Evolutionary Psychology and the Future of Evolutionary History

Chris Haufe

Submitted in partial fulfillment of the
Requirements for the degree
of Doctor of Philosophy
in the Graduate School of Arts and Sciences
COLUMBIA UNIVERSITY
2006

Abstract

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This work highlights a number of problem areas within the research program known as "evolutionary psychology." I focus on the differences between the use of those patterns in evolutionary biology (which I endorse) and their use in evolutionary psychology (which I condemn). First, I describe the methods by which we arrive at reliable accounts of evolutionary history. as well as why these methods are seen as reliable and why a researcher might favor one particular kind of account over another. I then show via comparison how far evolutionary psychology is from doing this kind of work. Following that, I provide separate philosophical treatments of a number of popular rhetorical tools used by evolutionary psychologists to give their research the veneer of evolutionarily-informed psychological investigation. I close with a critical assessment of some of the more famous results in evolutionary psychology

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Acknowledgments

This work owes a special debt of gratitude to the following entities: the Department of Philosophy at the University of Michigan — particularly Eric Lormand; the Department of Philosophy at Columbia University — particularly Philip Kitcher and Alison Wylie; the Columbia Metaphysicist Society — particularly Matthew Slater and Neil Williams; and my family — particularly my wife, Maysan Haydar. It is with affection and thanks that I dedicate my dissertation to her.

1. Introduction

Lewontin, Rose, and Kamin (1984) begin the final chapter of their critique of human sociobiology with these remarks:

> Critics of biological determinism are like members of a fire brigade, constantly being called out in the middle of the night to put out the latest conflagration, always responding to immediate emergencies, but never with the leisure to draw up plans for a truly fireproof building. Now it is IQ and race, now criminal genes, now the biological inferiority of women, now the genetic fixity of humans. All these deterministic fires need to be doused with the cold water of reason before the entire neighborhood is in flames" (265-266).

Thanks primarily to these authors and to Philip Kitcher's merciless *Vaulting Ambition*, we now live in a world in which the term "human sociobiology" is, by and large, without a referent. Lamentably, however, the conflagrations continue to rage under a different banner.

The new generation of critics of what Lewontin *et al.* call "biological determinism" (whether or not this name is apt) have been called into the service of quelling infernos ignited by a new movement known as *evolutionary psychology*. The character of evolutionary psychology can be informatively divided into two fundamental principles. The first such principle is that our cognitive architecture is composed predominately of mental "modules," which are best understood as psychological mechanisms which process a limited range of informational inputs and (ultimately) produce a limited range of behavioral outputs. The second fundamental principle of evolutionary psychology is that these mental modules were directly selected by nature to perform the functions characterized by their particular input-output relationships. Each of these instances of direct selection are assumed to have happened at some point during the Pleistocene era.

Lots of things have changed since the Pleistocene, and what may have been adaptive back then may not be adaptive now. Much has been made by evolutionary psychologists over the fact that a trait need not be adaptive in the present environment in order to qualify as an adaptation. Recognition of this principle

> is especially important in the study of human behavior. Our species spent over 99% of its evolutionary history as hunter-gatherers in Pleistocene environments. Human psychological mechanism should be adapted to those environments, not necessarily to the twentieth-century industrialized world (Cosmides and Tooby 1987: 280).

The take-home lesson in these and similar statements by Cosmides and Tooby as well as others (e.g., Thornhill and Palmer 2000: 7) is that nonadaptive or maladaptive results are a natural (though not a *necessary*) consequence of placing traits in an environment different from the one to which they are adapted. It may be that there is some adaptive challenge in the present which our Stone-Age adaptations are unequipped to deal with, causing our reproductive success to decline relative to what it might have been during the era in which those adaptations evolved—the Era of Evolutionary Adaptedness (EEA). For example, evolutionary psychologists Steve Gangestad and Randy Thornhill have remarked that

> one overarching function of the propensity to form long-term sexual relationships is that such relationships provide a social context in which childrearing would have been efficient and successful within ancestral environments

> [cite]. Of course, in this age of readily available and reliable contraception, long-term sexual relationships can be completely unlinked with reproduction and parenting. This fact, however, in no way gainsays a historically adaptive, reproductive significance of the psychological design that underlies the formation and maintenance of sexual relationships (Gangestad and Thornhill 1997: 70).

While the introduction of contraception into human sexual behavior has severed to a significant degree the adaptive relation between long-term sexual relationships and the production of and care for offspring, the presence of contraception in the modern environment does not undermine the status of long-term sexual relationships as adaptations.

Another kind of case is one where an adaptive challenge which played an important formative role during the EEA is absent in our present environment, resulting in inappropriate resource-wasting behavioral responses. Many sociobiologists and evolutionary psychologists have suggested that our visceral reaction to the sight of snakes or spiders is a consequence of an age-old psychological adaptation designed for avoiding lethal bites. Few of us today live among deadly spiders, yet many still flee at the first glimpse of eight legs creeping up the wall—a wholly unnecessary and perhaps even maladaptive response.

Conversely, evolutionary psychologists have emphasized that "[t]o whatever extent, great or small, a particular present behavior is still adaptive, it is because present conditions still happen to resemble ancestral conditions" (Tooby and Cosmides 1990a: 382). The fact that the present environment is relevantly similar (i.e., similar in the aspects towards which our adaptations were originally oriented) to the EEA means that our psychological adaptations can be adaptive in the present, even though the adaptations themselves were formed thousands of years ago. The crucial factor is not when the adaptations evolved, but *whether the relationship between a particular behavior and reproductive success is the same in both the past and present environments.*

Accordingly, an important thing to keep in mind when thinking about the relationship between adaptations formed in the past and their performance in present environments is the distinction between changes in *selective value* and changes in *behavioral response.* On the evolutionary psychological account, environmental dissimilarities *do not* change the naturally selected behavioral response to an environmental cue. Rather, dissimilarities often change the selective value of those responses, rendering a response nonadaptive where it was once adaptive. For this reason, we cannot use present adaptiveness as evidence of past adaptation. But behavioral response *Y* in the presence of environmental cue *X* is just as much evidence of adaptation under modern world conditions as it would be if we were able to exactly recreate the EEA. Tooby and Cosmides provide clarification:

> in viewing cases of behavior, the adaptationist question is not, 'How does this or that action contribute to this particular individual's reproduction?' Instead, the adaptationist questions are, 'What is the underlying panhuman psychological architecture that leads to this behavior in certain specified circumstances' and 'What are the design features of this architecture--if any--that regulate the relevant behavior in such a way that it would have constituted functional solutions to the adaptive problems that regularly occurred in the Pleistocene?' (Tooby and Cosmides 1992: 55).

In other words, ask not what a behavior *can* do for its possessor. Rather, ask what the mechanisms which produce that behavior *could have done* for its possessor "in certain specified circumstances"—viz., those of the EEA.

1.1. The Context of The Present Critique

I hope evolutionary psychologists will be happy with what I have portrayed as the core commitments of their field, as well as the manner in which I have portrayed them. I similarly hope they will be happy to learn that, for the most part, I think that much of what they say is correct. Specifically concerning the nature of adaptation, I think that their conception of the mechanics of natural selection is quite crisp and accurate, and that it does not deviate from what evolutionary biologists today believe about adaptation and the past.

Other critics have found less to agree with in evolutionary psychology. The present critique comes on the heels of a growing resistance in the academic and mainstream press to the work being done by evolutionary psychologists. Much of this resistance has been directed at the perception that evolutionary psychology represents us as "hopelessly maladapted" to the present environment and thoroughly constrained in our thoughts and behavior by what natural selection saw as important to think about and to do roughly 2 million years ago. The antidote to these evolutionary excesses, claims the resistance, is a reformation of (1) the notion of what, precisely, our minds are adapted *to*; and (2) the degree of significance attributed to biology's influence over what is humanly possible. The reformatory antidote has received its most potent concentration in David Buller's recent *Adapting Minds*, which provides painstaking reviews and recommendations for how to improve evolutionary psychology.

I think Buller's book is, in Jerry Fodor's words, "a lost opportunity" for the reason that what seems necessary is not reformation but entombment (Fodor 2005). Buller clearly has the insight and the work ethic to have undertaken such a task, but his sympathies for the evolutionary study of mind and behavior led him in a more nurturing, less destructive direction. Buller is "unabashedly enthusiastic about efforts to apply evolutionary theory to human psychology" and frequently endorses "one or another hypothesis about the evolution of some aspect of human psychology" (Buller 2005: x). But I think there is little to be gained at present from the study of human behavior in an evolutionary framework, and even less to be gained from the "just-so" storytelling in which Buller himself engages. It is this last aspect of his book—his willing endorsement of particular hypotheses regarding the evolution of certain psychological properties—that makes *Adapting Minds* in many places an exercise in, rather than a critique of, evolutionary psychology. I don't think Buller would disagree with this characterization, but then it should not be surprising that his evolutionary hypotheses fall victim to many of the same problems which plague evolutionary psychology—indeed, many of the problems which plagued human sociobiology.

Failure to appreciate the deep congruence between evolutionary psychology and its predecessor, sociobiology, leads Buller to mistakenly assert that "Kitcher's critique of sociobiology doesn't apply to evolutionary psychology" (*ibid.*: x). Kitcher helped us develop a clear understanding of what is at stake in determining whether a given evolutionary hypothesis is true—what he called "the confirmation of particular Darwinian histories. The main strategy in justifying particular scenarios for the history of life is one that is well known to practicing biologists...Darwinian histories win their way to the top through the elimination of rivals" (Kitcher 1985: 66). The elimination of rivals by a particular Darwinian history occurs through the accumulation of different types of evidence which comport with that history but which do not simultaneously comport with rivals. To the extent that two or more rival Darwinian histories can account for the evidence, evidentiary considerations alone cannot confirm a particular history.

What is therefore at issue in deciding whether a given Darwinian history is true is whether there is evidence to support the component propositions of that history and whether that evidence could also be taken to support the component propositions of other Darwinian histories. In this regard, the task of human sociobiologists of the '70s and '80s was no different than that which lies before today's evolutionary psychologists: to show what evidence supports their preferred account of the evolutionary history of some human property and to show that rival histories are not equally well supported by that evidence. It is this common thread that forms the substance of my critique.

1.2. Magic Bullets Vs. Local Critique

I began this introduction with a quote from Lewontin *et al.* (1984), but in fact I think that the approach taken in their book is misguided. Indeed, the reasons why it is misguided are what makes the "fire brigade" analogy so wonderfully appropriate. Just as the notion of a fireproof building is a fireman's pipe dream, the search for a fundamental flaw which, if corrected, would prevent sociobiological/evolutionary psychological conflagrations from breaking out has amounted to a lot of wasted effort. This is because, as is the case with fires, the kinds of problems created by sociobiologists/evolutionary psychologists have different types of causes, and what is required to douse the flames of one problem may fan the flames of another. Lewontin, along with the late Stephen Jay Gould, has sought a "magic bullet" that could expose a common cause of these problems and forestall future instances of ignition. Over the last thirty-or-so years, both Gould and Lewontin have fired many a round at the heart of what they labeled "biological determinism," but time after time have they failed to hit their mark.

Missing their target in this case does not indicate the need for target practice on the part of either Gould or Lewontin. Decades in the trenches have proven their marksmanship to be both reliable and lethal when aimed at smaller targets. Thus, argues Kitcher (2004) in his memorial essay for Gould, what is needed is a return to the approach of which Gould was the consummate master: case-by-case analysis and debunking (what Kitcher calls *local critique*). John Earman has emphasized the importance of local critique in another, more general connection (in fact, one which is often taken up by critics of evolutionary psychology)—namely, the magic bullet strategy pursued in an effort to separate genuine science from pseudo-science:

> it does not much matter what label one sticks on a particular assertion or an enterprise; the interesting questions are whether the assertion merits belief and whether the enterprise is conducive to producing well-founded belief. The answers cannot be supplied by a simple litmus test, but can only be reached by detailed, case-by-case investigations (Earman 2000: 3).

Likewise, what seems important when confronting evolutionary psychology is whether, for any particular Darwinian history, the appropriate kind and degree of support has been provided. This is the form of confrontation I attempt in what follows. (Of course, where certain principles or methods are shared across the discipline, as is becoming increasingly common among evolutionary psychologists, the neighborhood affected by local critique will often be far-reaching.) What seems unimportant (at least from a philosophical perspective) is what a particular group's motivations are or whether the implications of their hypotheses are politically or morally palatable. As the evolutionary psychologists are constantly reminding us, the commitment to the scientific worldview is a commitment to believing what the evidence tells us to believe. But it is equally a commitment to *not* believing *until* the evidence tells us to believe. This latter aspect of the commitment, I will argue, has been severely neglected by evolutionary psychologists.

The discussion to follow can be broken up into roughly two parts. In the first part (chapters 2-4), I describe how different types of researchers go about accumulating support for a hypothesis concerning some aspect of an organism's evolutionary history, and why we should view their methods and conclusions as reliable. I then show by way of comparison with this research why parallel work conducted by evolutionary psychologists is woefully deficient. The second part of the discussion (chapters 5-8) is devoted to matters more internal to evolutionary psychology. Here I examine some of the rhetorical tools they have used in the place of actual evidence to give their work an edge over other approaches to human behavior. The unmasking of the rhetoric shows evolutionary psychological hypotheses to be no better off (or worse) than other types of accounts of the same phenomena.

2. Demonstrating Adaptation

Introduction

Researchers attempting to demonstrate that some feature of an organism is the product of adaptation through natural selection employ a wide range of methods. These can be divided roughly into three categories: (a) direct demonstrations of natural selection, (b) indirect demonstrations via demonstrations of homology or homoplasy, and (c) demonstrating "functional design" (Williams 1966: 9). Some of these, if employed with sufficient care, can lead to reliable conclusions about whether some feature was selected for. Others, even when applied perfectly, cannot.

The discussion below is designed to serve as a backdrop to subsequent chapters but its significance is rather more general, for it depicts what is perhaps the principal divide between work in evolutionary psychology, on the one hand, and the overwhelming majority of work in the rest of the evolutionary sciences, on the other. The truth of hypotheses about which of our psychological properties are evolved adaptations—the stock in trade in evolutionary psychology—is to be evaluated according the rules for assessing the truth of hypotheses about all other kinds of adaptations (insofar as these rules lead to reliable conclusions). This chapter documents the differences between the kind of support provided by traditional evolutionary biologists and the kind provided by evolutionary psychologists, differences which hold implications for the reliability of evolutionary psychologists' claims about natural selection. Evolutionary psychologists have, with little or no justification, rejected the traditional methods by which researchers have tested hypotheses about adaptation, favoring instead one which has a number of theoretical problems and no history of success to recommend it.

The structure of the chapter breaks down as follows: I first outline in some detail the concept of an adaptation as it is understood in evolutionary biology. The distinctions drawn here will be important for understanding, among other things, (1) the difference between a property's being useful and a property's being an adaptation; (2) whether the appropriate evidence for testing an adaptation hypothesis has been sought; and (3) how successful a particular method for demonstrating adaptation is likely to be. These issues will play a significant role throughout the remainder of the dissertation, so clarity here is particularly crucial. Following that, I review many of the traditional methods by which researchers draw inferences about the influence of natural selection and discuss, for each method, the likelihood of success were we to apply it to humans. In the final section, I describe and critically assess the ways of demonstrating adaptation to which evolutionary psychologists are partial.

2.1. Adaptation

2.1.1. Natural Selection is Necessary to Produce Adaptation

Our discussion begins with a few remarks on what it means for a trait to be an adaptation. First, whether some property *P* of an organism *O* is an adaptation depends on that property's *causal history* (Brandon 1990: 41). The relevance of causal history to adaptation can be illustrated in the following way.

Suppose that the initial appearance of *P* is the result of a genetic mutation. Luckily, *P* causes an increase in the reproductive success of *O*, some of whose descendants might also possess *P* through genetic inheritance. Because *P* tends to increase and individual's reproductive success in this population, those descendants of *O* who possess *P* will, in turn, have increased reproductive success relative to members of the population who lack *P*. Through this process, *P* eventually becomes widespread in the population. Only properties whose causal history fits this description qualify as adaptations (Brandon 1990; Sober 1984).

For example, imagine that a male bird is born with an unusually bright red spot on its chest, much brighter than the plumage of any other member of the population. Because of this bright red spot, females find themselves drawn to him in a way they are not attracted to other males in the population. He mates with a few of them, and some of his sons also possess such a spot. Assuming the females in the population retain their preference for this spot through the generations, after a while the bright red spot will become widespread in the population. Thus, it qualifies as an adaptation.

Now imagine a slightly different causal history. Just as before, the male's bright red spot causes females to be strongly attracted to him. But unfortunately for this handsome young beau, before he can mate with any of these females he is killed by one of the predatory cats living in the area. Even though the bright red spot has in this case the same causal *properties* as in the case where he was able to reproduce, it lacks the same causal *history* in that the spot does not become widespread; its history dies with him. Lacking the appropriate causal history, the bright red spot fails to qualify as an adaptation.

There are several other ways in which a property, no matter how useful or fitness-enhancing, may fail to qualify as an adaptation. The primary distinction here is between adaptations on the one hand, and properties that have "fortuitous benefits" on the other (Sober 1984; Williams 1966). Consider the phenomenon of "correlated characters," or properties that are for some reason or other (e.g. pleiotropy, developmental constraints) linked to one another. We may find through careful observation and experiment that a certain widespread property *C* tends to increase the ability of its possessor to attract mates. But it might be the case that, rather than having spread through the population because it causes an *increase* in attractiveness, *C* merely evolved because it was genetically linked to another property *P* that actually *was* selected for because of the benefits it confers on its possessor (such that *C* would not have been selected for in the absence of *P*). Note Price and Langen:

> ...a character whose intraspecific variation is thought to be of major adaptive significance based on comparative or functional studies may have evolved from some ancestral state entirely by correlated response—evolution by correlated response does not necessarily imply neutrality" (Price and Langen 1992: 307).

It need not be the case that a property has low or no utility simply because it evolved through correlation with another property on which selection operated directly. Indeed, the "hitchhiking" property (in this case, attractiveness) may be highly beneficial. Nevertheless, because it lacks the appropriate causal history, because its spread is not explained by its contribution to reproductive success, it is not an adaptation.

Another process by which phenotypic properties may spread is random genetic drift, where some genes may become fixed not because of selection for them but simply due to chance. Occasionally, the prevalence of some phenotypic feature may appear to suggest the hand of selection when in fact the actual explanation is genetic drift. If genetic drift *does* turn out to be the cause of a certain property's evolution, that property, even where beneficial, is not an adaptation (Lauder 1996).

2.1.2. Natural Selection is Sufficient to Produce Adaptation

Just as *only* properties whose spread is due to direct selection for them are worthy of the label, "adaptation," it is also the case that *all* properties with this causal history are worthy of that label. What this means is that if some property *P* caused an increase in reproductive success at time t_1 and consequently spread through the population, then *P* remains an adaptation even if at time t_2 in the future *P* no longer increases reproductive success. Although *P*'s effects at t_2 are no longer beneficial and may even *decrease* fitness, the fact that *P* arose via the particular causal history required of an adaptation allows it to maintain its status as an adaptation. One way of understanding this distinction is to say that adaptations need not always be *adaptive*:

> An adaptation may cause problems for the organisms that have it; a changed environment may mean that an adapta-

> tion is no longer advantageous...To say that a trait is an adaptation is to make a claim about the cause of its presence; to say that it is adaptive is to comment on its consequences for survival and reproduction (Sober 1984: 210-211).

Recall the lucky male bird in the previous example who was born with a bright red spot which females found strangely attractive. Suppose that he and his red-spotted descendants mated successfully such that after several generations, at time t_2, most male birds in the population had the bright red spot, and that once again the prevalence of the red spot is due to its attractiveness to the females in the population. Males with red spots are more likely to attract mates than are males without red spots. The red spot has achieved “adaptation” status.

Now imagine that, after several generations and subsequent to the red spot achieving "adaptation" status, a feral cat is introduced to the birds’ habitat and the bright red spot makes it easy for the cats to detect and consequently kill red-spotted males. The red spot becomes such a liability that increased likelihood of being killed by a cat dwarfs the increased likelihood of mating. Because of the danger now posed by the red spot, generations subsequent to the introduction of the cats actually contain *fewer* red-spotted males; most of them die before they can pass down their red spot. The spot has clearly become maladaptive. Yet because of the manner in which it became prevalent in the population, it remains an adaptation.

2.1.3. *Adaptation and Function*

In addition to necessarily implying direct selection for a property, the label "adaptation" implies that there is a certain task to which the property is adapted. Property *P* qualifies as an adaptation if and only if the spread of *P* is due to the superior performance of organisms with *P* with respect to some task *T* (Sober 1984: 208). It makes no difference whether *P would be* good for task *T'*, were the performance of *T'* to have been or to become necessary for members of a population. Nor does it matter that *P* currently allows those who bear it to excel at task *T"*. These properties do not explain how *P* became prevalent in the population, and are thus irrelevant to the questions of whether *P* is an adaptation or what *P* is an adaptation for. Only its *actual* benefits for performing *T* explain how it spread through the population.

Returning to the red-spotted birds, we can say that red spots are an *adaptation for* attracting females because the spread of red spots in this population of birds is *due to the fact that* the red spot caused males to excel at the task of attracting females. Now suppose that on an island somewhere there is another, unrelated species of bird (species *B*), some of which have bright red spots. Species *B* has a bitter taste which makes it unpalatable to the predators there. After several generations, many predator species have acquired the ability to correlate unpalatability with bright red spots, which causes them to avoid the local species of bird which possess such spots. This in turn results in the spread of red-spotted birds on the island, now virtually unencumbered by the threat of predation. Given that red spots are adaptations for avoiding predators on this island, does it follow that if we brought to the island a species whose red spot was due to a history of female preferences for the spot (species *A*), then *their* red spots are also adaptations for avoiding predation? Certainly not. Although *A*'s red spots *would* allow them to excel in predation avoidance on the island, that fact does not explain why *A*s have red spots in the first place.[1]

Similarly, suppose that red spots no longer have the same effect on females they once did but now make it easier for members of this species to identify conspecifics. Even though red spots confer some current utility on their bearers in terms of being able to be readily identified, that utility did not play a role in the spread of red spots in the population. Thus, red spots would not be considered an adaptation for species recognition.

We have seen that *only* properties which spread through a population because of direct selection for those properties qualify as adaptations. In addition, we have seen that *every* property which spreads through a population because of direct selection for that property qualifies as an adaptation. Thus, natural selection is both necessary and sufficient for producing adaptations. Finally, we saw that any adaptation is an adaptation only for some particular task, such that

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[1] The vagueness lurking beneath the surface of this example is interesting. Suppose that after arriving on the new island, *A*'s spots stop being attractive to females. Yet, the spots persist in subsequent generations because of the predator avoidance advantage. To what environmental factor are *A*'s spots an adaptation—female preferences or predator avoidance? If we are able to say that the spots would not have persisted if not for the predator avoidance advantage, it seems natural to think that they are now an adaptation for predator avoidance. But predator avoidance does not explain the *proliferation* of spots among *A*s. Perhaps we want to say here that had there been no preference for spots among *A* females, and had a red-spotted male arisen on the new island, spots *would have* proliferated among *A*s for the purpose of predator avoidance. But that seems to violate the principle that whether a property *P would be* good for a task *T* is irrelevant to determining whether *P* is an adaptation for *T*. The confusion here suggests that there is something intuitive about the idea that counterfactual causal histories play some role in determining a trait's status as adaptation.

the superior performance of that task by individuals with the property relative to individuals without it caused the property to spread throughout the population.

