
- Dennett, D. C. (1989). *The international stance*. The MIT press.
- Dochtermann, N. A. (2011). Testing Cheverud's conjecture for behavioral correlations and behavioral syndromes. *Evolution*, 65(6), 1814-1820.
- Dray, W. (1957). *Law and explanation in history*. Oxford: Oxford University Press.
- Drewnowski, A., & Rock, C. L. (1995). The influence of genetic taste markers on food acceptance. *The American journal of clinical nutrition*, 62(3), 506-511.
- Driscoll, C. (2004). Can Behaviors Be Adaptations?\*. *Philosophy of Science*, 71(1), 16-35.
- Driscoll, C. (2009). On our best behavior: optimality models in human behavioral ecology. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 40(2), 133-141.
- Dupré, J. (2001). *Human nature and the limits of science*. Oxford: Clarendon.
- Ewald, P. W., & Williams, W. A. (1982). Function of the bill and tongue in nectar uptake by hummingbirds. *The Auk*, 99(3), 573-576.
- Fawcett, T. W., Hamblin, S., & Giraldeau, L. A. (2013). Exposing the behavioral gambit: the

- evolution of learning and decision rules. *Behavioral Ecology*, 24(1), 2-11.
- Fenster, Charles B. (1991). Selection on floral morphology by hummingbirds. *Biotropica* 23. (1) 98-101.
- Forber, P. (2010). Confirmation and explaining how possible. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 41(1), 32-40.
- Fullard, J. H., Otero, L. D., Orellana, A., & Surlykke, A. (2000). Auditory sensitivity and diel flight activity in Neotropical Lepidoptera. *Annals of the Entomological Society of America*, 93(4), 956-965.
- Gigerenzer, G., & Gaissmaier, W. (2011). Heuristic decision making. *Annual review of psychology*, 62, 451-482.
- Gintis, H. (2007). A framework for the unification of the behavioral sciences. *Behavioral and brain sciences*, 30(1), 1-15.
- Grafen, A. (1984). Natural selection, kin selection and group selection. *Behavioural ecology: an evolutionary approach*, 2.
- Gray, R. D., Heaney, M., & S., Fairhall. (2003). Of Adaptive Explanation. *From mating to mentality: Evaluating evolutionary psychology*, 247.
- Griffiths, P. E. (1993). Functional analysis and proper functions. *The British Journal for the Philosophy of Science*, 44(3), 409-422.
- Griffiths, P. E. (2009). In what sense does 'nothing make sense except in the light of evolution'?. *Acta Biotheoretica*, 57(1-2), 11-32.
- Godfrey-Smith, P. (1993). Functions: consensus without unity. *Pacific Philosophical Quarterly*, 74(3), 196-208.
- Godfrey-Smith, P. (1994). A modern history theory of functions. *Nous*, 28(3), 344-362.
- Godfrey-Smith, P. (2006). The strategy of model-based science. *Biology and Philosophy*, 21(5), 725-740.
- Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford University Press.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, 205(1161), 581-598.

- Gould, S. J., & Vrba, E. S. (1982). Exaptation—a missing term in the science of form. *Paleobiology*, 4-15.
- Hadfield, J. D., Nutall, A., Osorio, D., & Owens, I. P. F. (2007). Testing the phenotypic gambit: phenotypic, genetic and environmental correlations of colour. *Journal of evolutionary biology*, 20(2), 549-557.
- Hinde, R. A. (1982). *Ethology: Its nature and relations with other sciences*. New York: Oxford University Press.
- Jablonka, E., & Lamb, M. J. (2005). *Evolution in four dimensions: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. MIT press.
- Kaplan, J. M. (2002). Historical evidence and human adaptations. *Philosophy of science*, 69(S3), S294-S304.
- Kimura, M. (1968). Evolutionary rate at the molecular level. *Nature*, 217(5129), 624-626.
- King, J. L. & Jukes, T. H. (1969). Non-darwinian evolution. *Science*. 164. 788-798.
- Kiritani, O. (2011). Function and modality. *Journal of Mind and Behavior*, 32(1), 1.
- Kitcher, P. (1985). *Vaulting ambition: Sociobiology and the quest for human nature* (pp. 29-ff). Cambridge, MA: Mit Press.
- Laland, K. N., & Brown, G. (2002). *Sense and nonsense: Evolutionary perspectives on human behaviour*. Oxford University Press.
- Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21(10), 542-547.
- Lennox, J. G. (1991). Darwinian thought experiments: A function for just-so stories. *Horowitz and Massey, 1991*, 223-245.
- Longino, H. (2012). Knowledge for What? Monist, Pluralist, Pragmatist Approaches to the Sciences of Behavior. In *Philosophy of Behavioral Biology* (pp. 25-40). Springer Netherlands.
- Longino, H. E. (2013). *Studying Human Behavior: How Scientists Investigate Aggression and Sexuality*. University of Chicago Press.
- Lorenz, K., translated by Lorenz, K & Rickert, R.W. (1982). *The foundations of ethology: the principal ideas and discoveries in animal behavior*. Simon and Schuster.
- Machery, E. (2007). Massive modularity and brain evolution. *Philosophy of Science*, 74(5), 825-838.