2.2. Adaptation and Natural Selection

Given that the only properties that qualify as adaptations are those which became prevalent in a population because of the operation of natural selection on them directly, it follows that demonstrating that there has been natural selection for a property *P* is sufficient for demonstrating that *P* is an adaptation. Endler's (1986) *Natural Selection in the Wild* provides a masterful tour through the literature on and methods of demonstrating natural selection, describing and assessing the completeness of each method and providing examples of instances in which the method was used to successfully demonstrate natural selection and thus adaptation. In what follows, I will draw heavily on Endler's book in hopes of clarifying the evidentiary demands placed upon researchers interested in demonstrating natural selection. In addition, I will also examine the problems we might run into when applying traditional methods to the study of the evolutionary history of human psychology.

METHODS FOR STUDYING PAST SELECTION

2.2.1. Correlation with environmental factors (Method I)

This method is designed to test the hypothesis that "geographically varying selection results in a correlation between traits and the selective environmental factors" (Endler 1986: 56). If the correlation between them is significant, this suggests that selection may be acting on that trait. For example, suppose we find that in environments which contain a vast array of exceptionally bright colors, the red spots on male birds are much brighter than they are on males of the same species in environments where the spectrum of colors is drab and muted. If we find that this correlation between brightness of spot and brightness of environment persists in many different kinds of environments in which the birds are found, this may suggest that selection is responsible for the degree of brightness of red spots found in males.

Because the focus of this method is a particular kind of correlation, researchers must always remain sensitive to the possibility that any correlation they find may simply be the result of chance rather than causation. The best way to avoid the confounding effects of chance is to sample "over a large geographic area that follows geographically complex environmental variation" (*ibid.*: 57). By performing a multitude of tests in a variety of environments, one lessens the likelihood of mistaking mere statistical accidents for the presence of natural selection.

Yet even if one is able to confidently rule out chance correlations, there may be other results that appear to suggest selection when in fact there is some other type of causal process at work. For example, to the naive researcher, variation in condition-dependent traits will give the appearance of selection because they tend to exhibit the same type of trait-environment correlation one finds when selection is at work. This type of error is liable to occur when the form of genotype-environment interaction is unknown. Additionally, it is possible for there to be a correlation between variation in environmental factors and variation in traits that are not heritable, which may lead one to infer selection when it does not exist.

Finally, it should be noted that the suggestion of selection proffered by a successful implementation of Method I does not *demonstrate* selection. "[E]ven if the correlation is very good, other methods are always needed to demonstrate a *causal* relationship" (Endler 1986: 58). There will be more said later on about which methods can work in conjunction with Method I to demonstrate selection.

Prospects for Human Psychology

Setting aside for the moment the fact that trait-environment correlation is insufficient for demonstrating selection, are there good reasons for thinking that human psychological traits are amenable to study through Method I? Let us first consider this warning given by Endler:

> [I]gnorance of genetics and development, in conjunction with method I, can give a very misleading picture of the dynamics of morphology and natural selection. Both the heritability and the nature and form of any genotype-environment interaction must be known for the proper use of method I, as well as for all methods (Endler 1986: 58).

This makes the application to human psychology a rather difficult task. We must have some genetic-developmental information about the psychological trait in question if its correlation with a particular environmental factor can be taken to indicate that selection is operating on it. When, for example, David

Buss notes that there is a suggestive correlation between jealous behavior and adultery, he does so without the kind of genetic-developmental knowledge required for the correlation to have any probative value in the first place (Buss 2000). Thus, there is no basis for concluding that the trait-environment correlation in this case is the result of selection for jealous behavior in certain environments.

2.2.2. *Comparisons Between Closely Related Sympatric Species (Method II)*

This method involves the comparison of responses in closely related phenotypes to similar environments. Given that "closely related species are likely to have similar genetics and development," we have reason to suspect that those species will react similarly to the same environmental variables (Endler 1986: 59-60). In cases where we find that homologous traits (traits similar through descent) show a common response to some environmental factor, natural selection presents itself as a possible causal factor. Like Method I, however, homological comparison can only provide indirect evidence for natural selection. The lack of knowledge of fitness differences between carriers of the trait and those without it will prevent one from knowing whether the trait has (or had in the past) positive effects on fitness or is instead simply a benign homology, thus providing an incomplete basis for an inference of selection. Another problem for this method is that it alone will not offer an ecological explanation as to why there is (or was) selection for the trait (Brandon 1990; Endler 1986: 62).

Prospects for Human Psychology

The principal problem for application of this method to human psychology is the fact that we are largely ignorant of the ancestry of modern humans, which makes comparison of homological characters impossible (Lewontin 1998; Potts 1987). Because we lack knowledge as to whether there are intermediate phenotypes between us and our closest known relative, we simply cannot know whether any of our traits (psychological or otherwise) evolved from a similar trait T_k in, say, chimpanzees or from an intermediate phenotype which may have possessed its own unique adaptation T_a from which our trait T_h is derived. If the truth lies in the latter scenario, it makes no difference whether our trait appears more similar to T_k than to T_a. T_k and T_h are *not* homologous in this case, so we cannot apply Method II here. Even if it appears that psychological traits of contemporary humans vary in the same ways as do those of their closest known relative, our ignorance of the phylogeny rules out an inference of natural selection.

2.2.3. Comparison Between Unrelated Species Living in Similar Habitats (Method III)

This method compares traits that are analogous (similar without descent) rather than homologous. The reasoning behind it is fairly clear: traits that are functionally equivalent will take on similar forms when subject to equivalent selection pressures. There are different considerations to take into account depending on whether the focal species live in the same geographical area.

Hence, I divide my comments between issues relevant to allopatric species and those relevant to sympatric species.

Allopatric Species

Ascertaining convergence is especially difficult when comparing species who live in different geographic locations. The main problem is defining "habitat equivalence" (Endler 1986: 63). Where selective factors are not defined with sufficient rigor, researchers run the risk of engaging in "progressive ad hoc optimization" (Lewontin 1979a), meaning that one needs only to relax the parameters on what is required for equivalence until he has what appears to be a law-like relationship between traits which perform a certain function and "equivalent" environmental factors. When we find similar nesting behavior in two unrelated allopatric bird species, we may seek to provide a single explanation for both species' behavior. Some researchers may be tempted to look for *any* pair of superficially similar environmental factors and attribute to them equivalent selective pressure. This mistake ignores the fact that what appears similar to us often turns out not to be so in the eyes of natural selection (Coddington 1994). A related difficulty posed by this method concerns the attribution of functional similarity to two traits in unrelated species, where ad hoc optimization dangers also loom large. As we will see below, however, both problems are less serious when comparing unrelated sympatric species.

Sympatric Species

As Endler points out, the best demonstrations of natural selection by comparing unrelated sympatric species come from species which mimic each other. One type of mimicry (Batesian) occurs when there is a species which predators generally avoid. Other species in the area will evolve to mimic that species in some way (usually through color or odor), consequently causing predators to avoid the mimic as well (Endler 1986: 63). In cases like this, the problems of functional and habitat equivalence are more easily avoided. With respect to function, we have good evidence for equivalence because both traits are directed towards the same predator species and have the same effect on that species. And because the species are sympatric, issues of habitat equivalence do not pose as serious a worry as in allopatric species (although there is always the possibility of microhabitat differentiation). The best strategy is to formulate hypotheses of both functional and habitat equivalence with as much precision is possible, thereby decreasing the risk of ad hoc curve-fitting in order to produce the veneer of regularity in nature (Coddington 1994: 74; Endler 1986: 63).

Prospects for Human Psychology

There are three kinds of data required for comparing humans with unrelated species: (1) paleoenvironmental data concerning the climate, terrain, and biota which characterized early human habitats; (2) data regarding the social structure of early humans; and (3) performance data regarding the human psychological trait in question. Where the particular human trait is an adaptation unique to humans, comparison with other species will be impossible because of the lack of an appropriate analogue (Coddington 1994: 61).[2]

Any comparison involving humans which relies on a notion of habitat equivalence will need to provide a detailed account of the environment of early humans. If we are going to draw an analogy between the role of the environment in natural selection *vis a vis* humans and its role *vis a vis* other species, we are obviously going to need to know what the environment of early humans was like.

So, what *was* it like? The answer to this question is difficult to assess for a variety of reasons. First, because humans evolved millions of years ago, the environment which gave rise to them is not something to which we have direct access. We are thus forced to reconstruct their environment from the surviving fossil and geological evidence, and this reconstruction itself faces problems (Potts 1987: 30). Perhaps the most serious obstacle is the lack of a consistent relationship between a given type of paleoenvironment and a given type of hominin fossil (Potts 1998b: 116). Human origins scholar Rick Potts laments:

> Linkage in time and space between these two types of data is imprecise. Rarely do samples for paleoenvironmental analysis come from the exact loci and sedimentary environment in which hominin fossils were originally buried or, based on taphonomic analysis, in which the hominins may actually have lived and died (Potts 1998b: 116).

Without a regular correlation between environment type and fossil type, it is difficult to draw conclusions as to what the early hominin environment was like.

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[2] This last point makes it especially clear why a complete phylogeny (including knowledge of the descent of psychological characteristics) is absolutely critical. Novel adaptations such as might be found in human beings are, by definition, *not* the product of the suite of selection pressures which may have shaped a superficially similar trait in some other lineage. In such cases, we learn nothing by comparing the novel trait with a seemingly similar trait because the traits do not derive from a common environmental cause.

The lack of a consistent fossil-environment correlation may suggest that the earliest hominins were "associated with a diverse range of habitats—forest, woodland, open savana and mosaic habitats" (Potts 1998b: 116). This idea is further supported by the fact that unlike the stable ecosystems we find today, the era in which humans evolved was one characterized by rapid, violent, and ecologically disruptive change (Potts 1996, 1998a). We are therefore left with a depressing epistemic situation: (1) the available paleoenvironmental data does not suggest a unique answer to the question of what the early hominin environment was like, and (2) our current best guess suggests that that environment was in important respects nothing like anything we find today. Clearly, finding a species living in an equivalent habitat will be no easy task.

The social structure of early humans should be included in the notion of "habitat" because social demands are thought to have been of high selective importance. Chapter 4 will be devoted to discussion of this topic, but a few short remarks here should serve the present point. Most of our knowledge of early social structure comes from evidence indicating the use and manufacture of stone tools, and from conspicuous deposits of animal bones scattered across parts of eastern Africa. Their association with faunal remains suggests that the first humans ate more meat than their closest nonhuman primate ancestors, although it is entirely unclear how this meat was procured, how *much* of it was procured, or what role the eating and procuring of meat played in society. For example, no one knows how often or even *whether* early humans hunted (O'Connell 1997; Potts 1984, 1987). Current data derived from modeling is thought to indicate that meat could not have been consumed often enough or in high enough quantities to have constituted a significant dietary contribution (O'Connell *et al.* 2002).

In addition to lingering questions regarding what role these animals bones might have played, it is also unclear why they are often found collected together. Where it had been previously thought that the bone accumulation was evidence of "home bases" where early hunters brought their kills to be devoured by the community (Isaac 1978), it is now known that there are a variety of ways in which bones accumulate.

Our current state of ignorance is only compounded by the fact that an incomplete phylogenetic record tracing the evolution of the human-chimpanzee common ancestor to modern humans prohibits us from inferring what early humans must have been like from how our closest living relatives actually are. The possibility of unique behavioral adaptations somewhere in the ancestral line makes modern chimpanzees an inappropriate analogue upon which to base inferences about the behavior and social structure of early humans (Foley 1999; Potts 1987).

In order to determine whether traits in unrelated taxa are analogous, we need to find out whether they actually perform similarly with respect to the task to which they are supposed to be adapted. The data we seek will depend on the hypothesized function. If, for example, the function of a trait is thought to be for guarding impregnated mates, we will need to show either through observation or experiment that (1) the trait under examination actually facilitates mate guarding in a way that cannot be accounted for by any other trait, and (2) there is no function other than mate guarding which the trait in question could be performing which might account for its evolution (Lauder 1990, 1996). Even if the analysis supports our performance hypothesis, however, this will not tell us whether selection is currently operating on or has in the past operated on the trait. The results of our analyses could merely indicate some selectively irrelevant beneficial effect. For example, a functional analysis may point to one variant rather than another even though the variation is not heritable and thus not an object of selection. Nevertheless, these analyses may help in reconstructing the trait's evolutionary history.

How are we to acquire the relevant performance data on human psychological traits? As we noted above, whether a trait is currently adaptive cannot tell us whether there was selection for that trait in the past (Williams 1992: 40). Thus any performance data relevant to assessing the function of an aspect of human psychology must come *not* from analyses of the performance of that trait in contemporary humans but from performance analyses carried out on humans during the period in which that particular trait was supposed to have been selected for. This may not be impossible, but it is certainly unfathomably difficult at present. Just to put things in perspective, performance analyses are rarely performed on *living* organisms because of the difficulties involved (Lauder 1990; Lewontin 1998).

The fact that there are many significant features of the early *Homo* habitat for which we have little to no data means that it is an open question whether there is some species which occupies a similar habitat and through which we could come to understand why we have the properties that we do. Furthermore, the barriers to performance analyses of our psychological traits suggests that, were we to find a properly analogous species, a whole new set of inferential problems would be waiting for us.

METHODS BY WHICH ONE CANNOT STUDY PAST SELECTION BUT WHICH CAN BE USED TO STUDY PRESENT SELECTION

2.2.4. Deviation from Formal Null Models (Method IV)

A variety of population genetics models make predictions about the distribution of certain alleles in a population assuming there is no selection acting on them. If the actual distribution of alleles diverges from what is predicted in the case of no selection (i.e., if the null hypothesis is rejected), this may indicate that selection is occurring in that population. The strength of the evidence for selection provided by rejection of the null hypothesis will depend upon other assumptions of the particular model; rejection might simply indicate that one of the assumptions (other than the assumption of no selection) is false (Endler 1986: 64-73).

Prospects for Human Psychology

There are at least two major impediments to applying this method to human psychology. First, unlike all the methods discussed thus far, which look for selection at the level of the phenotype and leave questions about genes for another time, population genetics models require explicit knowledge about the genetic bases of the traits under investigation. The requisite genetic knowledge in the case of human psychology is entirely lacking. Consider again the hypothesized adaptation of jealousy. We cannot apply a population genetics model to the study of jealousy because we do not know its genetic basis, assuming it even *has* an identifiable genetic basis.

Second, these models test for current selection and are therefore of no use in the study of human psychological adaptations, which are hypothesized to have reached fixation thousands of generations ago and which are therefore not the object of current selection (Cosmides and Tooby 1987; Tooby and Cosmides 1990b). We would find the distribution of the relevant genes (assuming we knew which ones to look for) to be at one hundred percent, which would tell us absolutely nothing about whether the trait was under direct selection at anytime in the past.

2.2.5. Long-term Studies of Trait Frequency Distribution (Method V)

Long-term studies of trait frequency distribution follow trait distributions over many generations. Evidence for current selection is suggested either by little or no change in the distribution (which could indicate selective equilibrium, in which there is constant selection *against* deviation from the current distribution), or by consistent change in one direction over the generations studied (which could indicate the operation of selection) (Endler 1986: 73-75).

Prospects for Human Psychology

Here we encounter familiar problems. Again, the trait distribution for most psychological adaptations is hypothesized to have been one hundred percent since the end of the Pleistocene (roughly 11,500 years ago). Even though this is a case of long-term stability, we cannot attribute the stability to selective equilibrium because the lack of phenotypic variation implies that there would be long-term stability whether or not the trait was at equilibrium. In addition, the lack of phenotypic variation rules out the possibility of directional change.

For psychological adaptations which may be present in less than one hundred percent of the population, long-term study may be possible in principle. Some psychologists have alleged that an aptitude for music may represent one such adaptation (Miller 2000a: 43-44; Miller 2000b). A study designed to determine whether selection is operating directly on musical aptitude would require us to have data on the distribution of musical aptitude for a large number of generations. A comparable study done on chromosomal inversion in *Drosophila robusta*, for example, used information on trait distribution which spanned a thirty-four year period, which is the equivalent of *thousands* of generations of *D. robusta* (Etges 1984). We have no such data on human musical aptitude, nor are we likely to acquire any.

2.2.6. *Perturbation of Natural Populations (Method VI)*

The idea behind this method is similar to that of Method V—*viz.*, that conspicuous changes in trait frequency distributions may indicate the presence of natural selection. In this case, we investigate to see whether a perturbation of either the environment or the trait distribution itself results in a return from the post-perturbation distribution to the original pre-perturbation distribution, which we assume to represent an equilibrium. So long as we can rule out random drift, natural selection would seem to be the only cause that could explain why the distribution returned to pre-perturbation levels. If used carefully, perturbation studies can be particularly illuminating in that they clearly implicate the selective agent causing the change in trait frequency distribution (i.e., the perturbing variable) (Endler 1986: 75-76).

This method of demonstration has been applied by Endler himself with striking success. Endler distributed roughly eighteen hundred guppies *Poecilia reticulata* with different-colored spots over ten ponds. He predicted that ponds containing certain predators would result in a directional change in color patterns such that they would "converge on the color patterns of natural populations of guppies living with the same predators" (Endler 1980: 78), whereas the distribution of color patterns among guppies in predator-free ponds would follow a different path (one which turned out to imply rather strong *sexual* selection for the same colors most likely to result in predation). After following the population for ten generations, the results were consistent with his predictions. A longer field experiment supported his findings.

Prospects for Human Psychology

Perturbation studies seem rather promising candidates for demonstrating selection for some human psychological trait, so long as we focus on a trait with sufficiently high heritability. A few practical problems remain, though. First, a human study on par with Endler's guppies would take at least a couple of centuries and would require a stringently controlled experimental setting for that time. Second, we would, for ethical reasons, need to find a perturbing variable that would be acceptable to the entire sample and their descendants (predation is unlikely to be a popular candidate).

2.2.7. Genetic Demography or Cohort Analysis (Method VII)

This method allows us to gain substantial understanding of lifetime fitness and life history trends, but it is very difficult to apply. Any successful application requires complete data on survival, fertility, fecundity, and mating success for a large number of individuals in every relevant trait group (Endler 1986: 81). In the simplest case, subjects will either have the trait or not have it (discrete variation), in which case we will only need to obtain data for those two groups. Whether selection is operating on the trait is best determined by comparison of lifetime reproductive success between groups (Clutton-Brock 1983: 463-464), with the assumption that the more successful trait group excels because of its possession of the trait in question. Measurement of reproductive success over an entire lifetime avoids making arbitrary distinctions in life stages that may not be recognized by nature itself and thus, causally irrelevant (Brown 1988: 439). As always, extrinsic environmental variables must be held constant between the two groups in order to separate the effects of biological inheritance from those of environmental factors (Lewontin 1998: 120).

Prospects for Human Psychology

As in previous methods, whether there is genetic variance in the human psychological trait, investigation will at least be possible in principle. The obstacles are mostly practical in nature. Unique to this method is the difficulty of obtaining anything near complete data on lifetime reproductive success for a robust sample of individuals. Lewontin (1998) has stated that

> to measure a one percent difference in reproductive rate in a species like *Homo sapiens*...would require the complete survivorship and reproductive histories, from birth, of an impractically large number of individuals in the contrasting [trait: CH] groups (of the order of 100,000), an enormously costly enterprise that has never been carried out for any human trait (120; Lewontin 1974: 240).

This nuisance is further complicated by seemingly insurmountable environmental intrusions familiar to those working in the human sciences.[3] There is no realistic possibility of controlling for environmental influences in groups this large and geographically disparate (Lewontin 1998: 120-121).

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[3] Lewontin *et al.* (1984) engage in an illuminating discussion of the serious difficulties posed by environmental variables in the study of identical twins, which are normally considered the *easy* cases for human genetics.

2.2.8. Comparison Among Age Classes or Life-History Stages (Method VIII)

Age class comparison is essentially the “lazy man’s” demographic analysis. The primary difference is that age class comparisons provide estimates of fitness differences based on trait frequency distributions across generations, where demographic analysis measures fitness differences directly (Endler 1986: 83).

Prospects for Human Psychology

See "Prospects" for Method VII.

2.2.9. Nonequilibrium Predictions of Changes in Trait Distributions (Method IX)

Predictions from Independently Estimated Fitness (IXa)

If we have estimates of either the strength of selection or fitness differences, we can use this knowledge to make predictions about what the trait frequency distributions will look like in subsequent generations. The actual distribution should correspond to what is implied by our estimates. Unlike all other methods discussed so far, *selection* is the null hypothesis for Method IX. If we test a prediction and find it to be false, then it must either be the case that “(1) the selection model is incorrect or inappropriate, or (2) there is no selection” (Endler 1986: 86).

Nonequilibrium Predictions about Fitness Differences (IXb)

This version of Method IX uses general facts about "anatomy, physiology, energetics, behavior, etc.," to predict either equilibrium distributions (see section 2.2.10 below) or changes in trait frequency distribution (Endler 1986: 89). The basic idea here is that types which are thought *a priori* to be able to outperform other types will in fact enjoy disproportionate representation in a population. If our predictions turn out false under this method, it signals either that (1) we were wrong about which types will be favored, or (2) there is no selection. One very useful aspect of version IXb is that, because we expect certain types to be favored for a particular *reason*, we are potentially able to see *why* selection is occurring when our *a priori* expectations turn out to be true (Endler 1986: 89).

A good example of the successful application of this method is Endler's (1980) guppy study mentioned above. He used knowledge about the color range of guppies and the visual capacities of predators to predict a directional change in the distribution of guppy color—a prediction which turned out to be true.

Prospects for Human Psychology

In order to use Method IXa on humans, we would need to obtain direct data on fitnesses in a population. This is a hard thing to do, as the problems we faced in sections 2.2.5-2.2.8 make clear. Reliable fitness estimates for humans would require an impracticably large sample size or a smaller long-term study of absurd duration.

There are two worries attached to Method IXb. First, our intuitions about what types of human behavior are likely to be outperformed by others may not correspond to what nature has in fact chosen to favor. Endler provides a nice example using willow trees. Willows have poor structural integrity, characterized by soft wood and a high tendency for branches to break. This fact about willows may suggest to us that they are poorly designed and thus unlikely to be favored by selection. What we would have missed in this case is that this "poor" design actually *increases* willow fitness: "more frequent limb loss (and the ability to sprout)" will result in willows having "a larger Malthusian parameter than those that do not fragment" (Endler 1986: 44). In the human case as well, we are always in danger of underestimating the value of a trait in the eyes of nature. From the perspective of functional design, we might expect bashfulness to have adverse effects on a man's ability to acquire mates, when in fact it may make him *more* attractive to women than a confident man who finds approaching women very easy. Whichever is the case, the truth is not knowable *a priori*. Poor *a priori* appraisal of trait utility can easily result in false positives as well. We may suspect a trait as being favored by selection for one reason, when in fact it is favored for another. As we will see in the remaining chapters, these sorts of worries arise repeatedly for evolutionary psychology.

Second, the high degree of behavioral plasticity in humans affords them a vast repertoire of responses for each ecological problem. Humans may not require something as drastic as favorable genetic mutation in order to outperform conspecifics in certain tasks relevant to fitness. Hence, someone may appear to be better "designed" when he just happened to be a little more clever than his fellows on that day or had learned a good trick. Plasticity has the potential to grossly mislead researchers who assume that different behavioral responses represent heritable variation in a trait.[4]

2.2.10. Equilibrium Predictions about Trait Frequency Distribution (Method X)

This method is similar to Methods IXa and IXb in that it uses selection (rather than none) as its null hypothesis. The first step in applying this method is to construct a model composed of four assumptions:

(1) *state space:* this is a description of the possible trait values and their distributions based on evidence gathered from the population being investigated.
(2) *strategy set:* the strategy set lists the organism's options for employing whichever trait value it has been blessed with.
(3) *variable(s) to be optimized:* the model predicts that optimization of this variable will maximize fitness.
(4) *constraint set*: a list of constraints on the *absolute* optimization of the variable to be optimized. The idea is that we are trying to predict an optimal state, "all things considered." (Endler 1986: 91; Kitcher 1985: 229; Oster and Wilson 1978: 295-307)

If the predictions of the model correspond to what is found in the natural population, this may suggest that the model's assumptions are true, and "nature can be regarded as reasonably well understood" (Oster and Wilson 1978: 294). In particular, what the researcher has come to understand is the cause(s) of the outcome of direct selection (Endler 1986: 96).

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[4] See the essays contained in Foster and Endler (1999) for a glimpse of the research problems associated with competing explanations of behavioral variation

Prospects for Human Psychology

Optimality analysis has certainly had its share of critics over the years, and not just when applied to human traits (e.g. Brandon and Rausher 1996; Lewontin 1979b; Lewontin 1987; Pierce and Ollason 1987). In this section, I'll try to focus on only those features of optimality modeling that make application to human psychology a rather daunting task. It should be noted, however, that any critique of optimality analysis *per se* will usually apply *a fortiori* to the study of humans.

The first problem we are likely to encounter will be constructing the state space for a particular psychological trait. Often it is assumed in the literature on the evolution of human psychology that human psychological traits have a bivalent structure, where individuals simply either have the trait or they don't. This assumption could lead to trouble. One worry is that many psychological traits (e.g. musical aptitude) exhibit variation that is highly non-discrete. It is not as if some people simply have musical talent, and the others simply don't. Rather, musical talent comes in *degrees*, where individuals have more talent than some but less talent than others. Assuming that the state space divides conveniently into two trait values (the haves and the have-nots) constrains the range of possible predictions of the model to an absurd degree and cannot be representative of the reality of human psychological life. The optimality analysis which assumes bivalence is likely to obscure the true optimum value, which normally lies somewhere between the maximum and minimum conceivable trait values.

A second worry for the application of optimality models to humans is located in the selection of an appropriate fitness proxy. An optimality model assumes that the variable being optimized is being optimized because optimization of that variable leads to fitness maximization. For example, we expect animals to optimize their foraging strategies or courtship behavior because optimal performance in these categories will maximize fitness. When we attempt to apply an optimality model to a particular population, we determine which of its behaviors fit into the optimizing category and see whether actual performance of the behavior conforms to what is predicted by our model. Suppose we wish to see whether courtship display for some species of bird is optimal. We look for which behaviors best fit into this category, and assess whether they match with the predictions of the model.

How do we know which behaviors qualify as "courtship display"? We *could* use our untutored intuitions and assume that whichever song and dance sequence typically precedes copulation is the mating display, but this research strategy runs a high risk of rolling roughshod over potential subtleties found in the mating system. Perhaps the dance and song sequence which precedes mating also precedes other forms of social interaction, like species recognition or food sharing. If we had been more careful in our assessment, we might have discovered upon closer inspection that only when the dance and song was accompanied by a conspicuous series of blinks and winks did it signal mating intentions.

Determining which behaviors fit into the optimizing category will undoubtedly be a much heftier task when it comes to humans. The subtleties and immensely complex structure that are characteristic of human social life would seem to make it virtually impenetrable to the kind of analysis we think ourselves capable of conducting on non-human species. For example, which human behaviors properly fit into the category of "courtship behavior"? Phone calls? Flowers? Online instant messaging? (The philosophical upshots of classification difficulties will be the focus of chapter 7).

A related problem derives from the supposition that humans possess unique kinds of adaptations (e.g., language or music) not found in other species. We commonly conduct optimality analyses by focusing on a category which is typically optimized across taxa and then finding which behavior falls under that category in the relevant species. If a human adaptation is in some novel ecological category, we have no comparative basis for believing that that category will be optimized. We cannot base our choice of category on past history of optimization in that category for other taxa, because the novel human category *has* no past history. We will have to provide some independent justification for why we would expect that behavior to maximize fitness, one that of necessity does not make reference to instances of optimization in the category for other species.

TABLE 1.1

	a	b	c	d	e	f	g
I						√	√
II						√	√
III						√	√
IV					√		
V					√		
VIa*	√		√		√		
VIb†			√		√		
VII			√		√		
VIII			√		√		
IXa					√		
IXb	√				√		
X	√				√		√

a) can provide evidence for why selection is occurring in the present
b) can provide evidence for why selection occurred in the past
c) direct demonstration of current selection
d) direct demonstration of past selection
e) can provide evidence for current selection
f) can provide evidence for past selection
g) cannot distinguish between past and current selection

* perturbation of trait frequency distribution
† perturbation of environment

2.2.11. Summary

Table 1.1 summarizes some of the important features of the methods discussed so far. Of particular importance are the findings that (1) no method is capable of directly demonstrating past selection; (2) no method is capable of providing direct evidence for why selection occurred in the past; and (3) none of the methods which can be used to study adaptations that may have been produced in the past is capable of indicating whether those adaptations *actually were* produced in the past or rather whether there is selection for those traits in the present. (Obviously, this is only a problem for extant species.)

This does not bode well for the study of the evolutionary history of human psychology. In addition, the veritable void of data which constitutes our knowledge of the genetics, development, and genotype-environment interaction makes theorizing about human psychological adaptations seem particularly academic, even from a philosopher's point of view. Without knowledge of whether the trait we're investigating has a genetic basis, our conclusions about the presence of selection for that trait cannot be reliable (cf. Grafen 1991). Of the twelve methods that can be used to detect natural selection, only *three* of them can be applied to instances of past selection (I, II, and III). But even when applied perfectly and with exceptional rigor, these three methods "can only suggest that certain traits are worthy of further study," because they do not provide any kind of direct evidence for selection, such as fitness differences or biological inheritance (Endler 1986: 62). The best these methods can do is suggest certain trait-environment correlations which may or may not indicate that a trait is or was adaptive.

2.3. The Design Inference Method

Does this mean the end to the search for human psychological adaptations? Never! Many proponents of the evolutionary psychology research program have defended a method for detecting adaptation which allows one to infer that some feature of an organism is an adaptation if that feature exhibits "functional" or "special" design, or "conformity to *a priori* design specifications" (Williams 1992: 40. See also Andrews *et al.* 2002; Cosmides and Tooby 1995; Pinker and Bloom 1990; Thornhill 1997; Tooby and Cosmides 1992; Tooby and Devore 1987). The article of faith for this method is, "if [a trait: CH] shows functional design, then neither drift, mutation nor incidental effect are responsible for the existence of the trait" (Thornhill 1997: 20). The design inference method (DIM) is also used to discern the function of a trait. Indeed, some have claimed that DIM is the "leading evidentiary standard for inferring function from the analysis of a trait's features in relation to its effects" (Andrews *et al.* 2002: 496).

DIM can be nicely divided into two different approaches to demonstrating adaptation. The first is the discovery of adaptation through recognition of the sheer complexity of the property as judged by a given researcher. The second is to demonstrate that a property would be good for performing a given function. I discuss both approaches in turn.

2.3.1. Recognizing Adaptation

This element of DIM is akin to many of the methods we discussed previously (I-V, VIb-IXa) in that it seeks merely to demonstrate *that* some feature of an organism is an adaptation and says nothing about the task to which it is adapted, i.e., its function. Recognizing adaptation begins with recognizing a naturally existing pattern in either behavior or morphology (Lauder 1996: 61). The symptoms of a naturally existing pattern include "specificity, proficiency, precision, efficiency, economy, reliability of development, complexity of design" (Andrews *et al.* 2002: 496), "extremely low-probability arrangements of matter" (Pinker and Bloom 1990: 455), or "organization"—"an improbable state in a contingent...universe" (Pittendrigh 1958: 395). Pattern recognition can come from either (1) the intrinsic properties of the trait or (2) the effects of the trait.

As far back as William Paley[5], people have inferred from the intrinsic properties of a trait that it was a product of design. A common analogy drawn in this context is between the properties of the trait and those of an artefact.[6] In Paley's classic formulation, we immediately infer from the precision and complexity of a watch that it is not the product of mere chance. By the same reasoning, the even greater complexity of the vertebrate eye should license the inference that the eye is an adaptation produced or "designed" by natural selection. Of course, Paley's (1836) argument was intended to provide evidence for *divine* design, not design by natural selection.

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[5] Even before Paley, in fact. See Ibn Rushd (Averroës), "On the Harmony of Religion and Philosophy."

[6] The scope and limits of this analogy are explored in penetrating detail in Lewens (2004).

A conspicuous pattern of effects may also license an inference of adaptation. For example, the eye would be fascinating enough if it was a merely super-complex and delicate structure with several finely integrated working parts. But the magic doesn't stop there. Eyes have the happy consequence of allowing organisms to represent their environment. DIM takes the fact that eyes everywhere have this effect to warrant an inference of adaptation. Notice that warrant for an inference of adaptation from a conspicuous pattern of effects should obtain even when we do not find the kind of precise and complex arrangement characteristic of the eye. We could even infer adaptation if the thing which regularly causes seeing was a mass of "undifferentiated fetal tissue" (Cosmides and Tooby 1995: 21).

One area of concern over whether DIM can reliably detect adaptation is that "[b]iological adaptations are built piecemeal [cite] and yet we must typically disassemble them to apply the argument from design in ways that do not mirror the pattern of construction" (Lauder 1996: 84). Thus, it might be true that we are quite talented with respect to recognizing "complexity," "specificity," and so forth, but when it comes to the historical order of assembly our intuitions aren't going to be of much use to us. And yet this order of assembly is critical to whether the structure under investigation is an adaptation, because it tells us whether the structure itself was the subject of direct selection, or whether its component parts were each the subject of different selective regime, or whether a combination of these scenarios is closer to the actual truth (Lauder 1990, 1996).

Even Williams, a strong proponent and in many ways philosophical godfather of DIM, stresses that this kind of analysis "would not proceed far without the use of historical data. The analysis would disclose much that is functionally inexplicable" (Williams 1966: 263-264). We might, for example, impute adaptive significance to the inversion of the vertebrate eye or to the elongation of the mammalian sperm duct, when these "low-probability arrangements of matter" merely reflect the combination of chance and developmental constraint—both of which are essential and still largely unappreciated components of the evolutionary process (Gould 2002; Gould and Lewontin 1979). Alternatively, that which suggests the designing hand of evolution to us may be nothing more than the chance fixation of certain alleles. If we cannot rule out genetic drift as an explanation for the prevalence of a trait either through fossil evidence or modeling, we cannot claim the trait is an adaptation, no matter how complex or functionally organized it might appear to us (Lande 1976).

In order to fully appreciate the scientific poverty of DIM's criteria for recognizing adaptation, which Andrews *et al.* (2002: 496) claim are "surely sufficient to demonstrate that a trait has been designed *by something* to perform a task," let us contrast those criteria with cohort analysis (Method VII, section 2.2.7). The comparison is apt because cohort analysis is also claimed to be sufficient for demonstrating adaptation, while remaining silent about function.

As mentioned above, cohort analysis is an enormous undertaking requiring complete reproductive data for a large number of individuals in order to yield reliable results (over 100,000 in each trait group). An analysis of the data collected provides us with information about actual fitness differences between types that bear one trait and types that bear another. The facts about fitness differences are observer-independent—they are simple calculations that would come out the same no matter who was doing them. Most importantly though, it is these facts about fitness differences that are the substance of adaptation. Without fitness differences, it matters not how complex or "improbably functional" a trait appears; unless there was some period in its history when it caused its bearers to outreproduce those without the trait, it is not an adaptation.

In contrast, judgments of complexity and special design are destined to be observer-dependent and thus highly subjective, as pointed out by Williams himself. Now there might be some "threshold of complexity" beyond which no one would deny that some feature is objectively complex. Paley seems to have that as much about the eye. But where this threshold lies, and which features of organisms are beyond it, is something that will have to be argued for, not merely assumed. Assumptions like these have a long tradition of being overturned, and Paley's own theological argument should serve as a reminder of that tradition.

Even if we *could* agree on when a feature is complex, though, there is no necessary connection between that complexity and a history of fitness benefits conferred upon organisms who possessed the feature. Complexity is neither a necessary nor a sufficient condition for qualifying as an adaptation; the two notions are entirely conceptually distinct. Complexity and other DIM heuristics for recognizing adaptation tell us nothing about fitness differences, which are precisely the kind of data we need to demonstrate adaptation. Now, it is certainly true that whether a trait has positive effects on fitness in the present has no necessary bearing on whether it did in the past and therefore no bearing on whether it was an adaptation produced by a past selection regime (section 2.1.2). But it nevertheless remains the case that at *some* point, fitness differences *must* come into the picture. Those differences, and not complexity, are constitutive of adaptation.

We have faith in the reliability of cohort analysis to demonstrate adaptation because it tests specifically for whether the conditions for adaptation are met. If we do not even regard the comparative method (sections 2.2.2 and 2.2.3) as so much as providing *some* direct evidence of adaptation because it does not address whether the necessary conditions are met, on what basis ought we to regard DIM as *demonstrating* adaptation? At least the comparative method demonstrates some kind of correlation which may be relevant to the (past or present) facts about selection. There is no theoretical foundation for thinking that DIM can even give us *that* much.

2.3.2. *Methods for Recognizing Function and Their Accompanying Problems*

There are, in general, three types of inferences DIM uses to determine function: (1) “conformity to *a priori* design specifications,” (2) conformity to an “adaptive target” (Tooby and Cosmides 1992: 72) (aka "Adaptive Thinking"), and (3) predictive success of models derived from hypotheses of function (aka "Reverse Engineering"). My criticisms here will be brief and are intended as a preview of objections developed in more detail in subsequent chapters.

Williams has stated that "[a]daptation is demonstrated by observed conformity to *a priori* design specifications" for a particular function, conformity which can be "intuitively comprehended" (Williams 1966: 260; Williams 1992: 41). He offers the human hand, which is "an adaptation for manipulation because it conforms in many ways to what an engineer would expect *a priori* of manipulative machinery" as an example of how we can infer function from this kind of conformity (Williams 1992). In a similar vein, Thornhill and Palmer have written that the function of the human thumb can be intuited with "a moment's reflection" (although apparently they did not have a moment, as they do not specify a particular function for the thumb) (Thornhill and Palmer 2000: 15).

The belief that one can specify *a priori* which design criteria must be met in order to perform a given function assumes that all forms capable of performing that function will have at least a few common structural features—viz., those that are relevant to performance. But this assumption is false. Nature selects for particular functions, and discriminates between forms only insofar as they are relevant to function. Therefore, we cannot assume that any structure capable of performing a particular function will possess certain nontrivial structural features relevant to performing that function.

To demonstrate the poverty of this assumption, Lauder compares the human hand—Williams' example of *a priori* specifiability—with the arms of octopi. Both are "capable of fine manipulative function," and yet could not be more distinct structurally (Lauder 1996: 74). If we assume that structures designed for manipulation will conform to design criteria *derived* from the model of the human hand, as Williams seems to have done, then we will necessarily miss any functionally analogous structures that fail to meet these criteria. This prospect makes for a rather unreliable method for identifying function. (We will see in chapters 3 and 4 how severe this problem becomes in the context of adaptations designed by mate preferences.)

The idea behind inferences of type (2) is that an organism's behavior will reflect the outcome of selection for a favorable response to a particular selection pressure known to affect the organism or to have affected the organism's ancestors. Because of their tendency to focus on adaptations produced in the distant past, evolutionary psychologists typically look for conformity to *ancestral* adaptive targets. For example, some psychologists think that early human males faced selection for ensuring paternity. The perceived ability of jealous behavior to conform to this adaptive target may license us to infer that the function of jealousy is to ensure paternity.

In order to demonstrate that some property of an organism exhibits conformity to some adaptive target, we need specific information for at least two categories: (1) the ancestral environment, and (2) performance relative to other phenotypes with respect to the alleged target. First, if we are going to demonstrate that some organismal feature comes favorably close to hitting an adaptive target, then we need to know which adaptive targets in fact needed to be hit during the period in which that feature (the alleged adaptation) was produced. For traits which reached fixation long ago (as is hypothesized for most human psychological adaptations), knowledge of adaptive targets is going to be very difficult to come by. As I argued briefly in section 2.2.3 (discussed more fully in chapter 4) , the data for humans is virtually nonexistent.

Second, assuming we know what adaptive targets there were, we need to know (a) whether this particular feature was even *capable* of hitting it, and (b) whether it was capable of hitting it better than other variants that existed at the time. There have been excellent attempts to demonstrate (a), for example in Kingsolver and Koehl's modeling of the performance of several variants of insect wings for both thermoregulation and aerodynamic effect (Kingsolver and Koehl 1985. See chapter 6 for discussion). While Kingsolver and Koehl's experiment is a triumphant example of performance modeling, they themselves are acutely sensitive to the fact that they have little to offer in the way of demonstrating whether some wing variants actually were better than others, because there is no fossil evidence of intermediate phenotypes between wingless insects and fully winged ones. The most their experiment shows is that, *if* certain variants had existed contemporaneously, some would have outperformed others.

Of course, in the case of humans we have nothing analogous to the data Kingsolver and Koehl offer us. We do not, for example, have any data which would suggest that jealousy facilitates ensuring paternity or that it did at any time in the past. No attempt has been made to model the relationship between jealousy and ensuring paternity in any remotely rigorous way, and it is difficult to see how such a project might get off the ground. Moreover, even if we could be reasonably sure that jealousy was an effective paternity-ensuring mechanism, we still would need to show that it outperformed other ancestral variants in order to even have *indirect* evidence that jealous behavior was selected for. In the literature, jealousy and other hypothesized adaptations are simply compared to their negation (a comparison which, by the way, assumes without argument that some variants *lacked* the trait in question) in a verbal model that has absolutely zero scientific significance.

Reverse engineering is perhaps the most popular method of deducing the function of a trait under DIM. In this case, we proceed by laying out coarse-grained *a priori* design requirements that would need to be met in order to successfully navigate a particular adaptive challenge (these are the model's predictions), and then test to see whether species members meet those requirements. The first step is to formulate a hypothesis regarding what *else* would be true of a species if it had a certain adaptation. The form of the hypothesis will usually look something like this: if the species has an adaptation *P* designed meet selective challenge *F*, then members of the species will exhibit phenotypic features *X, Y,* and *Z* that would have been a favorable response to *F* or are symptomatic of being capable of a favorable response to *F*. We then test for whether species members actually do exhibit features *X*, *Y*, and *Z*. If our results are positive, we can infer both that the species has adaptation *P* and that the function of *P* is to perform favorably in the face of selection pressure *F*.

All good hypotheses generate testable predictions, but not all true predictions provide evidence which is capable of distinguish the target hypothesis from alternative hypotheses. In order for an instance of predictive success to provide critical evidence for a hypothesis—evidence which sets it apart from others—the prediction must be one that, if true, could only be explained by the hypothesis which generated it. If hypothesis *H* yields a prediction *E* that turns out to be true, and if hypothesis *H*' could explain why *E* turned out to be true, then we cannot use the fact that *H* generated true prediction *E* as evidence for the truth of *H*, because *H*' could just as easily explain why *E* is true. The fact that *H*' may have been constructed *post hoc* would seem quite irrelevant to whether it truly explains *E*. True novel predictions certainly seem to have strong probative force, but the strength of that force still cannot trump that of alternative hypotheses. To think otherwise is to attribute to prediction a strange truth-conferring power that it obviously does not have.

If we apply these platitudes to instances where successful predictions have been offered as demonstrations of the function of an adaptation, we see that there is a very narrow range of predictions which, if true, can provide critical evidence for the hypothesis which generated them. Consider jealousy once again. Suppose we predict that if jealousy is an adaptation designed to ensure paternity, then people who are jealous will keep a close eye on their mate and attempt to control their reproductive activity. Could this prediction only be true if jealousy is an adaptation designed to ensure paternity? Obviously not. It could be true whether or not jealousy is an adaptation. For example, a man with low self-esteem might live in constant fear that his wife is going to leave him. His vigilance with respect to her whereabouts need not be explained by reference to his age-old psychological adaptation for paternity assurance. His behavior is consistent with the hypothesis that his own feelings about himself cause him to assume similar feelings towards him on the part of others.

The mere fact that in this case the prediction was derived from an adaptation hypothesis rather than the self-esteem hypothesis does not in any way imply that jealousy is an adaptation. No one expects hypotheses to generate predictions, which, if true, would rule out any *possible* alternative explanation. We do, however, expect predictions derived from a particular hypothesis to at least give us some reason to raise our degree of belief in the hypothesis relative to its negation. Predictions about trait frequency distributions which deviate from null models, for example, allow us to do this. We should increase our confidence that selection is taking place if we find that the distribution of traits in a population differs significantly from what it would be if there were no selection. By contrast, coarse-grained qualitative predictions which could easily be true if the hypothesis from which they are derived is false should not carry much weight if in fact they do turn out to be true.

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Conclusion

The point of the survey strategy pursued above was to suggest that the proper response to the difficulties raised for demonstrating human psychological adaptation is not, as proponents of DIM have done, to reject those methods which have on so many occasions led to triumphant advances in our understanding of evolutionary history, choosing instead to employ unsubstantiated and quite clearly unreliable techniques which do not even attempt to test for known indications of the operation of selection. What is needed is to focus our efforts on gathering evidence for things which we know will be true of a trait if it is an adaptation, and to do this with care and humility.

We began this chapter by going through the conceptual components of adaptation and natural selection in some detail. Following that, we were given a glimpse of how aspects of these concepts have been used to formulate methods for demonstrating whether some trait is the direct result of natural selection. Specifically, we saw that whether researchers take a method to be reliable for demonstrating adaptation depends on whether that method tests for what must be or must have been true of some property if that property is an adaptation.

For each method discussed, there were any number of problems which awaited researchers attempting to use that method to demonstrate the direct influence of natural selection on an aspect of human psychology. The specific problems vary depending upon which method one uses, but we can extract a couple of general unifying themes which cut across the individual methods. The first problem is our overall ignorance of the genetics and developmental patterns of human psychological traits. Many of the methods require specific information about changes in gene frequencies, and nearly all of them require knowledge of the conditions under which a trait develops. Even if we had a comprehensive understanding of these dynamics however, the inaccessibility of these data for the relevant population (Pleistocene hominins) would render our understanding ineffective for learning about the history of selection for the traits in question. This represents the second general problem for application of the standard methods. The third problem is the ethical obstacles involved in pursuing research via these methods in cases where the necessary data is, in principle, attainable. Standard features of experimental and observational studies of natural selection such as control of environmental factors and phenotypic manipulation will simply not be within the scope of what is morally permissible when it comes to human subjects. I will not have much to say about this last problem in the chapters to follow. The former two, however, will occupy a central role in my critique. Their presence will be felt in a number of problem areas in evolutionary psychology.

In addition to these general trends, we were also introduced to a number of specific concerns regarding the probability of evolutionary psychologists' preferred methods to lead to reliable conclusions. A few responses were hinted at above which will be given more detailed treatment in subsequent discussion. One important theme which emerged from these responses was that where reliability is concerned, DIM fails precisely where the traditional methods used by evolutionary biologists succeed—namely, in gathering the kind of evidence one would need in order to rule out alternative hypotheses. As we shall come to appreciate, nearly all the failings of evolutionary psychological research can be viewed as variations on this theme.

3. Selection in Relation to Sex

Introduction

Two aspects of human life in particular have featured prominently in evolutionary psychology: (1) the link between one's biological sex and one's behavior, and (2) the dynamics of intergender relations, specifically in the context of what evolutionary psychologists refer to as "human mating," which encompasses (for reasons described below) all sorts of behavior which one might not immediately associate with mating (e.g., going to work, getting a good job, being kind to others and their children, and a variety of other commonplace human activities).

Most of the research on sexual dimorphism and mating conducted on nonhumans has appealed to the family of theories which make up the field of sexual selection. Similarly, evolutionary psychologists have found sexual selection theories to be felicitous in accounting for ostensibly widespread gendered behaviors among humans. Theories in the field of sexual selection, it is supposed, shed light upon human sex differences and the upshots of those differences for reproduction.