- Machery, E. (2008). Discovery and confirmation in evolutionary psychology. *Oxford Handbook of Philosophy of Psychology*. Oxford University Press, Oxford.
- Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 14(2), 54-67.
- Melo, G.A.R., Hermes M.G., Garcete-Barrett, B.R. (2011) "Origin and occurrence of predation among hymenoptera: A phylogenetic perspective" In: Polidori, C. eds. *Predation in the Hymenoptera: An Evolutionary Perspective* (ch. 1) Transworld Research Network, Trivandrum-695 023, Kerala, India.
- Millikan, R. G. (1984). *Language, Thought, and Other Biological Categories: New Foundation for Realism*. The MIT Press.
- Millikan, R. G. (1989a). An ambiguity in the notion "function". *Biology and Philosophy*, 4(2), 172-176.
- Millikan, R. G. (1989b). In defense of proper functions. *Philosophy of science*, 288-302.
- Mitchell, S. D. (1989). The causal background of functional explanation. *International Studies in the Philosophy of Science*, 3(2), 213-229.
- Mitchell, S. D. (1993). Dispositions or etiologies? A comment on Bigelow and Pargetter. *The Journal of Philosophy*, 90(5), 249-259.
- Mitchell, S. D. (1995). Function, fitness and disposition. *Biology and Philosophy*, 10(1), 39-54.
- Nanay, B. (2010). A modal theory of function. *Journal of Philosophy*, 107(8), 412
- Nanay, B. (2013). Function Attributions Depend on the Explanatory Context. *The Journal of Philosophy*, 109(10), 623-627.
- Neander, K. (1991). Functions as selected effects: The conceptual analyst's defense. *Philosophy of science*, 168-184.
- Neander, K., & Rosenberg, A. (2013). Solving the Circularity Problem for Functions. *The Journal of Philosophy*, 109(10), 613-622.
- Orzack, S. H., & Sober, E. (1994). Optimality models and the test of adaptationism. *American Naturalist*, 361-380.
- Owens, I. P. (2006). Where is behavioural ecology going?. *Trends in Ecology & Evolution*, 21(7), 356-361.
- Parker, G. A., & Maynard Smith, J. (1990). Optimality theory in evolutionary biology. *Nature*, 348(6296), 27-33.

- Pincock, C. (2012). Mathematical models of biological patterns: Lessons from Hamilton's selfish herd. *Biology & Philosophy*, 27(4), 481-496.
- Pinker, S., & Bloom, P. (1992). Natural language and natural selection. *The adapted mind*, 451-493.
- Ramsey, G. (2013). Culture in humans and other animals. *Biology & Philosophy*, 1-23.
- Richardson, R. C. (2007). *Evolutionary psychology as maladapted psychology*. Cambridge, MA: MIT Press.
- Rolando, A., Maffei, G., Pulcher, C., & Giuso, A. (1997). Avian community structure along an urbanization gradient. *Italian Journal of Zoology*, 64(4), 341-349.
- Shear, W. A. (1994). Untangling the evolution of the web. *American Scientist*, 82, 256-256.
- Sober, E. (1984). The nature of selection: evolutionary theory in philosophical focus. *Bradford books*.
- Sober, E. (2000). Philosophy of biology. Dimensions of philosophy series. 2<sup>nd</sup> edn. Boulder, CO: Westview Press.
- Stanford, P. K. (2006). *Exceeding our grasp: Science, history, and the problem of unconceived alternatives* (Vol. 1). Oxford: Oxford University Press.
- Temeles, E. J., & Kress, W. J. (2003). Adaptation in a plant-hummingbird association. *Science*, 300(5619), 630-633.
- Tinbergen, N. (1942). An objectivistic study of the innate behavior of animals. *Bilbioth. Biother.* 1, 39-98.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20(4), 410-433.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. *The adapted mind: Evolutionary psychology and the generation of culture*, eds. Barkow, J. H., Cosmides, L. E., & Tooby, J. E., 19-136.
- Tooby, J., & Cosmides, L. (2005). Conceptual foundations of evolutionary psychology. *The handbook of evolutionary psychology*, 5-67.
- Trestman, M. (2010). *Goal-Directedness, Behavior and Evolution: A Philosophical Investigation*, University of California, Davis, 132 pages; 3427484
- Trestman, M. (2011). Two strategies for investigating the evolution of behavior. *Biology & Philosophy*, 26(6), 871-889.

- Trut, L. (1999). Early Canid Domestication: The Farm-Fox Experiment Foxes bred for tamability in a 40-year experiment exhibit remarkable transformations that suggest an interplay between behavioral genetics and development. *American Scientist*, 87(2), 160-169.
- Trut, L. N., Plyusnina, I. Z., & Oskina, I. N. (2004). An experiment on fox domestication and debatable issues of evolution of the dog. *Russian Journal of Genetics*, 40(6), 644-655.
- van Gils, J. A., Schenk, I. W., Bos, O., & Piersma, T. (2003). Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. *The American Naturalist*, 161(5), 777-793.
- Weber, M. (2005). Holism, Coherence, and the Dispositional Concept of Functions. *Annals in the History and Philosophy of Biology*, 10, 189-201.
- Weber, M. (2012). Behavioral Traits, the Intentional Stance, and Biological Functions: What Neuroscience Explains. In *Philosophy of Behavioral Biology* (pp. 317-327). Springer Netherlands.
- West, P. (2005). The Lion's Mane Neither a token of royalty nor a shield for fighting, the mane is a signal of quality to mates and rivals, but one that comes with consequences. *American scientist*, 93(3), 226-235.
- Wright, L. (1973). Functions. *The Philosophical Review*, 82(2), 139-168.
- Zach, R. (1979). Shell dropping: decision-making and optimal foraging in northwestern crows. *Behaviour*, 106-117.