The general strategy pursued in this chapter will resemble that of chapter 2 in that the weaknesses of evolutionary psychology in this area are exposed by way of comparison with work done by researchers outside of human evolutionary psychology who work on similar problems. In addition to comparison with other research, a look at the important models in sexual selection theory reveals a variety of confusions among evolutionary psychologists which will themselves prove instructive for understanding some of evolutionary psychology's deeper problems.

3.1. What Sexual Selection Is

Although the terms "natural selection" and "sexual selection" are typically used in different contexts, the dynamics of these processes are one and the same. In both "sexual selection" and "natural selection," superior performance in some category (e.g. attractiveness to females or survival, respectively) causes an increase in reproductive success—the currency of selection. The particulars of each instance of selection do not change the underlying mechanics. The fact that a trait which females find attractive increases reproductive success via a rather direct relation to mating and another (e.g., strength) increases reproductive success somewhat less directly (through longevity) is immaterial; decoupled from its effects on reproductive success, neither trait is of any selective value. Nature does not pay attention to *how* an organism increases its reproductive success, only *whether* it increases its reproductive success. Part of what we mean when we say that there has been "selection for" a particular trait *P* is that the prevalence of *P* has increased in a given population. When selection is the dominant influence, the manner in which *P*'s prevalence increased will be the same no matter what *P* is and no matter to which aspect of the organism's performance *P* is related: *Necessarily,* P *caused an increase in reproductive success for organisms that possessed* P.

Keeping in mind that there is no particular kind of selection that is uniquely sexual, let us now discuss instances of selection to which the term "sexual selection" refers. Rather than describing a special process distinct from natural selection, "sexual selection" is (or at least ought to be) used in reference to standard natural selection, restricted to a specific set of selection pressures—in particular, the set composed of pressures resulting from intrasexual competition over mates (Andersson 1994: 5-9; Clutton-Brock 2004: 26). Whenever there is competition for mates, those members of the population who are able to outperform others will tend to have higher reproductive success than the competitors they have bested. If the superior performance of these more successful individuals is due to heritable differences between them and those less successful at reproducing, selection for the trait(s) which caused the differences in reproductive success can occur. This is Darwin's "selection in relation to sex."

> ***Sexual Selection*:** differences in reproductive success, caused by competition over mates, and related to the expression of the trait (Andersson 1986: 7)

While this much is agreed upon by most workers studying sexual selection, exactly *why* competition over mates occurs remains a subject of considerable debate. Below I make an attempt to outline some of the principal theories aimed at explaining competition over mates. My intention here is to give a glimpse of some of the relevant theory, not a survey of the entire field. There are surely important contributions to the literature which space and scope have prevented me from mentioning.

Parental Investment

The *locus classicus* for explaining why competition over mates arises is an essay written by Robert Trivers in 1972 in which he argued that the "relative parental investment of the sexes in their young is the key variable controlling the operation of sexual selection" (Trivers 1972: 92). On Trivers' view, members of the sex which invests less in the rearing of progeny will compete for reproductive access to members of the more heavily investing sex. The extent to which a parent invests in the survival of an individual offspring limits that parent's ability to invest in the production and maintenance of other offspring. When one sex invests more heavily into offspring generally, the ability of its members to produce and maintain additional offspring is diminished relative to the lesser investing sex, which in turn constrains the reproductive opportunities of the lesser investing sex. Consequently, members of the lesser investing sex

> will compete among themselves to breed with members of the sex investing more, since an individual of the former can increase its reproductive success by investing successively in the offspring of several members of the limiting sex (Trivers 1972: 56)

In addition, the sex which invests more heavily will tend to be discriminate when granting access to its reproductive capacities, what is typically called "choosiness."

The Operational Sex Ratio

Clutton-Brock and Parker (1992) suggested that Trivers underestimated the number of factors determining the direction of competition and choosiness. They argued that parental investment was but one factor influencing a more fundamental cause of competition—viz., the *operational sex ratio* (OSR), the ratio of males available for mating to females available for mating (Emlen and Oring 1977).

Clutton-Brock and Parker's (1992) model is based on the relationship between scarcity and competition. In general, the word "scarcity" connotes a dearth of some kind. In the economic sense, "scarcity" describes the unavailability of a particular resource, not in *real* terms, but rather with respect to the demand for that resource. We can think of a population of organisms as a market racked by economic scarcity. Workers who study sexual selection are concerned primarily with scarcity of mates. Since there is enormous pressure upon organisms to increase their reproductive success, the demand for mates will always be high. When demand for mates exceeds the supply of mates—i.e., when the OSR is biased in one direction—scarcity has occurred (Clutton-Brock 1983: 461). Scarcity, in turn, gives rise to competition. Because there is not enough of the desired resource to simultaneously satisfy all demand, individual consumers must try to outperform one another in order to ensure that they will be able to acquire a portion of the vanishing supply. The more scarce the resource—the more biased the OSR is towards a particular sex—the more intense the competition is likely to be between members of the biased sex. Correspondingly, choosiness in the scarce sex will also increase. (Clutton-Brock and Parker 1992; Gowaty 2004).

The important point of departure between Clutton-Brock and Parker (1992) and Trivers (1972) is with respect to how important parental investment is in determining the OSR (Clutton-Brock and Parker 1992: 453). Clutton-Brock and Parker argued that, while parental investment may often be *the* dominant factor determining the OSR, there are forces other than parental investment which, where significant, can override the effect of parental investment on an individual's reproductive rate. Perhaps surprisingly, this suggestion is actually consistent with Trivers, who was only interested in parental investment to the extent that it was a factor which limited an individual's reproductive rate. He just happened to be wrong in thinking that it is “the only relevant variable” (Trivers 1972: 56).

Costs of Breeding

In contrast to Clutton-Brock and Parker's supply-and-demand argument, Kokko and Monaghan (2001) and Kokko and Johnstone (2002) argue that, on a sufficiently robust interpretation of the concept of "parental investment," Trivers' (1972) explanation for what causes competition and choosiness is correct. If we understand parental investment to be "the mortality costs of breeding" (Kokko and Johnstone 2002: 326), it can be shown that parental investment is the fundamental determinant of competition and choosiness in a population, rather than the OSR. For example, imagine a species where the OSR is heavily biased towards males. In Clutton-Brock and Parker's (1992) supply-and-demand model, this implies that the surplus of males will compete with each other for access to females, with whom they will mate indiscriminately. On Kokko's *et al.* view, however, that will only be true in the special case where the only difference between the sexes is their relative representation in the mating pool (Kokko and Johnstone 2002: 327). In species where the OSR is heavily male-biased but where males experience sufficiently high mortality costs to breeding (e.g., difficulty finding mates or severe energy drain from copulation), these costs can override the tendency of a male-biased OSR to, *ceteris paribus*, promote indiscriminate mating preferences among males, causing them to be choosy. A male who faces high copulatory costs may reserve his copulation efforts for just the right female (understood in terms of whichever mate qualities are most preferred in the focal population), even in cases where receptive males outnumber receptive females (Kokko and Monaghan 2001: 163).

Dynamic Individual Response

The model developed by Patricia Gowaty and Stephen Hubbell over a series of publications represents a significant departure from those outlined above, which they call "classical sexual selection hypotheses." Whereas the models of Trivers, Clutton-Brock and Parker, and Kokko *et al.* emphasize the importance of costs of parental investment incurred in virtue of being a member of a particular sex, Gowaty and Hubbell's model focuses on the mating costs of being a particular *individual*, regardless of sex. Rather than nature selecting for (e.g.) competitiveness in one sex and choosiness in the other, what should be selected for is the individual's ability to exhibit *adaptive* choosy or *adaptive* indiscriminate behavior in response to "changing social and life-history situations" (Gowaty and Hubbell 2005: 17 (draft)). Thus, in contrast to classical hypotheses which view sex roles as fixed, Gowaty and Hubbell's model predicts that sex roles will be flexible in real time, depending on what constitutes an adaptive response in the contemporary environment (*ibid.*: 32).

The preceding survey is intended to illustrate the range of variation in theories of what drives sexual selection, which is in fact even more substantial than I have been able to portray (cf. Hubbell and Johnson 1987; Sutherland 1985)). In addition, none of the critical variables for these models (parental investment, effects of the OSR, and adaptive flexibility) have received a significant amount of empirical support (Clutton-Brock 1991; Cunningham and Birkhead 1998). Suffice it to say that there is at this point no consensus on what causes sexual selection.[1]

3.1.1. *Evolutionary Psychology and the Theory of Sexual Selection*

The impression one gets from reading literature on the evolutionary psychology of human mating is that, in 1972, Robert Trivers proved deductively that the difference in magnitude of parental investment between males and females is the chief causal determinant of sex differences. Thus, we can read that "Trivers

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[1] *Pace* Kappeler and van Schaik (2004: 4), whose assertion that "[i]n the end, variation in sex roles was convincingly linked to sex differences in potential reproductive rates" is contradicted multiple times in their own edited volume.

realized that, from this difference in 'parental investment,' all else follows" (Miller 2000b: 85), that he "provided the basic theory of what governs the extent of...sexual selection (Thornhill and Palmer 2000: 33).

Evolutionary psychologists focusing on sexual selection appear to have read Trivers' paper correctly. Unfortunately, this is not sufficient for understanding the dynamics of sexual selection. One problem with the exclusive focus on Trivers' (1972) notion of initial parental investment is that a lot of theoretical work has been done in this area in the past three decades, much of which is at odds with Trivers' thesis. Some of the other contributions to the theoretical literature have been reviewed above. These theories, which are either inconsistent with or significant refinements of Trivers' original framework, scarcely receive a mention from evolutionary psychologists. In order to avoid the appearance of preferential attention to Trivers' model for ideological reasons, it needs to be acknowledged that there are a variety of interesting and rich theoretical perspectives which, insofar as they are internally consistent and are framed with biologically plausible assumptions, deserve as much attention as that of Trivers' (1972) ideas.

Plausible assumptions present another problem for the exclusive focus on Trivers (1972). One major assumption built in to Trivers' notion of parental investment and the descendants of that notion is the belief that differences in gamete size (what is called *anisogamy*) are what give rise to differences in parental investment and competition for mates. This assumption, which is explicit in Trivers' (1972) paper, receives slavish and triumphant repetition in the service of human evolutionary psychology. The story is that men have an endless supply of tiny, metabolically inexpensive sperm which they can deploy to inseminate females virtually cost-free and then immediately return to the mating pool. Women, on the other hand, have a short supply of large, metabolically draining eggs which, if fertilized, require a minimum of nine months of high-cost physical investment which "forecloses other mating opportunities" (Buss 2003: 19)

> The great initial parental investment of women makes them a valuable, but limited, resource. Gestating, bearing, nursing, nurturing, and protecting a child are exceptional reproductive resources that cannot be allocated indiscriminately. Nor can one woman dispense them to many men (*ibid.*: 20).

As a result of these differences in initial parental investment, nature selected for "women who were highly selective about their mates." The genes of these women thrived, whereas "[a]ncestral women suffered severe costs if they were indiscriminate—they experienced lower reproductive success, and fewer of their children survived to reproductive age" (*ibid.*: 20). This situation resulted in an ESS equilibrium in which men maximize their fitness by providing little or no parental care, instead directing their resources towards acquiring additional mating partners, while women maximize their fitness by investing their energy and resources into rearing children. If there is selection against male desertion of mating partners (if, for example, women refuse to grant sexual access to a man who does not appear willing to commit),

> it is more likely that a mixed strategy will be the optimal male course—to help a single female raise young, while not passing up opportunities to mate with other females

> whom he will not aid (Trivers 1972: 62),

which explains why men are more likely than women to have extramarital affairs or, “extra-pair copulations.” Again, this is all supposed to *follow* from the assumption of anisogamy.

But the assumption that sex differences in parental investment follow from sex differences in gamete size is premature. There is a prior dynamic—viz., partitioning of energy expenditure—which determines how much parental investment an individual can or should engage in. Suppose that males have a fixed amount of energy which they can divide between male-male competition (call this "prezygotic investment"), on the one hand, and investment in gametes or offspring (call this "postzygotic investment"), on the other. Since competition for mates comes before parental investment (i.e., prezygotic investment comes before postzygotic investment), how much energy an individual male devotes to competition will determine how much energy he has left for parental investment. This indicates that it is not anisogamy itself that is responsible for differences in parental investment. Rather, it is the way in which a male chooses to divide his energy expenditure that determines his level of parental investment. In certain scenarios he may devote most of his energy to male-male competition, leaving little for parental investment. In other scenarios he may devote a smaller portion of his energy to competition, directing a significant portion to parental investment. As pointed out by Shuster and Wade (2003: 195), "[i]n such cases, postzygotic investment by males could equal or exceed that of females."

Contrary to Trivers' model, then, low or negligible levels of male parental care do not follow as a matter of necessity. Importantly, we can expect male parental care to evolve when the indirect fitness benefits (i.e., benefits to reproductive success of offspring) outweigh the direct fitness benefits of the highly competitive inseminate-and-desert strategy (Shuster and Wade 2003: 248). Thus it does not follow as a matter of logic that males will evolve to exhibit low parental investment owing to relative gamete size. It might be that men have evolved to engage in high levels of parental investment and low levels of male-male competition.[2] Whichever is the case depends on the historical facts about which strategy would have secured more fitness benefits. The fact that men provide far less parental care than women in the modern world does not confirm Trivers' theory.

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At the beginning of the this section, we mentioned that sexual selection was driven by competition for mates, and that the most reproductively successful phenotypes will be selected. Now, the precise form(s) which competition takes will vary depending on the population as well as the sex, and each form of competition can be thought of as a separate selection pressure. For example, if there is pressure on males in deer populationsw to defeat other males in combat, selection may favor larger antlers. In bird populations females may prefer larger nests, in which case selection may favor males who are able to build the most impressive structures. Even when males (females) in two populations face

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[2] Alternatively, the population might contain a stable polymorphism where both low and high investment strategies are employed in different circumstances, as suggested by Kitcher (1985).

similar selection pressures, however, the phenotypic effects may be radically different. Suppose we place half of the deer from Deer Island onto Island *Y* and half of them onto Island *Z*. Males on Island *Y* may be under pressure to defeat other males in combat, causing an increase in average body size. Males on Island *Z* may also face pressure to win male-male competitions, only here selection might favor increased antler size without a concomitant increase in average body size. The fact that *Y*-males and *Z*-males come from the same original population is not enough to ensure that their future development will be the same. The outcome of selection will depend on, *inter alia*, which variants arise in the new respective populations.

Now although each token event of sexual selection is its own unique process, the phenotypic effects of sexual selection can be roughly divided into three functional categories, first outlined by Darwin (1871). The first category is traits selected for for use in same-sex contests. Here we see the evolution of things like increased size and weaponry which can give animals an advantage over competitors in direct contests (fights), as well as improvements in sensory and locomotive capacities, which can assist animals in mating systems in which mating success depends heavily upon early and swift location of mates (so-called "scrambles") (Andersson 1994: 12). The second category of traits is those which have arisen as a result of selection operating upon "sex differences in feeding behaviour and habitat use" (Clutton-Brock 2004: 29. See also Shine 1989). These traits are typically only indirectly related to reproduction, and may in many cases only be weakly associated with sex roles (Darwin 1871). Finally, there are traits which are the products of mate choice.

3.2. The Study of Mate Choice and Mate Preference

> *The inherent plausibility of the hypothesis that mate choice is a common feature of the sexual behaviour of animals should make us especially cautious and critical in our evaluation of attempts to demonstrate its occurrence in nature* (Halliday 1983: 3).

Darwin's suggestion that the female preference for particular males has led to many of the life-threateningly exaggerated behavioral and morphological traits possessed by males was not one that he would live to see gain wide acceptance. And although an abundance of population genetics models have confirmed Darwin's suspicion (beginning with Kirkpatrick 1982; Lande 1981; O'Donald 1962), the relationship of these kinds of traits to mate preferences and mate choice remains one of the most controversial subjects in evolutionary biology (Maynard Smith 1991: 146).

Most theorists follow Halliday's (1983: 3) definition of mate choice: *any pattern of behaviour, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than with others* (see also Maynard Smith 1987: 11; O'Donald 1983: 55). Accordingly, a mate *preference* can be defined as the *disposition* to mate with certain members of the opposite sex, whether that disposition is manifested through mate choice. It is mate preferences which cause mate choice (Heisler *et al.* 1987: 100; Jennions and Petrie 1997: 286).

3.2.1. Observing Choice[3]

The fact that "choice" is operationally defined makes it relatively easy to know the conditions under which we can infer that some bit of behavior qualifies as an instance of choice. In the case of female choice, the first requirement for detection is that males in the population differ with respect to at least one property. For example, if we wish to demonstrate that females choose a male because he has a red spot, then it must be the case that some males in the population do not have red spots. Second, we must look for evidence of non-random mating in relation to the male phenotypic trait thought to be involved in choice. If red spots are relevant to female choice, it is necessary that females mate with spotted males in a manner that deviates significantly from chance. There is no canonical method for demonstrating non-random mating, but the most common form is the simultaneous "two-stimulus" test, wherein females are presented with two males with contrasting trait values and allowed to pick one or the other (Wagner 1998: 1032). If females show a bias towards spotted males over spotless males, this may support the hypothesis that spots are involved in female choice. Alternatively, evidence can be gained by observing whether the mating success of males with red spots is disproportionate to the

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[3] I will be conducting the discussion of choice in terms of female choice for males. This should not be taken to imply that the theoretical considerations with respect to male choice for females are different; they are not.

frequency distribution of red spots in the population (Cooke 1983). If spotted males make up 10% of the population but take part in more than 10% of the mating, we might attribute this asymmetry to female choice. This method does not afford as clear a result as the two-stimulus test for the reason that the disproportionality may be due to a variety of other factors, such as male mating effort or location. If spotted males tend to devote more effort than spotless males to acquiring females, a population in which females mate indiscriminately may still exhibit a mating success bias towards spotted males. Demonstrating nonrandom mating requires that we control for these kinds of externalities.

The third condition we need to fulfill is to determine whether the pattern of female choice associated with red spots is a result of females choosing males because of their spot or instead because of a trait which is phenotypically correlated with red spots (Cooke 1983: 288; Heisler *et al.* 1987: 100-101). It might be the case that females appear to be choosing spotted males when really they are choosing males with a particular kind of territory, which spotted males just happen to occupy. In order to show that females choose spotted males because of their spots, we need to control for territory quality. For instance, in a now-classic study on female choice in widowbirds, Malte Andersson was able demonstrate that females choose males based on tail length rather than territory quality by placing males of different tail lengths in similar territory quality (Andersson 1982: 818-819). Alternatively, we could employ statistical tools which allow us to simultaneously evaluate the causal influence of multiple factors on the pattern of female choice (see Arnold and Wade 1984; Endler 1986).

3.2.2. Problems with Inferring Preference from Choice

These measures are necessary for any successful demonstration of female choice for a particular male trait. Because preference is taken to be the primary causal factor involved in female choice (see Wagner 1998 for additional factors), demonstration of female choice is generally taken to be sufficient to establish that females have a genuine preference for the male trait on which they base their mate choices (Heisler *et al.* 1987; Jennions and Petrie 1997; Wagner 1998). Whether this is a reliable method of detecting preference is a subject of ongoing debate (Wagner 1998), but nevertheless it is the most widely used—and perhaps the *only*—method of detecting female preference.

Recent contributions to the literature (e.g., Jennions and Petrie 1997) have stressed the importance of distinguishing between *preference functions*, which represent the order in which a female ranks alternative mate types, and *choosiness*, "the effort an individual is prepared to invest in mate assessment." The combined influence of each of these components determines a female's *sampling strategy,* the set of rules which she employs when searching for a mate. For example, suppose that Shela, a female newt, prefers to mate with the male which has the most spots. In order to find this male she must sample each male in the population. But this will only be possible if she is sufficiently choosy, i.e., if she is willing to devote the effort required to find her most preferred male. Most likely she will be unwilling to do this (the costs in time and energy would forbid it), and so she will have to employ some kind of decision procedure which allows her to balance the strength of her preferences with the effort she is willing to invest into satisfying them. A variety of such decision procedures, or "sampling tactics," have been proposed (see Jennions and Petrie 1997: 310 for review) and which, if any, of these a female employs will have to be determined empirically. Now obviously, the requirements for demonstrating that a female uses a particular sampling tactic will vary depending on the tactic. In general, however, it will be necessary to observe females' responses to a broad range of males and under a variety of search conditions.

The importance of understanding a female's preference function and choosiness for determining her mate preferences can be seen more clearly if we examine them in the context of the two-stimulus test mentioned above. If females in a population have, say, similar preference functions but differ in their degree of choosiness, the two-stimulus test is likely to obscure important and potentially evolutionarily relevant subtleties which more careful and fine-grained manipulation might have revealed. Consider two females: *A* (who prefers *X*-males to *Y*-males and has a high degree of choosiness) and *B* (who also prefers *X*-males to *Y*-males but has a low degree of choosiness). The use of a simultaneous two-stimulus test on *A* and *B* may sure enough reveal their preference for *X*-males, but it will obscure the fact that *A* would have invested lots of resources into mating with an *X*-male, whereas *B* may only invest as much as is required by the two-stimulus test (i.e., nearly nothing). In another, more demanding setting in which *B* encountered a *Y*-male before an *X*-male, she may have chosen to mate with the *Y*-male. The costs which females incur when exercising mate choice have been shown in several models to have important effects on the direction of evolution of both the female preference itself as well as the male trait being chosen (Iwasa *et al.* 1991; Pomiankowski 1987b; Pomiankowski and Iwasa 1998; Pomiankowski *et al.* 1991), and to use this kind of test to infer the nature of *A* and *B*'s preferences would have led to serious errors, the implications of which go beyond mere misrepresentation of the form of female preferences. In order to avoid problems such as these, researchers must be sensitive to potential variation in both preference function and choosiness (Wagner 1998: 1036).

3.2.3. *The Study of Human Mate Preferences*

The largest and most prominent study of human mate choice is undoubtedly the one conducted by evolutionary psychologist David Buss. Published in 1989, this study contains data on 10,047 individuals in 37 different cultures located in 33 countries. Buss's strategy for detecting mate preferences was to administer a survey which asked people to provide information about a number of personal features which Buss believes have been shown to be theoretically important to mate choice. The information requested included:

- biographical data on age, sex, religion, marital status, number of brothers, and number of sisters
- age at which respondent preferred to marry, preferred age difference between respondent and spouse, whether the respondent preferred to be older than spouse, and desired number of children
- the importance of each of 18 different characteristics in potential mates, rated on a scale of "0" ("irrelevant") to "3" ("indispensable"). These included

  - ✓ "dependable character"
  - ✓ "sociability"
  - ✓ "chastity: no previous sexual intercourse"
  - ✓ "intelligence"
  - ✓ "good financial prospect"
  - ✓ "good looks"
  - ✓ "ambition and industriousness"
- a ranking of the relative desirability of 13 different characteristics in a potential mate ("1" being the most desirable), including
  - ✓ "good earning capacity"
  - ✓ "physically attractive" (Buss 1989)

Without going into the probative value of the results of a survey for establishing truths about evolutionary history, let's look at how useful this method might be in meeting the goals of detecting human mate preferences relative to the canonical methods applied to nonhumans.

First it should be noted that, whereas observing mate choices is essential in determining the mate preferences of nonhumans, *actual choice* between potential mates plays absolutely no role in Buss's study of mate preferences. It may seem *prima facie* that since we can simply *ask* humans what their mate preferences are it is unnecessary to use a proxy method such as patterns of mate choice on which we then base our inferences about human mate preferences. Such a possibility would certainly be appealing to researchers who work with nonhumans and who are sensitive to some of the difficulties involved in inferring psychological dispositions from patterns of behavior. If subjects' self-reports can give us direct access to their actual preferences, there would be no need to invest the significant quantities of time and resources that go into observing mate choice, not to mention the epistemological worries regarding whether some nonrandom pattern of choice does indeed indicate a deeper psychological preference.

The guiding principle of Buss's survey is that self-reports about mate preferences are reliable indicators of evolved mate preferences. There are at least two reasons to wonder whether this principle is well-founded. Let us start with a preliminary distinction between *having a preference for* a particular kind of mate, and *being attracted to* a particular kind of mate. Within studies of nonhuman mate choice behavior, this distinction does not exist. We infer that some animal has a preference for a particular kind of mate from their being attracted to a particular kind of mate. If done correctly, taking into account the possibility of extreme sensitivities of mate choice to context (as represented by the problems associated with two-stimulus tests), there is good reason to think that basing our inferences about nonhuman mate preferences on their mate choices will yield reliable conclusions.

Within studies of *human* mate choice, however, it is easy to see how important the distinction between preference and attraction is likely to become. At best, Buss' survey is capable of capturing respondents' *beliefs* about the kinds of mates they prefer in theory. However, when respondents are let loose into the actual mating pool, we may find that the mates to which they are actually *attracted* differ significantly from the mates they purport to prefer. We are then faced with the difficult choice of which piece of behavior—their attractions or their purported preferences—we are warranted in accepting as evidence of their *actual* mate preferences.

Whichever piece of behavior we turn out to be warranted in accepting as evidence of actual mate preferences, the upshot of the distinction between purported preferences and attractions is that we cannot simply unquestioningly accept respondents' reports about the kinds of mates they prefer. If evolutionary psychologists want to take self-reports as reliable evidence of human mate preferences, they must provide us with some explanation as to why they ignore actual human mate choices as evidence of human mate preferences. It should give us pause when that which is seen as *essential* to detecting mate preferences among the rest of the evolutionary biological community is viewed for the most part as *irrelevant* by evolutionary psychologists. The fact that humans are, unlike nonhumans, capable of offering verbal reports of their psychological dispositions does not underwrite the use of those reports as a reliable method for detecting mate preferences. As we will see in later sections (esp. chapter 4), this kind of polarization between evolutionary psychologists and other researchers working in the field of evolutionary history is all too common.

Buss is sensitive to the potential disconnect between "expressed desires" and "actual mating behavior" and acknowledges that

> there are many reasons why we would not expect a one-to-one correspondence between mating desires and behavior: (1) you can't always get what you want; (2) parents and other kin exert an influence on actual mating decision, regardless of the individuals' desires; (3) desirable

> mates are in rare supply compared with the large numbers that desire them, rendering only those high in mate value able to achieve their desires; and so on (Buss 1997: 192).

"Despite these real conceptual complexities," he assures us, "findings on desires in a mates [i.e., the results of Buss' study: CH] do a good job of predicting many different facets of mating behavior" (Buss 1997: 192-193). In support of this he cites studies which have shown, among other things, that "actual marriages confirm the universality of the age difference between brides and grooms" represented by the responses to his survey, and "that the single best predictor of the occupational status of the man a woman marries is her physical attractiveness" (192). Should the apparent consistencies between purported preferences or "desires" and "actual mating behavior" then allay any fears we might have that peoples' self-reports may not accurately reflect evolved psychological dispositions to mate with particular kinds of conspecfics?

There are two stark problems with this response. First, Buss does not even *attempt* to show why the "strong links between mating desires and actual mating behavior" exist independently of the potentially confounding variables he mentions in the excerpted portion above. For example, what reason do we have to think that the "strong links" between women's expressed desires for older men and the "universality of the age difference between brides and grooms" is explained by anything other than family influence (confounding variable (2) above)? Buss offers none.

Indeed, we have reasons to believe that family influence does play a strong role in traditional societies, and that, for example, women's husbands and men's wives may more accurately reflect their parents' mate preferences than their own. These sorts of family structures will often require that one consider a variety of extrinsic factors such as how well a potential mate is likely to get along with one's other family members, in addition to how a potential mate coheres with one's mate preferences. The end product (i.e., the actual mate) will be the result of a negotiation between what one desires in a mate (i.e., the kinds of things in which Buss is interested) and what kind of a mate would be good to have given one's particular familial situation. Whomever this turns out to be may be radically different from the individual one would have chosen independently of externalities.

Second, there is certainly cause to wonder whether the kinds of relationships we find among contemporary humans should properly be categorized as "actual mating behavior" caused by evolved mate preferences, rather than, say, peoples' attempts to realize their beliefs about what kinds of qualities might be *good for a mate to have*.[4] It's certainly plausible to think that much of what people believe to be "desirable" in a mate is the result of the internalization of dominant cultural or familial norms. This applies to physical characteristics as well as personality. The effect of such norms on peoples' beliefs about what constitutes a good mate will carry over to their actual mate choices (if we believe that mate preferences are what, in part, determine mate choices). So there *is* support for the position that people's actual mating behavior might not be the result of their actual mate preferences. Moreover, the support for this position does not derive

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[4] See Vickers and Kitcher (2003) for related comments.

from some outlandish skeptical possibility. Rather, it appeals to distinct and commonsense principles which are treated with the appropriate degree of care outside of evolutionary psychology.

What would *really* be useful is if we could find some kind of pattern of women making mate choices in a manner *inconsistent* with their "expressed desires." Such a result would go far beyond anything Buss's study has done in terms of uncovering deep-rooted psychological dispositions, for it would to some extent allow us to distinguish between peoples' *beliefs* about their preferences and *actual* preferences of the variety sought by those working with nonhumans.[5]

The serious concerns over the probative value of peoples' beliefs about their mate preferences cannot but erode our confidence in the ability of Buss's method to uncover human psychological dispositions to mate with certain members of the opposite sex (see Halliday's definition above). Just to fan the flames a bit, we should also consider the obvious fact that by limiting respondents' options in terms of which mate qualities they believe to be desirable to a list of less than 30 features chosen by Buss, his survey has absolutely no way of detecting preferences which do not appear on the list. This has important implications both for uncovering preferences themselves as well as for explaining *why* people have the preferences they have. Each of the possibly preferable qualities proffered to respondents can be (and *have* been) easily pressed into the service of one adaptationist explanation or another. In contrast, there would be

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[5] For problems related to self-report data, see Shields and Steinke (2003).

no way for Buss's survey to uncover nonadaptive, sensory bias-related, or context-dependent preferences (such as those exhibited in mate choice copying [Gibson and Hoglund 1992; Kirkpatrick and Dugatkin 1994; Servedio and Kirkpatrick 1996]) because no such things appear on the list. Suppose there is a panhuman preference for elbows larger than the mean value of elbow. Buss's study would not be able to uncover that, because it is not included among the features which people have been told they are capable of preferring.

3.2.4. Thornhill and Gangestad on Detecting Preferences

Evolutionary psychologists Randy Thornhill and Steven Gangestad's work on human mate preferences represents a significant improvement over that of David Buss with respect to uncovering deep-rooted psychological dispositions. Although nowhere near the magnitude of Buss's survey, Thornhill and Gangestad employ methods which are much more in line with those used to study mate preferences in other taxa. In their initial study (Gangestad *et al.* 1994), which tested for a preference for low degrees of fluctuating asymmetry (the extent to which bodily features deviate from perfect bilateral symmetry. See chapter 4), 8 subjects were asked to rate the facial attractiveness of 72 individuals by looking at a photograph of each individual and assigning a value of "1" ("not at all attractive") to "10" ("extremely attractive") (pp76-77). Consistent with the authors' hypothesis, the results showed that individuals with low fluctuating asymmetry were rated more attractive than those with high asymmetry.

One of the positive features of this study which Buss's survey lacks is the absence of confusion generated by the distinction between those features which people purport to prefer and those to which they are attracted. Subjects were simply asked which images they found more attractive, not whether they believed it would be good for a mate to possess specific features or how "indispensable" those features are. Setting aside worries about the veracity of responses, it seems that we have good reason to believe that the study does reveal something interesting about mate preferences, for the same reasons we are warranted in thinking that many studies conducted on nonhumans reveal truths about mating preferences—namely, that the method employed measures subjects' responses to the particular visual stimulus hypothesized to be involved in mate choice, rather than an abstract description of that stimulus. In addition, their method avoids the kinds of ambiguities mentioned above, which can arise either because of the nature of self-report (i.e., people are less likely to contemplate which of the subjects it would be good for them to be attracted to), or because of the immensely complex social milieu in which actual human mate choices get made (i.e., people do not have to worry about whether their mother would get along well with the man in the picture). This is, however, not to say that internalized cultural norms will be absent in the responses in Thornhill and Gangestad's study. To assert otherwise would be to deny the causal efficacy of social forces in this domain. The point is merely that Thornhill and Gangestad's set-up does not invite confounding factors to the degree that Buss's study does. Whether the responses of 8 individuals can be taken as representative of the whole of humanity is another matter, of course. For the purposes of this discussion, the only matter which should concern us is whether the methodology could lead to reliable conclusions about mate preferences.

Gangestad and Thornhill do not altogether avoid the problems which plague Buss's apparatus. Another episode in this research program (Gangestad and Thornhill 1997) raises concerns similar to those encountered in the discussion of Buss. In this latter case, Gangestad and Thornhill used mens' reports about how many times they had been the man with whom a woman cheated on her long-term partner to assess the link between the frequency of such an occurrence and a man's fluctuating asymmetry (discussed in detail below). It's not clear how reliable these reports are apt to be, for it seems natural to think that there is a very good chance that many times men have no idea whether the person with whom they are having sex is in a long-term relationship. The drunken "hook-up" at the fraternity party (Gangestad and Thornhill's subjects were college students) may not involve a lengthy preamble regarding the participants' other commitments, such there be.

This example along with Buss's difficulties point to a crucial but underappreciated infirmity in the structure of self-report data. We know that subjects' perceptions of researchers' expectations can affect their responses to questionnaires and that questionnaires will normally fail to detect when someone has lied. Insofar as the incentives either to lie or to tailor one's responses to their beliefs about what researchers would like to hear are negligible, we may consider these potential confounders relatively minor nuisances. But a more obvious and threatening factor, clearly brought out in the examples above, is the possibility that subjects may truly believe that their response reflects reality when in fact it does not. As we've seen, this possibility cuts right through to peoples' responses about their own preferences. I may report a "preference" for industrious women which is in fact a conglomeration of parental pressure, prevailing social values, and personal proclivities. Does this response reflect my actual preference? Either it does, in which case the link between my preference and my selfish adaptive motivations is mysterious (because we have no explanation for why my susceptibility to parental and social pressure would have been adaptive during the Pleistocene, or why the beliefs of third parties should track choices which would have been adaptive for me), or it does not, in which case self-report data are unreliable representations of mate preferences. Whichever disjunct turns out to be true, self-report data are unlikely to survive as useful proxies for mate preferences.

3.3. Detecting a Genetic Basis for Preferences

Let's return now to the kind of work characteristic of researchers studying the mate preferences of nonhumans. If you've shown that females in the focal population exhibit nonrandom mating patterns in relation to a given male trait, you're ready to take on the project of determining whether the preference for that trait has a genetic basis. The most reliable way to do this is to artificially select for the preference and see whether the trait frequency increases in subsequent generations. This kind of test requires that there be some variation in mate preferences among females and will not be possible unless we are able to first differentiate between alternative mating patterns within the population. Suppose we have done this, having discovered that some females prefer spotted males and some prefer spotless males. To see whether the preference for spotted males has a genetic component to it, we can remove females with a preference for spotless males from the population and consequently restrict mating to females with a preference for spotted males. If the proportion of females preferring spotted males increases in subsequent generations relative to the initial distribution, we have some cause to infer that the preference for spotted males has a genetic component to it. As always, it will be necessary to control for any potential external influence, such as the behavior of conspecifics (e.g., mate choice copying). If females exhibit the same pattern of choice whether they are raised in their natural habitat or in social isolation in a lab, this is strong evidence in favor of the view that the preference for spotted males is genetic. A less reliable method by which we can garner evidence for the genetic basis of preferences is through measuring the resemblance of parents and offspring, or full and/or half siblings to one another with respect to the preference in question (Bakker and Pomiankowski 1995: 132-133; Jennions and Petrie 1997: 291). Here we use covariation between the degree of genetic relatedness and preference (or the strength of the preference, if it varies continuously) to estimate how much of the phenotypic variation is due to genes alone (Mazer, 1999 #618: 96-97. See Bakker 1993 for example).

3.4. The Origin of Preferences

> *If instead of regarding the existence of sexual preference as a basic fact to be established only by direct observation, we consider that the tastes of organisms, like their organs and faculties, must be regarded as the products of evolutionary change, governed by the relative advantage with such tastes may confer, it appears...that occasions may be not infrequent when a sexual preference of a particular kind may confer a selective advantage, and therefore become established in a species* (Fisher 1958: 151).

If you've succeeded in demonstrating that females have a genetically based preference for certain male types (and *only* if you've succeeded in demonstrating this), you're ready to explain *why* females have these preferences. You will now be entering into the most controversial, divisive, and emotionally-charged area in the field of sexual selection. The stakes are high and the data are scarce, so watch your step.

Darwin (1871) gave us a characteristically powerful and parsimonious model for how conspicuous male traits were able to spread and persist even if they meant a severe reduction in the bearer's ability to survive, a model which was directly subsumable under the basic explanatory framework of natural selection. He suggested that the mating advantage gained by males through attractiveness of these traits to females might offset the disadvantage they incurred through the costs (usually physiological or predation) of maintaining them. Although the initial reception of this model was one of dismissive skepticism—skepticism which persisted well into the twentieth century—today it is generally held that the process first described by Darwin is one, if not *the*, dominant mechanism by which conspicuous male traits evolve (Ryan 1990: 160).

While Darwin's implication of female choice in the evolution of conspicuous male traits *did* meet the challenge those traits presented to the theory of natural selection, he failed to address a critical assumption of that model—viz., the origin of female preferences. It now seems intuitive that female choice can account for conspicuous male traits, but what accounts for the existence of female choice?

Early attempts to dispose of this dangling question focused on the selective importance of directing mating effort towards conspecifics. Fisher (1958: 144) observed that the "grossest blunder in sexual preference, which we could conceive of an animal making," would be to mate with a member of another species, given that the likely result would be either sterile offspring or no offspring at all. Thus there will be pressure on organisms to distinguish conspecifics from members of other species, and conspicuous male traits will evolve to help females make this vital distinction. This explanation, typically referred to as "species recognition," was the favored model of the framers of the modern synthesis, most likely owing to their preoccupation with the dynamics of species (Andersson 1994: 28; Maynard Smith 1987: 10). While species recognition is expected to play some role in the evolution of female choice, it seems unable to account for the extreme conspicuousness of many types of male traits, which are often amplified far beyond what would be required to differentiate between species (Andersson 1994: 28).

Today, researchers who study mate preferences have a variety of models from which they can choose to explain why females focus their mating efforts on some males rather than others, many of which are also connected to Fisher (1958). In this section, I discuss theoretical and empirical aspects of several of these models, paying particular attention to the requirements for successfully demonstrating that a particular model best explains why females have the preferences they do. I divide the discussion into two broad categories of preferences: (1) those which evolve because of selection operating on them directly and (2) those which evolve because of their genetic correlation with other traits which are themselves directly selected.

A section on mate choice models plays three important roles in my criticism of evolutionary psychology. First, it brings to light a number of powerful explanatory frameworks which occupy a central role in the study of nonhuman mate choice but which receive no mention in evolutionary psychology. The absence of these models in evolutionary psychology is suggestive. It indicates either that evolutionary psychologists are poorly acquainted with what is commonplace in the field in which they take themselves to be working, or that they are well-acquainted with what is commonplace but have chosen (without justification) to discuss a handpicked subset of models (notably, the ones which attribute an offspring viability-enhancing role to preferences). The second purpose served by a survey of models is to expose the mistakes committed by evolutionary psychologists when they *do* engage particular models. Third, in continuation with the spirit of what we've already seen, the rift between what is required to demonstrate the presence of a given mate choice mechanism, on the one hand, and what evolutionary psychologists bring to the evidence table, on the other, critically undermines any claims on their part to have uncovered the evolutionary origins or adaptive maintenance of human mating behavior.

3.4.1. *Directly Selected Preferences*

Some preliminary remarks on preferences which evolve through direct selection are in order. It should first be noted that, like all other sorts of traits, only preferences which evolve through direct selection qualify as *adaptations*. In order for a female preference to be an adaptation, that preference has to have been selected for its direct impact on the fecundity of females (Hall *et al.* 2000; Kirkpatrick 1987; Kirkpatrick and Barton 1997; Kirkpatrick and Ryan 1991; Kokko *et al.* 2003; Maynard Smith 1987; Ryan 1990,1994, 1997). In this respect, female preferences are just like any other adaptation produced by natural selection. If genetically based preference *P* was, for whatever reason (see below), directly responsible for the ability of the female to outreproduce contemporaneous variants which lacked *P* and thus caused it to spread through the population, then, and only then, *P* is an adaptation (discussed in chapter 2).

3.4.1.1. Direct Phenotypic Benefits

Discussion of benefits which affect the production of offspring directly is relatively rare in the literature on mate choice, probably because of how obvious the idea seems (Maynard Smith 1987; Ryan 1994, 1997). All we are doing in this case is applying commonsense essentials of natural selection to the context of mate choice. The notion that female types will be selected for if by some genetically based property they are capable of acquiring more food or better territory, or of making themselves better parents or more fertile, has an obvious and intuitive appeal. These kinds of benefits are typically considered the currency of selection. In the context of mate choice, then, rather than acquire these benefits themselves, females employ a male to do the work for them. When the genetically-based property by which some female types are capable of acquiring direct benefits is a preference for males who can give them these resources, the effect will be the same as if they had gone out and gotten the resources themselves (Heywood 1989; Hoelzer 1989). Just as selection would favor females who acquired beneficial resources themselves, so too will it favor females whose mate preferences facilitate the acquisition of beneficial resources.

Because the mechanism at work in this case is the same as direct selection outside the context of mate choice, the conditions for demonstration are similarly equivalent: show that females' reproductive success is augmented by choosing males who provide resources. This will require us to successfully employ some of the methods discussed in the previous chapter. (We need not demonstrate heritable variation among males with respect to resource-providing behavior, as genetic models (Hoelzer 1989; Iwasa and Pomiankowski 1999) have shown that female preferences of this type can evolve even when variation in male behavior is nonheritable.) Notice that if we are interested in explaining the evolution of female preferences, it will not be sufficient to demonstrate merely that females prefer resource-providing males. We must show that this preference spreads through the population because of its direct effects on reproductive success. It will only be possible to get direct evidence for these effects when there is heritable variation in the female preference.

3.4.2. *The Evolutionary Psychology of Directly Selected Preferences*

Claims that some behavior was directly selected for are numerous in the evolutionary psychological literature. Here I review one of the more prominent ones, arguing that it does not meet the evidentiary burden which demonstrations of direct selection are required to bear.

3.4.2.1. A Preference for Reliable Men Willing to Commit to a Woman

One of the central foci of Buss's writings is the distinction between "long- and short-term mating," which he considers to be "core components of the human strategic repertoire" (Buss 1998: 411). For Buss, the selective importance of a woman's long-term mate is captured in the following excerpt:

> Consider one of the problems that women in evolutionary history had to face: selecting a man who would be willing to commit to a long-term relationship. A woman in our evolutionary past who chose to mate with a man who was flighty, impulsive, philandering, or unable to sustain relationships found herself raising her children alone, without benefit of the resources, aid, and protection that another man might have offered. A woman who preferred to mate with a reliable man willing to commit to her likely had chil-

> dren who survived and thrived. Over thousands of generations, a preference for men who showed signs of being willing and able to commit to them evolved in women...This preference solved key reproductive problems, just as food preferences solved key survival problems (*ibid.*: 412).

The implication of direct selection is clear: women with a preference for a "reliable man willing to commit to her" were selected for because "the resources, aid, and protection" which those men provided caused her to have "children who survived and thrived"—a classic case of direct selection.

Now *pace* my criticisms of Buss's survey, let us suppose he actually has demonstrated that women have a preference for reliable men who are willing to commit to them. Let us suppose even further that he has satisfied that most difficult of requirements and shown variation in this preference to have a genetic basis (nevermind if the preference is hypothesized to be universal). The only question left to ask is, has Buss demonstrated that women's reproductive success is augmented by a nonrandom pattern of choosing men who are "reliable" in terms of providing resources, aid, protection, etc.—i.e., that the preference for reliable men "solved key reproductive problems" (*ibid,*: 412; see also Buss 2003: 19-48).

Buss offers us no actual data on reproductive success of women either with a preference for reliable men or without a preference for reliable men. Of course, we *at least* need these two data sets in order to evaluate his claim that these two types of women differ with respect to their reproductive success. In place of the necessary data, Buss submits, *inter alia*, two key pieces of evidence. One is the "discovery" that women "place a premium on a man's social status, his ambition and industriousness, and his older age—qualities known to be linked with resource acquisition," (*ibid*: 422) as well as love, which

> "some [unnamed: CH] studies have found...signals commitment of a host of reproductively valuable resources: economic (e.g., gifts, food), physical (e.g. ,protection), sexual, psychological (e.g., helping mate when he or she is down), and reproductive (e.g., such as [*sic*] having children together) (*ibid*: 420).

Thus, the preference for "reliable" men—"what women want"—turns out to be a composite of preferences for qualities "known" to be linked with resource acquisition, combined with a preference for men who love them, because love "signals commitment of...reproductively valuable resources" of all sorts. Whether there is a reliable link between a man's love and his willingness to furnish a woman with resources, as well as whether the resources Buss cites are "reproductively valuable," are assertions requiring demonstration but which Buss simply assumes are true. In particular, showing that some resource is "reproductive valuable" requires exactly the same kind of demonstration as does showing that Buss's putative preference for reliable men is adaptive—viz., a demonstration of differences in reproductive success *in humans* resulting from the focal variable (i.e., the valuable resource or the preference). Problems only multiply when we consider that the female preference for reliable, resource-giving men is supposed to have evolved sometime during the Pleistocene, thus making measurement of the relevant reproductive success differentials impossible.

The second piece of evidence is a description of the courtship behavior of the African village weaverbird *Ploceus cucullatus*, for which he cites as support a paper written by Nicholas and Elsie Collias in 1970 (Buss 2003: 7). The female weaverbird appears to be somewhat discriminating with respect to the male with whom she mates, and different aspects of a male's nest play a significant role in whether she mates with him (Collias and Collias 1970; Collias and Victoria 1978). On the basis of their description of the courtship process, Buss concludes that

> [b]y exerting a preference for males who can build a superior nest, the female weaverbird solves the problems of protecting and provisioning her future chicks. Her preferences have evolved because they bestowed a reproductive advantage over other weaverbirds who had no preferences and who mated with any males who happened along (Buss 1998: 412; Buss 2003).

Curiously, however, Collias and Collias (1970) make absolutely no mention of any sort of functional significance of females' preferences, nor do they suggest that the preference for certain males evolved to "solve the problems of protecting and provisioning her future chicks." These adaptationist yarns are spun from nothing other than the furiously productive loom that is Buss's imagination. To be fair to Buss, Collias and Collias (in a separate publication) *did* find evidence indicating that "strength of nest materials"[6] plays a role in female mate selection,

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[6] The variable called "strength of nests materials" is itself somewhat dubious. "Strength" in Collias and Victoria (1978) appears to be a bivalent property, where nests are either strong or not strong. Furthermore, whether a nest is "strong" in this study depends solely on whether it was constructed from fresh materials or from old, discarded nest materials. That is, there is no actual *test* of strength (e.g. no measure of load-bearing capacity or cohesiveness)—only a designation of strength based on the type of materials composing the nest. Thus, females may not actually be selecting nests based on how strong they are, further diluting adaptationist aspirations.

but they do not attempt to relate this to reproductive success (Collias and Victoria 1978).

To conclude this discussion, we can acknowledge Buss's contribution to the data on sex differences and even to our knowledge of sex differences without even so much as entertaining the notion that there is something to be inferred about human evolutionary history from Buss's work on mate preferences. The breadth of his survey (Buss 1989) is indeed formidable, and he is to be commended for attempting to meet the cross-cultural challenge which so many before him have simply ignored. But breadth and depth are two rather different dimensions.

3.4.3. *Pleiotropic Preferences*

Sometimes a preference will be directly selected for its effects in the context of mate choice, as in the above cases. Other times, direct selection for a preference will occur because of its effects outside the context of mate choice, for example, due to the effects of the preference on the ability of an animal to distinguish ripe from unripened food (or prey), dangerous predators from innocuous bystanders or even conspecifics from members of other species (Enquist and Arak 1993). When selection of this type occurs, the preference which is selected for may have concomitant effects in the domain of mate choice. For instance, females with an adaptation which causes them to prefer red fruit may also prefer red males. Here, the preference which causes them to prefer red males *was* directly selected, it just happens *not* to have been selected for its effects in the domain of mate choice (Endler 1992; Ryan 1990, 1994, 1997, 1998; Williams 1966).

Mate preferences may also derive from the effects of preferences whose adaptive value of are more domain-general in nature. For example, organisms might be more likely to favor signals of any kind which are easily detectable over those which are more cryptic. Of course there is no presumption that organisms have a general preference for "easiness" over "hardship" (although they may well have). Rather, the idea is simply that those signals which are easiest to detect are more likely to capture attention. Louder calls or brighter colors can give a signaler an edge in reaching potential recipients over competing signals as well as other ambient noise (Endler 1992: 125). If there is a general tendency to be attracted to easily detectable signals, this tendency can affect a female's mate choices; she may be drawn to more easily detectable males. This, in turn, will generate selection on males to produce increasingly amplified mating signals, which is one possible explanation for the conspicuousness of many male traits (Endler 1992: 141).

Finally, organisms may possess domain-general directional preferences as a result of certain basic properties of the nervous system, which may or may not have been selected for (Ryan 1998; Ryan and Rand 1993). For instance, animals across taxa exhibit a preference for symmetrical structures (Enquist and Arak 1994; Enquist and Johnstone 1997; Jansson *et al.* 2002). Additionally, stimuli which are "supernormal" can often evoke much stronger responses than naturally occurring stimuli, a phenomenon which is also prevalent across taxa (Arak and Enquist 1993, 1995; Ryan 1994, 1998; Ryan *et al.* 2001). One possible byproduct of the preference for symmetry can be seen in the fair number of cases in which females of different taxa have been shown to prefer more symmetrical males (although there is much debate as to how symmetry should be measured and whether particular studies do it accurately [Evans and Hatchwell 1993]). Moreover, the general preference for supernormality serves as a candidate explanation for exaggerated male traits, and is a key assumption in prominent models of sexual selection (Lande 1981; O'Donald 1983). Where these fundamental biases of the nervous system have been selected for, the mate preferences which follow from them will necessarily be the product of direct selection. In sum, "*any factor that directly influences the evolution of a sensory system implicated in mate choice could consequently bias female preferences*" (Ryan and Rand 1993: 193, my emphasis).

3.4.4. Demonstrating Pleiotropic Preferences

As indicated by the quote in the previous paragraph, female preferences are vulnerable to influence from a multitude of directions (see also Basolo 1995a,b, Basolo 1996). Preference patterns which have evolved as a result of either preference evolution in other domains or basic structural properties of perceptual systems are typically called “sensory biases,” “receiver biases,” or “response biases.” I will use these terms interchangeably.

There are a number of methods by which we can gather direct evidence for hypotheses of mate preference due to sensory bias. Some of these were alluded to already. Others are described below.

Phylogenetic Tests

One area in which hypotheses of female mate preferences due to sensory biases have been particularly successful is that of phylogenetic approaches to preference evolution. Strong evidence for these hypotheses can be obtained if part of the phylogeny of a particular species is known. Suppose we demonstrate that females in species X_n possess a preference for X_n males with trait T. If we want to see whether the preference for males with T is an adaptation in X_n females, we can test to see whether females in a ancestral species X_{n-1} in which T did not exist also possess a preference for males with T. If X_{n-1} females prefer males with T, even though there are no X_{n-1} males with trait T, the preference for T in X_n females is far more likely to be the result of shared ancestry with X_{n-1} than it is to be an independently evolved adaptation (Basolo 1996: 292).

This method has been carried out most famously by Alexandra Basolo on swordtail fish (see Basolo 1996) and by Michael J. Ryan on tungara frogs. Males in two sister species of frogs, *Physalaemus putulosus* and *P. petersi*, can add "chuck" calls to their introductory "whine," and those *P. putulosus* males which add chucks are preferred by females of that species. Females in a related species *P. coloradorum* also prefer chucks, but unfortunately for them (and for adaptationist hypotheses), *P. coloradorum* males do not produce chucks. Ryan

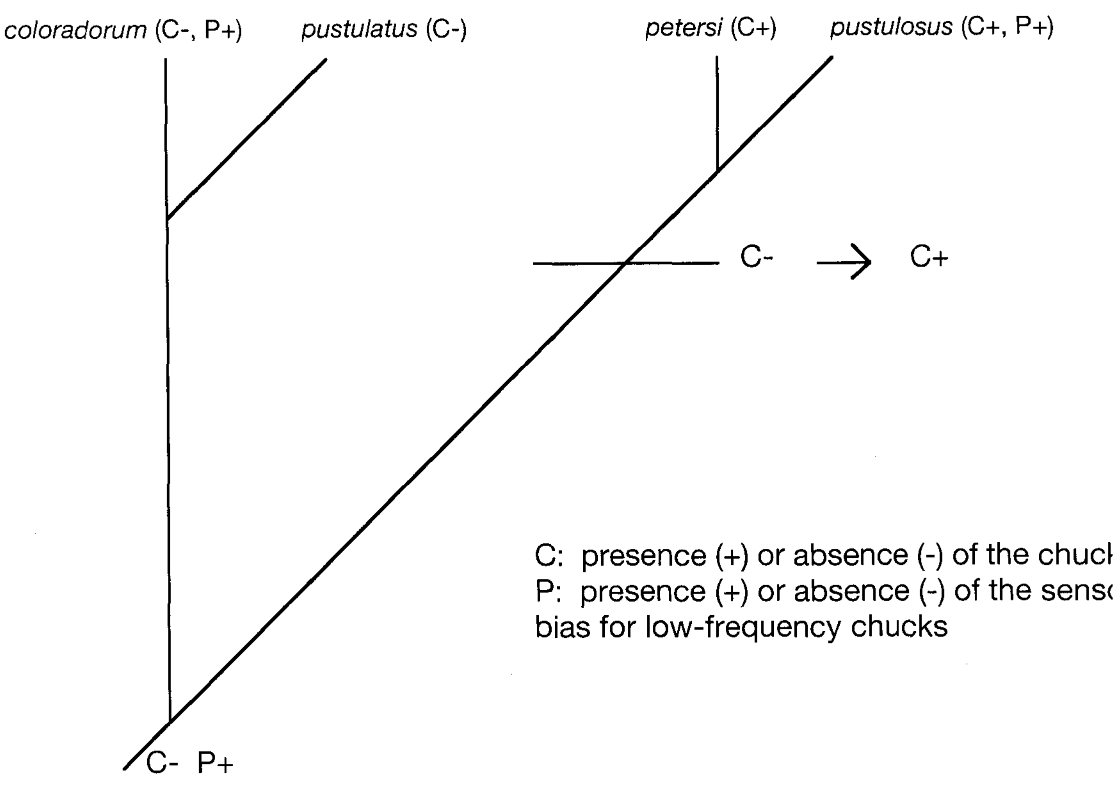

Figure 3.1 Phylogenetic distribution of chuck and preference in *Phylasaemus* (adapted from Ryan 1990: 183)

and coworker A.S. Rand inferred from this that the preference for chucks in all three species must have descended from a common ancestor in which the preference for chucks was present but the chuck was not. Thus, the preference for chucks would not be an adaptation in *P. putulosus*, but rather a byproduct of a more general sensory bias (Kirkpatrick and Ryan 1991: 36; Ryan 1990. See Figure 3.1).

The existence of homologous preferences suggests that a well-established phylogeny is necessary to make reliable inferences regarding the evolution of female mate preferences (Basolo 1995a: 308; Ryan 1996: 1; Ryan and Rand 1993: 189). In the case of Ryan's frogs, we could have easily been led astray had we failed to pay attention to the historical relation between the chuck and the preference for it. For example, in addition to preferring chucks *per se*, females also prefer chucks of relatively low fundamental frequency. Fundamental frequency decreases as male size increases, and

> more eggs are fertilized if the size difference between the typically larger female and the typically smaller male is minimized [cite]. To the extent that females are preferring lower-frequency chucks they are also preferring larger males...and thus might be gaining a reproductive advantage derived from their call preference (Ryan and Rand 1999: 545).

Ignorance of the relevant phylogenetic relationships in *Physalaemus* might well have resulted in an intuitive adaptationist inference to the effect that females in *P. pustulosus* have evolved to prefer lower-frequency chucks because of the fecundity benefits they receive due to the characteristically higher fertilization rates of the larger males associated with those lower-frequency chucks. The relationship of descent of the preference with respect to the chuck, however, precludes this as an explanation of why females prefer chucking males. What appears to explain the preference for lower-frequency chucks is instead a particular tuning bias of the female inner ear which is shared by all three species mentioned above (plus *P. pustulatus*), inherited from a common ancestor (Andersson 1994: 109-112).

Stimulus Training

Another way of testing for sensory biases is observing animal responses to different categories of stimuli. Jansson *et al* (2002; "Experiment 1") trained hens to prefer visual cues in the form of asymmetrical crosses by rewarding them with a tasty pellet each time they pecked a computer image of the cross (within 20mm of the symbol). After the hens had learned to peck at the asymmetrical cross with sufficient reliability (70% in three separate trials), Jansson and co-workers injected a *symmetrical* cross into the display sequence after every ninth reward dispensed. Pecking the symmetrical cross did not yield any reward. To control for an initial preference for symmetry ("Experiment 2"), hens were shown an asymmetrical and a symmetrical cross simultaneously on a computer screen, and rewarded with a mealworm for pecking within 20mm of *either* image.

All hens in Experiment 1 "showed a preference for the novel [nonrewarding: CH] symmetrical cross over the familiar [rewarding: CH] asymmetrical cross" (619). However, Experiment 2 showed that the rate of pecks at the symmetrical cross was "not significantly different from 50%, indicating no preference for the particular symmetry among naïve [untrained: CH] individuals" (620). Thus, the study showed that "a preference for symmetry can emerge in real animals as a result of particular visual experiences" (620), which

> cannot be explained by any benefits being associated with responding to the symmetrical stimulus since completely artificial stimuli were used and the symmetrical stimulus was not rewarded (620).

In this case, it is apparent that the preference for the symmetrical cross in Experiment 1 is due to its novelty relative to the asymmetrical cross. Thus the study vitiates the need to explain the widespread preference for symmetry by reference to "links between symmetry and quality" (620) as several authors have attempted to do (Moller 1993; Gangestad and Thornhill 1997. See discussion in chapter 4). The novelty of symmetry in nature is sufficient to explain its attraction.[7]

Comparison between Unrelated Allopatric Species

Evidence for sensory bias can also be gained by demonstrating that unrelated species have similarly oriented preferences. The idea here is that individuals of unrelated species living in different habitats are unlikely to have been selected to behave preferentially towards the same stimuli, as there should be no reason that the same stimulus would have exerted selective pressure upon two species with little in common in terms of genotype and environment.

Along these lines, in an experimental set-up similar to that described in the previous section, Ghirlanda *et al.* (2000) demonstrated that chickens prefer the same faces rated "most attractive" by college undergraduates. This result is important for a couple of reasons. A number of researchers have suggested that humans have an adaptation designed to garner information about mate quality from human faces (see chapter 4). Consequently, a preference for certain kinds of faces is essentially a preference for mates of a certain degree of quality, with the most preferred faces presumably being the highest quality

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[7] In a similar connection, Jansson and Enquist (2003) demonstrated the development of a bias for color stimuli which least resembled nonrewarding color stimuli.

mates. Now, it is unlikely that chickens would have been under strong selection pressure to be able to accurately gauge the quality of potential human mates based on their faces. Thus we can probably conclude with confidence that chickens do not have the same facial-recognition adaptation which is hypothesized in humans. Nevertheless, chickens prefer the same human faces that humans themselves prefer. Note Ghirlanda *et al*:

> From observed chicken behavior and knowledge of general behavior mechanisms we must in fact conclude that humans would behave the same way with or without the hypothesized adaptation. There would thus be no selection pressure for developing one (387).

It follows from the behavior of the chickens in this experiment that organisms without facial-recognition devices can be reliably drawn to the particular human faces which humans find most preferable. If preferences for particular human faces can be produced when the organisms are chickens, there should be no reason, argue Ghirlanda *et al.*, to posit the facial-recognition device in humans; *it is simply not necessary to produce the relevant preferences.* Moreover, even if we assume that it would have been adaptive for humans to reliably prefer mates with certain kinds of faces, the fact that they could do this without the aid of a facial-recognition device of the kind typically posited implies that individuals who possessed the device would have performed no better than those who did not possess the device, and would thus not have been favored by selection for their facial recognition abilities (see also Ryan 1998: 2002; Ryan *et al.* 2001).

3.4.5. Sensory Bias: Concluding Remarks

There is no specific experimental or observational paradigm for detecting the presence of sensory bias. These are just a few of the ways in which researchers have attempted to demonstrate the role of sensory bias in animal behavior, particularly in the context of mate choice. In general, however, it might be useful to adhere to the following strategy: First, demonstrate a pattern of nonrandom mating with respect to a specific male trait. Second, either (a) look for nonrandom female behavior with respect to other aspects of the environment which hold salient properties in common with the male trait (e.g, if females prefer red males, look for a preference for red in other domains. If they prefer symmetrical males, look for a preference for symmetry in other domains.), *or* (b) look for a similar pattern of behavior among females of closely related species where the male trait is absent, *or* (preferably) (c) do both. Third, if the strength of the female response is positively correlated with the *conspicuousness* (i.e., brightness, loudness, size) of the trait, then one should observe female responses to both (i) conspicuousness which is artificially augmented to a degree that does not occur in nature, and (ii) completely novel stimuli. The purpose of (i) and (ii) is to help distinguish between the effects of "indicator mechanisms" in which a male's quality is positively correlated with the conspicuousness of his trait (see discussion below), on the one hand, and a preference for novelty or "anti-monotony" *per se*, on the other hand (Arak and Enquist 1993; Endler 1992; Ryan 1990). If a female's response to novelty is strong, this may indicate that her preference for increasing degrees of conspicuousness in males is at bottom a domain-general preference for novelty. This kind of result would not, of course, completely *falsify* the view that females prefer males because of what is indicated by their traits, but it would undermine *prima facie* support for that view. That is, even if it were shown that male quality (in whatever sense) is positively correlated with conspicuousness, the fact that females exhibit a preference for novelty or exaggeration or simply greater stimulation suggests that a sensory bias may be behind their preference for conspicuous males.

Little has been said up to this point about the effects of female sensory bias on the development of male traits. As was stated earlier, female preference first appears in Darwin's work as a way of explaining how conspicuous, viability-reducing male traits can be selected for. Genetic modeling has confirmed Darwin's suspicions, even in cases where the viability costs of the male trait are quite high. This demonstrates the sheer selective force of which female preferences are capable. If female preferences can cause very costly traits to evolve, then they should *a fortiori* be capable of causing the spread of male traits that are relatively less costly. Thus, female preferences appear to run the gamut in terms of which kinds of male adaptations they can produce. Second, mate preferences are for a few reasons extremely sensitive to the influence of sensory biases. For one, as Ryan and Rand rightly point out, "any factor that directly influences the evolution of a sensory system implicated in mate choice could consequently bias female preferences." Sensory systems similarly incorporate a variety of subsystems in generating the sensations for which they're responsible, and each of these subsystems could potentially be modified by selective factors specific to *their* effects on the larger sensory system. This leaves room for mate preferences to be affected in innumerable ways by selection on sense modalities. Not only that, but

> [g]eneral properties of nervous systems might further affect mating preferences. For example, sensory systems can habituate to repeated stimulation, and some have suggested that songbirds have evolved complex song repertoires to release both male and female receivers from such habituation (Ryan 1997).[8]

The preponderance of influences which are, from the point of view of natural selection, extraneous to the function of female preferences (which, in the ideal case, would be to cause the female to mate exclusively with males who directly augment her reproductive success), results in the opportunity for female preferences to evolve in almost any direction. In turn, the terrifically diverse and unpredictable forms which female preferences are capable of taking give rise to equally diverse and unpredictable forms of male traits. For in many cases female preferences are the very *raison d'etre* of male traits, in much the same way that the abstract form which "resides in the soul of" Aristotle's "artisan" gives rise to a particular concrete structure (*Metaphysics*, Book Z.9, 1034^{a}24). Thus, if we combine the selective power of female preferences with the variety of forms which they are capable of imposing upon male traits, what emerges is a process which could, *in principle*, plausibly explain the origin of *any* male trait, even those which appear to have evolved to perform functions outside the context of mate choice.

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[8] See Arak and Enquist (1993) and Enquist and Johnstone (1997) for other kinds of habituation effects.

All this is, of course, not to say that sensory bias *does* account for every male trait. Rather, the point here is to underscore the distinct possibility of sensory bias as a dominant selective force in the evolution of male traits—particularly male traits geared towards attracting females. It would thus seem incumbent upon those working in the field of sexual selection and mate choice to explore the possibility that the focal trait, be it a conspicuous male trait or a nonrandom pattern of female mating behavior, exists either primarily or in part as a result of female sensory biases.

The effects of sensory bias on mate preferences and, consequently, on sexual selection are likely to be pervasive, although their precise role and physiological basis may often be extremely subtle and present serious challenges to measurement. The appropriate response to these difficulties is not skepticism with regards to whether we can know the evolutionary chronicle of preferences and sexually selected traits, but rather the path chosen by Ryan and numerous others referred to in this section—viz., more precise hypotheses and better, more discriminating tests of those hypotheses.

The only mention by an evolutionary psychologist of the causal role of sensory bias in mate preferences of which I am aware is Miller (2000), where sensory bias is introduced for the purposes of debunking it, recasting putative sensory biases in terms of adaptive preferences (see discussion below). One might rightly wonder why sensory bias receives no attention in evolutionary psychology given its important role in theoretical and empirical work on mate choice for at least the past twenty years. As I suggested above, either evolutionary psychologists are unaware of sensory bias models or they deliberately ignore them. If truth lies in the former disjunct, we have little reason to suppose that evolutionary psychological explanations of human mate choice are reliable because there has been no effort made to differentiate those models from alternative explanations. If, on the other hand, the latter disjunct is true, there needs to be some explanation on the part of evolutionary psychologists as to *why* they have ignored sensory bias (as well as other) models. The way things stand, evolutionary psychologists' explanations of human mate choice are in a similar position to that of their explanations for why sexual selection occurs; in order to avoid the appearance of adaptationist axe-grinding, evolutionary psychologists are obligated to account for their silence when it comes to alternative models.

3.5. Indirectly Selected Preferences

Most of the spotlight directed at mate preferences has been centered around mechanisms of indirect selection. Here I focus on the two most prominent mechanisms of indirect selection: Fisher's "runaway" process and the "indicator" or "good genes" process. Following Andersson (1994), I will use the term "indicator" rather than "good genes" as much as possible as some of the models under the "indicator"/"good genes" rubric focus on nongenetic benefits of mate choice (Andersson 1994: 54). However, these terms, where they appear, should be treated as coextensive.[9]

3.5.1. Fisherian Runaway

Imagine a population which in its initial state G_1 contains females of type P_1, who mate indiscriminately, and equal amounts of T_1 and T_2 males. At G_2, a female is born with a chance mutation P_2 which causes in her a preference of strength a_2 to mate with males of type T_2 over males of type T_1 (such that in a choice between two males she is a_2 times more likely to mate with T_2 males than she is to mate with T_1 males, where $a_2 > 0$). Some of the female offspring of this initial P_2T_2 mated pair possess P_2 through genetic inheritance, and the male offspring of this pair similarly inherit T_2. In the third generation G_3, T_2 males enjoy an increase in their chances of mating success, as there are more P_2 females now than in previous generations. Whereas T_2 males in G_1 enjoyed a likelihood no better than chance of mating with either P_2 females or P_1 females, in G_3 they retain their chance likelihood of mating with P_1 females but *augment* their chances of mating with P_2 females, thus increasing their overall chances of mating. Consequently, in G_4 there will be proportionately more T_2 males than there were in G_3—i.e., selection for T_2 males has been generated by the preference in P_2 females. In addition, the nonrandom pattern of mating between T_2 males and P_2 females creates a nonrandom positive association between the allele respon-

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[9] The discussion of these models in evolutionary psychology tends (suggestively) to favor the phrase "good genes." Hence, that phrase will dominate my discussion of evolutionary psychology.

sible for the male trait and the allele responsible for the female preference such that an individual carrying one allele will tend to carry the other, and selection for the male trait will thus drag the female preference to a higher frequency.[10] In turn, the increased frequency of P_2 females generates even stronger selection for T_2 males, which increases the frequency of P_2 females, and so on and so forth until the either all genetic variation in population is exhausted or, in cases where the male trait becomes increasingly exaggerated because of peak shifts in the female preference, there is a selective backlash against the conspicuousness of the male trait (Andersson 1994: 35; Fisher 1958: 152; Kirkpatrick 1982; Lande 1981).[11]

The process described above "suffices to produce the known diversity in male traits" (Andersson and Bradbury 1987: 2) and has, in addition, a number of interesting and important features, some of which have already been described.[12] First, the runaway process is an *inevitable* consequence of the co-occurrence of genetic variation in female preferences and preferred male traits (Kokko *et al.* 2002: 1338; Lande 1981). Second, runaway can occur even when the costs of T_2 are "nearly lethal" to its possessor (Kirkpatrick 1982: 9) and can continue even to the point where T_2 is so costly to males that the species is driven to extinction. Third, even where T_2 reduces survival, both it and the preference for it (i.e., P_2) can persist in the case where a new female preference for

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[10] Good explications of the process by which certain alleles can become correlated (as well as the process of runaway in general) are provided by Arnold (1983: 77-79) and Shuster and Wade (2003: 79-81).

[11] Kirkpatrick (1982) provides, I think, the clearest model of runaway. His notation is adopted here.

[12] Explanations of the features mentioned here, where not included, can be found in the references provided.

males who are "optimally designed" with respect to viability is introduced into the population (Kirkpatrick 1982). Consequently, *it does not follow as a matter of logic that females who prefer high-viability or "high quality" males will have higher reproductive success than females who prefer relatively low-viability males* (Arnold 1983: 88-89; Mark Kirkpatrick [pers. comm.]). If the preference for the less viable male type is sufficiently strong, the extra long life enjoyed by the "high quality" male will not be of much use to him since other males are much more attractive to females. Lastly, although Fisher originally described the runaway process in terms of "further development" (i.e., exaggeration) of the sexually selected male trait (Fisher 1958: 152), that male traits should increase in conspicuousness is not a

> necessary outcome of Fisher's hypothesis of runaway sexual selection. The essence of the runaway process is the genetic correlation of a male trait and a female preference through linkage disequilibrium...There is no inherent direction to the evolution of male traits under the runaway process alone, as many mathematical models have demonstrated [cite]. It is important to note that the runaway process applies to a specific mode of correlated evolution of trait and preference; this theory can accommodate, but does not predict, the exaggeration of male traits under sexual selection (Ryan, 1990: 169. See also Arnold 1983: 83-84).

Nor does it predict that females will evolve to *prefer* ever-greater exaggeration of male traits, although it can accommodate that result as well (Ryan 1994: 194).

3.5.2. *Runaway and Adaptationist Accounts of Preferences*

We can use the basics of Fisher's runaway process to expose a ubiquitous and fallacious argument in work on the evolutionary psychology of human mating, namely the *a priori* assumption that "high quality" males will as a matter of logic be selected for over "lower quality" males. Psychologist Geoffrey Miller provides by far the most extensive and sophisticated discussion found in evolutionary psychology on this topic. One of the more instructive passages occurs in his revisionist account of sensory bias. His views on sensory bias represent a radical departure from traditional discussions of the topic in that he sees what is normally considered either an arbitrary fundamental orientation of the nervous system (such as the swordtail's preference for swords) or a default attraction to (say) louder calls (because they are easier to detect) as actually having "evolved to help animals choose good sex partners" (Miller 2000b: 147).

> Many sexual ornaments may look as if they are merely playing on the senses. They may appear to be nothing but fireworks, sweet talk, eye candy, special effects, and manipulative advertising. But maybe we should give the viewers more credit. What look like sensory biases to outsiders may have a hidden adaptive logic for the animal with the senses (*ibid.*:147).

To wit, "[m]ost sensory biases are consistent with what we would expect from adaptive decision-making machinery that evolved for mate choice" (*ibid.*: 147). Traditional thinking in the field of sensory bias has shortchanged "viewers" by presuming that their attraction to "larger, brighter, and more symmetric visual ornaments" is based merely upon sensory biases, failing to realize that "[l]arge, healthy, well-fed, intelligent animals can produce" those kinds of traits. Notes

Miller, "As far as I know, there is no example of a sensory bias that leads animals to favor sexual partners that are smaller, less healthy, less energetic, and less intelligent than average" (*ibid.*: 147). Thus, the "hidden adaptive logic" behind so-called sensory biases unveils itself: "larger, brighter, and more symmetric visual ornaments" as well as "louder, deeper, more frequent, and more varied songs" are actually "fitness indicators" representing the advertiser's quality through the magnitude of his advertisement. This much should be intuitive, suggests Miller, adding that "[i]f sensory biases led animals to choose lower-fitness animals over higher-fitness animals, I suspect that the biases would be eliminated rather quickly" (*ibid.*: 147).

Genetic modeling of sexual selection does not confirm Miller's suspicions. In fact, it directly contradicts them. As we have seen, it follows analytically from the most basic Fisherian runaway model (as well as from other kinds of models)[13] that a preference which causes (say) females to prefer "lower-fitness" (i.e., lower viability) animals over "higher-fitness" (i.e., higher viability) animals can spread and *persist* in a population, even when a preference for "optimal" (in terms of viability) males is introduced. Not only that, according to the basic model the preference which initiated runaway will itself become exaggerated, causing males to have even *lower* viability. Miller presumably is aware of this feature of runaway (having written his PhD dissertation in psychology at Stanford on the evolution of the human brain via runaway sexual selection). However all of this gets tossed aside in pursuit of "hidden adaptive logic."

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[13] E.g. Servedio and Kirkpatrick's (1996) mate choice copying model, where the copying allele spreads even when it causes females to copy a choice for low-viability males.

The mistaken belief that a preference for a "higher-fitness" male will, as a matter of logic, replace a preference for a "lower-fitness" male is widespread in the evolutionary psychological literature (see the numerous examples in Buss [2003], including one mentioned in section 3.4.2.1). There can be little doubt that this fallacy is an instance of the general assumption that the "adaptive" will, *ceteris paribus*, replace the "nonadaptive." The preference for "higher-fitness" males is intuitively perceived as adaptive, and the reasoning seems obvious: it is better to prefer males with higher fitness than to prefer males with lower fitness; therefore, in the limit preferences for higher-fitness males will replace those for lower-fitness males.

The intuitive appeal of this argument coupled with its complete wrongheadedness makes this an especially instructive case. There is a consensus among workers in sexual selection that if the preference for higher-fitness males spreads in a population, it is not because the *preference itself* is adaptive. And in that case, the higher fitness of preferred males would be incidental to the evolution of the preference, which is due to increased fecundity—standard direct selection. Rather, the reason the preference for higher-fitness males will spread is because of the linkage which arises due to assortative mating. If anything, the preference for higher-fitness males is *maladaptive* when there is direct selection acting upon it in the manner which Miller suggests. Consider: the preference for higher-fitness males causes linkage, which results in the female being pulled away from the natural selection optimum which would have obtained in the absence of linkage disequilibrium (Kirkpatrick 1996: 2134).

The pedagogical value of this episode is twofold. First, it provides a clear illustration of what can go wrong in the perilous search for "hidden adaptive logic," "where every prospect pleases" (Kitcher 1985). Those who embark upon this quest will never be disappointed; it will almost always be possible to construct a story in which the seemingly nonadaptive is actually adaptive. But the "hidden adaptive logic," once found, comes at a price—in this case, direct contradiction with well-known theoretical results. Second, we are given another example of how seemingly intuitive arguments which fail to appreciate the assumption-exposing value of mathematical models can lead to conclusions which have no theoretical or empirical support.

3.5.3. *Demonstrating Fisherian Runaway in the Present*

There has yet to be a demonstration of Fisherian runaway either in the present or in the past. This is due, on the one hand, to the nature of the evidence required for demonstration (which is in part necessarily genetic) and, on the other hand, to the fact that episodes of runaway are expected to be relatively short. Additionally, it has been difficult to formulate critical predictions which would allow us to distinguish instances of runaway from those of other mechanisms (Kirkpatrick and Ryan 1991: 37).

Despite these challenges, it is nevertheless important to know what to look for when considering Fisherian runaway as a candidate explanation for a male trait or female preference. The essence of Fisher's (1930) idea is the genetic correlation (usually referred to as the "genetic covariance") between a female preference and a male trait. Thus, it is incumbent upon those seeking to demonstrate the presence of runaway to provide direct evidence for such a correlation. This, in turn, requires us to obtain specific information for a number of different components. First, we need to uncover the genetic basis for both the preference and the trait (discussed above). Gathering this kind of information will typically require that the species we are investigating is one "which can be reared in the laboratory in large numbers" (Heisler *et al.* 1987: 112). One reason for conducting such studies in the laboratory derives from the condition of assortative mating which is essential to the runaway process; it will be necessary to keep track of who is mating with whom in order to ensure that any genetic correlation between trait and preference is the result of assortative mating rather than some other process. In addition, the laboratory sample must be sufficiently large in order to avoid sampling errors. Once the preference and trait have been determined to have a genetic basis, we will need to obtain specific details on a variety of genetic parameters—e.g., distribution frequencies and heritabilities. Parametric information is particularly crucial in that these quantities are the primary causal determinants of not only the end results of the runaway process but even whether it can be initiated at all (Hall *et al.* 2000; Kirkpatrick 1987; Lande 1981; Pomiankowski 1987a).

We can arrive at an estimate of the correlation between mate preference and trait by employing statistical methods which allow us to gauge how likely it is that the presence of (for example) the mate preference in daughters is determined by the fact that their fathers had the preferred male trait (alternatively: the likelihood that the preferred trait in sons is determined by the fact that their mother had a preference for the trait). Alternatively, we can measure the mean expressions of the preference and trait of male and female offspring who share a father but not a mother (Arnold 1983: 80, 85-86; Heisler *et al.* 1987: 113). These averages are used as proxies for the trait value of the parent (what is called "breeding value"). The degree to which these averages are correlated with each other represents the degree to which the female preference allele and the male trait allele are correlated. This is the genetic covariance of trait and preference.

The existence of positive genetic covariance of trait and preference is necessary but not sufficient for demonstrating runaway. Beyond showing covariance, we must also demonstrate that the male trait exhibits a history of directional evolution, as originally suggested by Fisher (1930; Kirkpatrick 1996: 2135; Kirkpatrick and Ryan 1991: 37. See figure 3.2). If the runaway process is at work, male phenotypes should progress away from their viability optimum towards ever more extreme trait values, until the progression is checked by selection such that the benefit to males obtained from being preferred by females is equal to the viability (or other) costs incurred by males in virtue of the extreme development of their trait, or until all the genetic variation in trait value has been used up (Kokko 2001: 323).

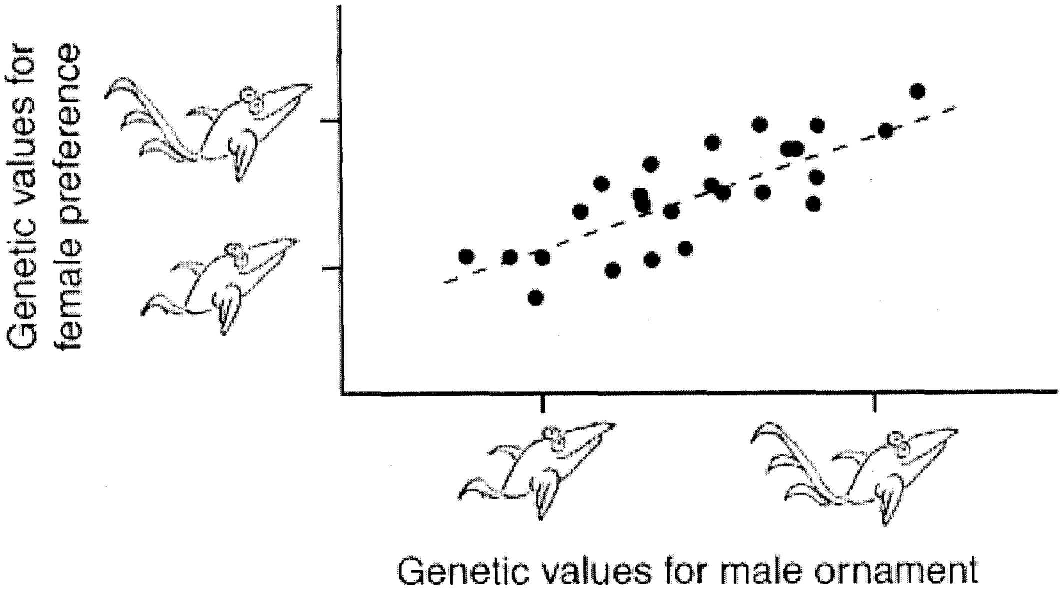

Figure 3.2 A hypothetical cluster of genetic values representing one trait expressed in males (tail ornament) and a second trait (preference) expressed in females. The dashed line is the regression B/G, where B is the genetic covariance between ornament and preference, and G is the genetic variance for the ornament. From Mead and Arnold (2004: 266).

There is an important distinction between what is being predicted here and the above comment by Ryan to the effect that “there is no inherent direction to the evolution of male traits under the runaway process alone.” While it is true that basic runaway models do not entail that male traits will necessarily evolve towards one particular extreme (e.g. larger rather than smaller), such models *do* entail that male traits will evolve towards *some extreme value or other*, either higher or lower than the viability optimum.[14] The proverbial fork in the road might serve as an illustrative analogy in this regard. That is, while arriving at a

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[14] I have chosen the term “viability optimum” rather than the occasionally used “natural selection optimum” in order to avoid the dubious natural selection/sexual selection distinction. These terms should nevertheless be treated as synonyms.

fork in the road does not itself entail that one will go, say, to the right, it does entail that one will go *either right or left*.

A third result of the process relates to heritable variation in total fitness. Because of the predicted balance between increased attractiveness and decreased survival mentioned in the preceding paragraph, overall there should be no direct correlation between fitness and attractiveness if the runaway process is at work. Anytime a male augments his attractiveness by increasing his display, he consequently decreases his viability; anytime he augments his viability by decreasing his display, he becomes less attractive (Lande 1981; Kirkpatrick 1982. See also Pomiankowski 1988). Thus his reproductive success will remain effectively the same no matter how attractive he becomes (Kokko 2001: 323). As is the case for the preceding predictions of runaway models, in order to be warranted in invoking runaway we must provide evidence for this condition—i.e., we must show that attractiveness and total fitness are not positively correlated.

3.5.4. Demonstrating that Some Male Trait Reflects Historical Influence of a Runaway Process which has Since Ended

If we are seeking to demonstrate a past history of a runaway process which is no longer active, we will need to satisfy evidentiary conditions which are rather different from the ones detailed above. The demonstration requirements mentioned in the preceding section only have probative value if we are attempting to catch a population *in flagrante delicto*, as it were. If we want to show that a trait reflects runaway activity at some time in the past, we will need to gather support for predictions for the long-term or end results of a runaway process. Because the direction in which male traits will develop as a result of runaway is completely unpredictable, it is nearly impossible to know what we might look for in the way of phenotypic properties which could indicate that runaway was responsible for the current state of a particular male trait. At present, no proposals have been offered in this regard, and there is little hope among researchers that this situation will change (Heisler *et al.* 1987: 109; Kirkpatrick and Ryan 1991: 37).

Actually, it is not quite accurate to say that there are *no* proposals for uncovering whether the runaway mechanism has shaped some aspect of the population in a past selection regime. Since writing his dissertation on the evolution of the human brain via runaway sexual selection, Geoffrey Miller has come to question whether the runaway process could thoroughly explain the brain's/mind's progression. Below I will review both Miller's reasons for believing that runaway was involved as well as his reasons for ultimately "burying" runaway as a candidate explanation (Miller 2000b: 98).

3.5.4.1. Positive Evidence: Evidence of Unpredictability

One of the reasons Miller thinks we have cause to suspect the influence of Fisher's runaway process on the brain/mind is that this trait shows indications of being the result of an "evolutionarily unpredictable" process (*ibid.*, 98). The reader can get a feel from what unpredictability looks like

> if you look at the diversity of sexual ornamentation in

> closely related species. Of a dozen species of bowerbirds, no two construct the same style of courtship nest. Of three hundred species of primate, no two have the same facial hair color and style. These differences cannot be explained as adaptations to different environments—they are the capricious outcomes of sexual selection," (77)

all of which are symptomatic of "[r]unaway's unpredictability" (77). In the context of human mate choice, unpredictability can be readily perceived if one considers that

> [m]any of the human mind's most interesting capacities do not appear in other apes, and those of most hominids are not discernible from the archeological record (98).

Human mental life is vastly different from others in the primate family—just the kind of thing one would expect from a process whose dynamics do not allow us to form any expectations regarding its direction or outcome.

The orthodox response to the unpredictability of runaway has typically been the pessimism mentioned above with respect to being able to form expectations about what the outcome of a process governed by runaway will look like and, therefore, whether we can know if runaway was involved in the formation of a particular evolutionary endpoint. The pessimism derives from the commonsense understanding of the concept of unpredictability. When a process is characterized by unpredictability, that usually means that there is some insurmountable epistemological barrier (sometimes due to systemic indeterminacy of the quantum mechanical variety, sometimes due to irremediable ignorance of deterministic yet unfathomably complex systems) which bars us from forming expectations as to the outcome of that process, even given knowledge of the initial conditions. Now for many systems which are typically thought of as unpredictable, we can form expectations about certain *kinds* of outcomes. Take the paradigmatic unpredictable process—dice rolling. Given two fair six-sided dice, we cannot predict what the pair will add up to once thrown. But we *can* make some other sorts of "predictions"—for example, we can predict the distribution samples, and we can predict that the pair will not add up to more than twelve, or that it will not add up to a dragon, or anything else that is logically entailed by the initial conditions or the governing dynamics. Of course, these predictions are trivial and therefore not very interesting.

If runaway produces unpredictable outcomes in the classical sense that dice rolling produces unpredictable outcomes, then we cannot form any expectations about what would be true of a particular evolutionary outcome if runaway had occurred, in the same way that we cannot form any expectations about what would be true of the outcome if someone had thrown the dice fairly (rather than, say, deliberately placing them both with "6" facing upwards). Thus the diversity of bowerbirds' nests or primate facial morphology cannot be suggestive of a runaway process, because the unpredictability of runaway means that we necessarily lack the kind of knowledge we would need in order to take something (e.g., "diversity") to be suggestive of its influence.

If, on the other hand, Miller is claiming that the runaway process allows us to form expectations about its outcome in the same way that dice-rolling allows us to form expectations about its outcome (trivial though they may be), then we need to see whether the kinds of things Miller is claiming to be evidence of the influence of runaway follow logically from the assumptions of runaway models.

Even a moment's glance at the items Miller offers in support of the notion that runaway was partly or entirely responsible for this or that feature of the natural world makes it clear that nothing he is giving us follows from the logical framework of the runaway process. What's more, the kinds of things he offers as indicative of runaway can be accommodated by any of the other major models of sexual selection. Indeed, most theorists see it as an essential goal of *any* model of sexual selection to be capable of explaining the kind of diversity which Miller takes as evidence of runaway. For example, Grafen's (1991a,b) model was designed to explain that diversity while axiomatically *excluding* any type of runaway effect.

At best, then, Miller's beliefs about the influence of runaway are entirely without support. Despite these failures, it is instructive to examine Miller's comments on why we cannot predict where the runaway process will lead:

> The runaway process is very sensitive to initial conditions and random events. Runaway's initial direction depends on the female preferences and male traits that happen to exist in a population. Runaway's progress depends on several kinds of random genetic events such as sexual recombination, which mixes genes randomly every time two parents produce offspring, and the evolutionary process called genetic drift, which eliminates some genes by chance in small populations, as a result of an effect called 'sampling error.' Because runaway is a positive-feedback process, its sensitivity to initial conditions and random events gets amplified over time. These effects makes runaway's outcome quite unpredictable. It never happens the same way twice" (Miller 2000b: 76).

This is a fine characterization of runaway, as far as it goes. But then, every evolutionary process is "very sensitive to initial conditions and random events" and "depends on several kinds of random genetic events." Consider the "good genes" process, which is traditionally posed as the antithesis of runaway. The progress of the "good genes" process "depends on several kinds of random genetic events" such as sexual recombination, genetic drift and a feedback loop. Yet only when the discussion turns to runaway—a process famed for its unpredictability—does the endemic randomness of evolutionary progress receive mention.

3.5.4.2. Negative Evidence: Directionality

One thing which leads Miller to reject the idea that runaway was involved in the evolution of the brain/mind is the rapid directional increase in the size of the human brain.

> It seems to me that the...trend toward larger brains should be explained rather than ignored. Pure runaway cannot explain it, because runaway does not have any intrinsic bias toward larger ornament size, higher ornament cost, or greater ornament complexity (*ibid.*: 81).

And later,

> Pure runaway is not biased in any particular direction, yet for the last two million years human brain evolution has shown a consistent trend towards larger size and higher intelligence. Runaway should not be so consistent (*ibid.*: 98).

Again, Miller gets the theoretical features of runaway roughly correct. There is no inherent bias in a runaway process which would necessarily cause the brain to consistently increase in size, cost, or complexity, and the mind to increase in intelligence. But it does not follow from this that we can *reject* the influence of runaway anytime we notice a directional trend. In fact, pure runaway *does* logically entail *some* kind of directionality (see section 3.5.1). It just doesn't logically entail that the male trait will increase. But that a trait does increase in (say) size is certainly *consistent* with runaway. After all, part of runaway's original mandate was to explain directional increases in male traits (Fisher 1930). The only way that the directional increase in brain size would rule out runaway as a candidate explanation would be if some logical feature of runaway actually *prevented* directional change from taking place. It simply does not follow from the fact that runaway has no "intrinsic bias" toward large brains that it cannot *accommodate* the evolution of larger brains. To repeat the quoted passage from Ryan (1990), "this theory can accommodate, but does not predict, the exaggeration of male traits under sexual selection."

3.6. Indicator Mechanisms

The passage attributed to Fisher at the beginning of section 3.4 continues:

> Whenever appreciable differences exist in a species, which are in fact correlated with selective advantage, there will be a tendency to select also those individuals of the opposite sex which most clearly discriminate the difference to be observed, and which most decidedly prefer the more advantageous type. Sexual preference originat-

> ing in this way may or may not confer any direct advantage upon the individuals selected, and so hasten the effect of the Natural Selection in progress. It may therefore be far more widespread than the occurrence of striking secondary sexual characters (151).

At the present time, the most common method by which researchers (certainly evolutionary psychologists) attempt to explain why females prefer certain males is via "indicator" or "good genes" models. These models are designed to explain how females might evolve to "clearly discriminate the differences" in males "which are correlated with selective advantage" and to make their mate choices based on those differences. Here I will quantify basic theoretical aspects of these differences in males and their correlative relationship with selective advantage. Following that, I examine the general process by which females putatively evolve to prefer males based on traits that are correlated with high viability (or some other selective benefit that is distinct from attractiveness). Lastly, I look at what is required to demonstrate that such a process is at work in a particular population, as well as what is required to show that females actually *do* choose their mates in the way proposed by indicator processes.

3.6.1. Indication

Let us define an "indicator" as anything which (a) allows reliable inferences to be made about some aspect of the world and (b) can be perceived by other organisms. Following Maynard Smith and Harper (2003), I divide the class of indicators into three subclasses:

> *Cue*: features of the world "that can be used by an animals as a guide to future action,"
>
> *Index*: some aspect of behavior or morphology which affords reliable inferences about quality because it is impossible to fake, and which evolved to alter some perceivers' behavior,
>
> *Handicap*: some aspect of behavior or morphology which affords reliable inferences about quality because it would be possible but unprofitable to fake, and which evolved to alter some perceivers' behavior.

In general, when we claim that some male trait is an indicator we imply that this trait affords reliable inferences about some component of male fitness upon which females base their mate choices. Now given that these three types of indicators differ conceptually, models which invoke one kind of indicator must necessarily make some predictions which differ from those of models which invoke another kind, in order that any probative value might accrue to the results of our experiments. Thankfully, differences among the three kinds of indicators *do* allow us to make critical predictions which, if true, would speak in favor of one kind rather than another. Here I outline which conditions need to be fulfilled in order to show that some trait is a particular kind of indicator used in female mate choice in the manner specified by indicator models of female preference.

3.6.1.1. Demonstrating Indication: General Requirements

The idea that a trait is an indicator (of any kind) used in mate choice implies that females have evolved to prefer males which possess this trait because of some type of law-like regularity between the trait and some component of male fitness (e.g., viability). This implication not only follows conceptually from the condition that the trait afford *reliable* inferences (for, if the link between the trait and male fitness were not law-like, inferences about fitness based on the presence or absence of the trait could not be reliable), but also from the fact that the link between the trait and the property indicated would have had to be relatively stable over evolutionary time in order for perceivers to have been able to garner information which would have been adaptive in many consecutive generations. Thus in substantiating any claim to the effect that trait *T* is a cue used in mate choice, we will have to demonstrate that there is some law-like regularity between *T* and a component of male fitness, *M*. In general, any such demonstration must proceed by first demonstrating (via methods discussed in chapter 2) that differences in *only M* between males cause differences in reproductive success. Having demonstrated this would establish that *M* is, in fact, a component of fitness. Next, in order to show that *T* actually does allow females to learn something about males which is selectively relevant, we would need to show that (either quantitative or qualitative) differences in *T* exhibit causal covariation with differences in *M*.

Following that, we would need to show that females are capable of perceiving *T*, and that those that perceive *T* use it as a guide to mate choice. Now, if *T* is used by females as a guide to the value of some *M* in males, females' responses to males should vary with the value of *T* (Maynard Smith and Harper 2003: 52), and any demonstration would need to include evidence of this. This may not always be possible. As Maynard Smith and Harper note, many male mating displays are extraordinarily complex, and quantifying differences in values of *T* (especially when *T* is some kind of dance or performance)

> is often difficult. For example, when a receptive female Silver-washed Fritillary butterfly encounters a male she releases a pheromone and then flies off in a straight line parallel to the woodland floor. The male follows, repeatedly swooping under her to emerge just in front of and above her head, before diving down again. He thus flies much further than she does. If the female accepts her suitor she simply drops to the ground to mate: otherwise she zig-zags away in flight. It would not be easy to demonstrate that the female's response varied with the male's performance (52).

Yet such a demonstration remains unquestionably the obligation of researchers who invoke indicator models.

There is an additional requirement for demonstrating that some trait *T* is an indicator which has not, to my knowledge, been mentioned by researchers, possibly due to the unimaginable difficulties involved in meeting it. On top of establishing each of the evidentiary components mentioned in the preceding paragraphs, it would also be necessary to show that *T* is used in mate choice by females *because* it affords reliable inferences about *M*. This amounts to a far greater burden than showing merely that females who base their mate choices on *T* have (or had at one time) fitter offspring than those that ignore *T*, a task which is trivial by comparison. Demonstrating that females who base their mate choices in *T* have fitter offspring would only serve to establish that, *ceteris paribus*, females should mate with those males which possess the most selectively advantageous values of *T*. This is quite a different thing from showing that females actually *use* the information about fitness represented by *T* in the manner described, much in the way that human consumers might use information about the engineering quality of a number of different cars in order to choose among them.

Prima facie this requirement might be slightly extreme. For, might it not be enough to show that (1) *M* is a determinant of fitness, (2) *T* causally covaries with *M*, and (3) females base their mate choices on *T*, and infer from these three premises that females prefer *T*-males because *T* causally covaries with fitness?

Recall the discussion of Ryan's work on *P. pustulosus* in section 3.4.5. Ryan reports that there is a law-like regularity between lower-frequency chucks and higher reproductive success, owing to fact that chuck frequency is an inverse function of size, and pairs in which the size difference between males and females is smallest (she is usually larger) tend to have fewer unhatched eggs (Andersson 1994: 110; Ryan 1985). Although Ryan showed that females prefer lower-frequency chucks *and* that lower-frequency chucks are causally linked to a determinant of fitness (number of eggs hatched), the fact that females from phylogenetically prior species in which males do not chuck also prefer chucks severely undermines the notion that *P. pustulosus* females base their mate choice on chuck frequency *because* it is linked to a component of male fitness. Thus, even where the above premises (1), (2), and (3) all turn out to be true, we cannot reliably infer that females prefer *T* just because *T* causally covaries with fitness.

This is where we run into problems. Most of the time, our principal evidence that a given trait (be it behavioral or morphological) *T* was selected to perform a particular function *P* is the fact that *P* is a determinant of fitness and that differences in *T* produce large differences in performance values of *P*. In the case of Ryan's frogs, however, while differences in *T* (the female preference for chucks of low-frequency chucks) do, in fact, produce large differences in *P* (finding a reproductive success-maximizing mate), we know from the fact that the preference for low-frequency chucks was widespread among sister species of *P. pustulosus* before chucks even existed that the preference *T* could not have been selected to perform *P*. Thus, in instances where some male trait *T* causally covaries with some component of fitness *M* it is likely that we will need to break the causal link between *T* and *M* and then see if, after several generations, the female preference for *T* persists. If it does not persist, this may be good evidence that females based their mate choices on male possession (or degree of possession) of *T* because differences in *T* indicated differences in values of *M*. If *T* was used by females in mate choice because it reliably indicated a male's *M*-value, once the link between *T* and *M* is broken, subsequent generations of females should evolve *not* to use *T* in mate choice so long as the selective forces which promoted the evolution of *M*-linked mate choices (via *T*) are still operating.

3.6.2. Demonstrating Indication: Indices

Along with inheriting all of the conditions for demonstration detailed in the preceding section, showing that some trait *T* is an index will carry additional burdens of its own. In establishing that *T* is an index we will need to show that *T* *evolved to inform perceivers* about some feature of the world. In the context of female mate choice, generally what is required is evidence that *T* was selected for the purpose of informing females about some component of male fitness *M*. On top of that, we must also show that the information conveyed could not be faked, given what we know about the focal species. An excellent example of this condition is provided by Maynard Smith and Harper (2003). Tigers can often be seen making scratch marks on a tree as high up as they can reach, a behavior which is thought to be for territory-marking purposes. Given what we know about tigers (for example, that they are incapable of finding boxes and standing on them in order to reach higher), the information conveyed by the height of scratch marks cannot be faked; it will always be a veridical representation of tiger size (*ibid.*: 46-47). To establish that *T* is an index, we must show that it bears this kind of unfakeable relation to the information it conveys, such that *T* could not vary independently of *M* (*ibid.*: 33). This property of unfakeability is what makes indices reliable sources of information for females. For example, if tigers somehow did acquire the ability to stand on boxes in order to mark trees, the unfakeable relation between scratch marks and tiger size would be broken; scratch marks could vary independently of tiger size. Thus, scratch marks would not afford reliable inferences about tiger size, and their role as indices of male quality would be undermined.

3.6.3. Demonstrating Indication: Handicaps[15]

Following Zahavi (1975) and Grafen (1990a), a *handicap* is an indicator of male quality which is reliable because the costs of faking the level of quality represented by the trait outweigh the benefits of faking it—i.e., it is possible but *unprofitable* to fake. Suppose that T_a is a male trait and that different values of a indicate corresponding levels of phenotypic quality, Q_q, which also differ among males (such that T_a indicates Q_q). In addition, suppose that the strength of a female's preference for a particular male varies directly with the value of q which she perceives him to have. But while a is readily perceivable by females, q is not—to get information about q they must rely on the value of a. Now, while males with lower values of q are *capable* of values of $a > q$, the costs to a male when $a > q$ are greater than those for a male when $a = q$—i.e., the costs of advertising at a given level are higher for lower-quality males (Grafen 1990a,b). Thus, the costs of advertising at a given value of a ensure that only males with a level of quality indicated by a will invest in advertising at that level. This corresponds to Zahavi's (1975) original idea that signaling is reliable because it is costly. Grafen then found an ESS in which natural selection alters the amount of a male's resources devoted to advertising until $a = q$.[16] When this strategy obtains, the male quality advertised represents his actual quality (signaling is "hon-

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[15] In fact, the only known workable model of the handicap mechanism is one where the female preference is directly selected. Thus discussion of that model could have been included in the section on directly selected preferences, rather than indirectly selected preferences. I have chosen to include it in the latter section because it seemed to me that continuity with the discussion of the dynamics of indication was more important than continuity with the broader category of directly selected preferences. I include this note so as to ensure that the reader is not confused on the matter of whether the Handicap mechanism is related to direct or indirect selection.

[16] It should be pointed out that Grafen (1990a) also found an ESS in which males will not devote any resources to developing T and females will not develop a preference for T.

est"), and females can make reliable inferences about male quality based on the value of *a*.

A peculiar feature of establishing that T_a is a handicap is that, contrary to the conditions for showing a trait to be an index, we must demonstrate that it is possible for a male to fake the relation between the level of quality indicated by *a* and the actual level of quality, and that the reason he does not fake his level of quality is *because* it would not pay to do so, rather than for some other reason.[17] Maynard Smith and Harper state that, where we find that a male *could,* but *does not,* fake the relation between his quality and the quality indicated "it is because it would not pay the signaler to make a dishonest signal, and this in turn implies that the signal must have a strategic cost" (Maynard Smith and Harper 2003: 33).[18] As carefully reasoned as Maynard Smith and Harper's (2003) *Animal Signals* is, it must be pointed that the mere fact that a male *could* produce a signal which suggests better quality than he actually has is not sufficient grounds for inferring that this signal is part of a handicap system. The distinctive premise of Zahavi's handicap principle is that costs of representing oneself as having a particular level of quality are only worth paying if one *does* have that level of quality. This idea makes quantifying the costs involved in a given level of signaling crucial to any demonstration of the handicap mechanism in operation. Now, costs in this domain are no different conceptually from costs incurred by other types of behavior, and hence the criteria we need to meet in order to measure them

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[17] I have no idea how showing that some male could possibly fake the relation between quality indicated and actual quality might be accomplished, but I imagine that it would have to involve showing a physiological upper limit on a male's capacity for display and then showing that he is not displaying at that capacity.

[18] See below for definition of "strategic cost."

will not differ. What we are looking for, then, are differences in *reproductive success* caused strictly by differences in costliness of various levels of advertisement for particular individuals (i.e., controlling for any impact on reproductive success caused by increased attractiveness due to better advertising). Here we must measure the development costs (cost in resources required to develop a given value of *a*) and vulnerability costs (predation risk incurred in order to develop a given value of *a*) (Maynard Smith and Harper 2003: 8) for each set of trait and quality combinations (a, q) (e.g, $[a_1, q_1]$, $[a_2, q_1]$, ...). If some type of handicap signaling system is in place, costs should increase along with increasing values of *a* for a given value of *q*, and, for sets in which *a* is greater than *q*, males should have lower reproductive success than they would had they adjusted their level of advertisement to accurately represent their quality. If we find that males do not have lower reproductive success when they advertise themselves as being of a higher quality than they actually are rather than advertise honestly, then the costs for advertising at a given level are *not* higher for low-quality males, implying that there is no handicap mechanism in place.

Occasionally one sees confusion in the literature with respect to whether costs need to be involved if signals are going to remain reliable. For example, Grafen (1990b: 521) himself takes his model to show that "[i]f we see a character that does signal quality, then it must be a handicap." But this simply cannot be correct. Costs are neither necessary nor sufficient for ensuring honest signaling. First, we saw earlier that indices are perfectly reliable signals of quality, yet they can very easily be cost-free, and thus not handicaps. Making scratch marks for a tiger 2.5m certainly is a reliable signal of quality, but because it is unfakeable, rather than because it is costly. Second, just because there are costs involved in producing a signal does not imply that those costs are what makes that signal reliable. Take warning calls, for instance. There can be heavy costs involved for an animal who alerts conspecifics to the presence of a predator, but those costs are not there because, "otherwise, someone would be tempted to lie" (Maynard Smith and Harper 2003: 16). Rather, they are necessary in order to transmit the information to receivers. It will be of the utmost importance to discern between *these* kinds of costs (what Maynard Smith and Harper call "efficacy costs"), which are required merely to get a signal across, and additional costs which are necessary to prevent cheating (what Maynard Smith and Harper call "strategic costs").

3.7. The Evolution of Female Preferences for Indicators: Indirect Selection

When discussing the evolution of the female preference for an indicator of male quality, it is important to keep in mind the distinction between (a) the indirect selection of a female preference for an indicator via genetic correlation with the male quality indicated, and (b) the direct selection for a female preference via increased reproductive success. In line with Fisher's verbal argument, mathematical modeling has confirmed that females can evolve preferences for male traits indicating viability, which will, through linkage disequilibrium, eventually cause the exaggeration of indicator and the female preference (Pomiankowski

1987a, b; Pomiankowski 1988). In these models, a sufficiently frequent female preference for a male trait which is genetically correlated with a component of male fitness (i.e., other than attractiveness—e.g., viability) becomes genetically correlated with those same fitness alleles through linkage disequilibrium brought on by assortative mating. In this respect, then, the evolution of female preferences for viability indicators proceeds in the same manner as does the evolution of female preferences for male traits which are not genetically correlated in any important respect with viability. It follows, then, that the conditions for demonstrating the responsibility of an indicator process for the evolution of female preferences will not differ from those outlined for demonstrating instances of the runaway process—with one exception. The major distinction between the two types of models (or, perhaps more accurately, between the two poles of a "sexual selection continuum" [Kokko *et al.* 2002]) is that, in indicator models, offspring of females with a preference for viability indicators experience enhanced mean viability because of their fathers' "good genes" (Kirkpatrick 1987: 73; Kokko *et al.* 2002; Ryan 1994; Ryan 1997: 193). Thus, in order to ascertain whether a "pure" (i.e., viability-neutral) runaway or Indicator process is involved (assuming one of them is), we need to show whether there is a generational increase in mean offspring viability (Kokko 2001: 323).

3.7.1. *The Evolution of Female Preferences for Indicators: Direct Selection*

Whether there can be direct selection for a female preference for an indicator depends *inter alia* on whether the female preference for a particular male trait causes a direct increase to her fecundity (as in Grafen's 1990a model) or some other determinant of her reproductive success. It is only in this case that females with the preference will outreproduce females without the preference, and hence only in this case that the female preference of an indicator will qualify as an adaptation. If a model features a viability advantage accruing to offspring because of their mothers' tendency to mate with high-quality males, that model describes a process of *indirect* selection, *not* direct selection. Thus, it would be incoherent to suggest that females "were selected to prefer males with good genes," for it runs together two incompatible types of selection. Furthermore, insofar as direct selection improves the mean fitness value in the population, it is also at odds with a good genes process, which "generates indirect selection on the preference, dragging it from its fitness optimum (Kirkpatrick and Ryan 1991; Pomiankowski *et al.* 1991). Evolution of the preference under the good genes process does not produce a eugenic benefit to the population" (Kirkpatrick 1996: 2134).

3.7.2. Assumptions of Cost and the Cost of Assumptions

By now the reader should have at least a partial appreciation for the amount of careful and patient work that goes into the theoretical and empirical study of mate choice and sexual selection. On the theoretical side, difficulties in formulating realistic models arise from several places. First, the complexity inherent in biological systems as well as the variety of systems makes it difficult to know how well a particular model will apply to a given system. Models may be based on parameters which somewhat accurately describe one population but which have only moderate causal influence on the dynamics of another, closely related population (Clutton-Brock 2004). Second, the amount of work involved in measuring crucial parameters impedes our understanding of how well a particular model describes *any* biological system. Nowhere has this been more of an area of controversy than in the context of the costs to reproductive success (as opposed to, for example, energy costs, which may or may not impact reproductive success [Heisler *et al.* 1987]) of mate preferences—what can be more properly thought of as the strength of direct selection on mating preferences (Hall *et al.* 2000; Kirkpatrick 1996; Mead and Arnold 2004; Pomiankowski 1987b; Pomiankowski 1988). Depending on the costs involved, models may not only by unrealistic but actually *invalid*. It is known, for example, that preferences for suboptimal males will not persist where there is a weak genetic correlation between trait and preference and the costs of the preference are particularly high (e.g. Kirkpatrick 1996). At present, there is no empirical data on the strength of direct selection on female preferences (Kirkpatrick 1996: 2135; Mead and Arnold 2004: 269), as well as for a host of other parameters.

Assumptions of cost also play important roles in other areas of mate choice, particular with respect to the handicap principle. The costs required for males to advertise at a given level is the lifeblood of the handicap principle, which makes measuring them all the more important. All too often it is assumed that some male trait functions as a "handicap" simply because it appears burdensome. There is absolutely *no* reason to make this kind of inference. For one thing, we've already seen (section 3.6.3) that the existence of costs *per se* is not sufficient for us to infer that some male trait is a handicap, owing to the difference between an "efficacy" cost and a "strategic" cost. For a trait to be a handicap, the costs involved must be *greater* than what is required merely to get the desired signal across. The only way to determine whether this difference obtains is through direct tests (see above). One cannot "eyeball" it, as it were.

The formidable criteria for demonstrating a handicap mechanism in action can be instructively contrasted with the evidence advanced by evolutionary psychologists towards this end. What we invariably find is that seemingly maladaptive behavior is transformed through clever adaptationist yarn-spinning into some sort of display used for the purposes of showing off one's prowess in some domain for the evaluative benefit of potential mates. This in and of itself need not be seen as a problem within evolutionary psychology. For, as I have been arguing, it behooves researchers to explore available alternative models. The problem in evolutionary psychology is that there are no cost measurements to accompany the adaptationist yarns. The yarns themselves are considered probative.[19]

Conclusion

The extant work on the evolutionary psychology of human mating behavior can be nicely captured by the word "inadequate": inadequate grasp of the conceptual issues, inadequate representation of available explanatory frameworks,

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[19] The Zahavis' (1997) monograph is the gold standard in this regard.

inadequate attention to alternative explanations, and inadequate evidence offered in support of hypotheses.

In addition to these, there is yet another aspect of evolutionary psychology which is terribly inadequate for the purpose of uncovering the evolutionary history of human mating, one which was introduced in the last chapter but which has gone unmentioned in this one. This inadequacy is the design inference method (DIM) itself. There are two central limiting factors for DIM's success in producing reliable conclusions: (1) our knowledge of ancestral selection pressures, and (2) how good we are at formulating *a priori* design criteria and matching the properties of organisms to those criteria. The preceding discussion has revealed the many ways in which mate preferences and sexually selected characters can take arbitrary sorts of forms for which there could be no *a priori* design criteria, for the sole reason that these traits often do not serve the kinds of useful purposes which make the search for conformity to *a priori* design specifications a reasonable strategy (insofar as it *is* a reasonable strategy). Formulating *a priori* design criteria in the context of mate choice is somewhat akin to telling an engineer to describe the set of criteria a thing would need to satisfy if it were designed to be completely useless. This problem will take center stage in my critical comments in the next chapter.

4. Finding a Beginning: Evolutionary Psychology and the Origins of *Homo*

Introduction

The relevance of the past to evolutionary psychology is best understood by appreciating its general importance to the study of adaptation (see chapter 2). Evolutionary psychologists have been at pains to emphasize that adaptations which exist in the present are the result of what a species experienced during *past* selection regimes. Additionally, extant adaptations are influenced by the line of descent of the organism, a point which has received comparatively little attention from evolutionary psychologists but with which we could expect them to agree, given their commitment to the principles of evolutionary theory. These two components of a species' evolutionary history—past selection regimes and line of descent—together determine which adaptations we find in contemporary phenotypes. With respect to our own species, then, evolutionary psychology's interest in the past should be clear: knowledge of what our evolutionary ancestors were like and what sorts of adaptive problems they faced is essential for explaining why contemporary humans have the adaptations they have, including their psychological adaptations.

As mentioned in 2.3.2, evolutionary psychologists use a method called "adaptive thinking" to reveal the function of an adaptation. The essence of adaptive thinking is to find which of an organism's traits are the result of selection pressures known to have affected the evolution of the organism. According to Tooby and Cosmides "we know with certainty thousands of important things about our ancestors and the world they inhabited," (Tooby and Cosmides 2005: 23) which can be used to guide our adaptive thinking.

A significant portion of evolutionary psychologists' adaptive thinking is predicated on the notion that the attainment of meat through hunting was a major influence on the evolution of our earliest hominin ancestors. Thus, we can read that "[a]ncestral people got their vegetables from gathering and their meat from hunting" (Buss 2003: 14), which they procured for their kin (*ibid.*, 7) and "for whom the resources derived from hunting were critical to survival" (*ibid.*: 28) because "[i]ts absence creates problems for nourishment and sustenance" (*ibid.*: 33).

I pursue two goals in this chapter: (1) to demonstrate that there is little support for what evolutionary psychologists believe about the hominin diet (and whatever is thought to follow from those beliefs), and (2) to show that preferred evolutionary psychology methodology cannot provide support for hypotheses regarding evolutionary history. As the following discussion will make clear, we know very little about the lives of our earliest hominin ancestors, how they interacted with each other and with local flora and fauna, or what was selectively important for them. Moreover, at present it is unclear how much we will *ever* know. As evolutionary biologist Michael J. Ryan has expressed in another connection, "[i]t is unfortunate, but the passage of time results in serious constraints for those interested in historical sciences" (Ryan 1996: 6). The relevant constraint with respect to our knowledge of early hominins is a general lack of data concerning virtually every aspect of their behavior and its selective consequences.

4.1. The Early Hominin Diet: Food for Adaptive Thinking in Evolutionary Psychology

The story in evolutionary psychology is that meat procured through hunting was of enormous value to Pleistocene women. A woman who was able to obtain a portion of Man the Hunter's kill would have aided her survival as well as that of her children (Buss 2003: 20-21). Women who were biased towards mating with men who provided them with life-giving resources such as hunted meat had higher reproductive success relative to women who chose mates indiscriminately (*ibid*.: 20). Eventually, women evolved a preference for men with resources. This adaptation sees its modern-day realization in the cross-cultural female preference for men with large amounts of economic resources (*ibid*.: 24). We see a complementary strategy in contemporary men all over the world, who display their resources in order to attract women. Whereas in prehistoric times men needed to kill large game animals in order to demonstrate their value as a mate and provider, modern men can get by simply by "flashing a lot of money to impress women, driving an expensive car, telling people how important they are at work, and bragging about their accomplishments" (*ibid*.: 99-100). All of this is, of course, in addition to the routine hunting that is common to contemporary hunter-gatherer societies.

Because hunting was so crucial for the early hominins, our ancestors evolved a sexual division of labor which allowed men to engage in "intensive hunting...with females exploiting the more sessile food sources" (Tooby and De-

Vore 1987: 224. See also Tooby and Cosmides 2005: 24). The "archaeological and paleontological data show that across evolutionary time, males predominantly hunted and females predominantly foraged" (Silverman and Eals 1992: 534). "During the days, women would have gathered fruits, vegetables, tubers, berries, and nuts" while "[m]en would have tried to show off by hunting game" (Miller 2000b: 181).[1] Relatedly, the "sexual division of labor between hunting and gathering during hominid evolution" was the "critical factor in selection for spatial dimorphism in humans," attested to by the fact that "various spatial measures showing male bias (e.g., mental rotations, map reading, maze learning) correspond to attributes that would enable successful hunting" (Silverman and Eals 1992: 535).

As the designated hunter, Man the Hunter was depended upon for the precious meat which only he could provide and with which he was able to retain his mate. "Meat that is suddenly not available because an undependable mate decided at the last minute to take a nap rather than to go on the hunt is a resource that was counted on but not delivered" (*ibid.*, 33).

> A man's ability and willingness to provide a woman with resources are central to his mating value, central to her selection of him as a marriage partner, central to the tactics that men use in general to attract mates, and central to the tactics that men use to retain mates. In evolutionary terms, a man's failure to provide resources to his wife and her children should therefore have been a major sex-linked cause of marital dissolution (*ibid.*, 177).

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[1] Although Miller explicitly affirms a sexual division of labor with men hunting and women gathering, it is not clear from Miller's writings whether he attributes the emergence of a division of labor to the nutritional importance of meat. Accordingly, I do not attribute this view to him.

Given that one of Man the Hunter's primary functions was to provide the Pleistocene's most important resource—meat—a man who was not coming home with a prodigious helping of meat was simply not allowed to come home. If he was not fulfilling his adaptive duties, he was of little use to a Pleistocene woman. As their female ancestors before them, women in the modern era stand by their evolved expectations for men to supply them and their children with resources. When these expectations are not met, or when they make more money than their husbands, women's psychological adaptations compel them to initiate divorce. Consequently, a study of divorce in 160 societies (Betzig 1989)

> found that a major cause of divorce is inadequate economic support in twenty societies, inadequate housing in four societies, inadequate food in three societies, and inadequate clothing in four societies. All these causes are ascribed solely and exclusively to men. In no society does a woman's failure at providing resources constitute grounds for divorce (Buss 2003: 178).

For hunting to have had the adaptive importance maintained by evolutionary psychologists, "there must have been a home base" at which "food exchange and meat provisioning" could occur (Tooby and Devore 1987: 224). Big game which was successfully hunted would have yielded a food supply well in excess of what a single hunter could have consumed. This created the opportunity for hunters to use their kills to barter for other things, such as sexual access (Buss 2003). Alternatively, Man the Hunter could have used his hunting success not to provision potential mates, but to show them (a) how much energy he could expend and how much skillful and risky behavior he could engage in, signaling to females how good his genes must be; and (b) share his kills with others to show females how generous he was (Miller 2000b: 312-313, 327-340). Either of these strategies would have required a place for our ancestors to congregate and observe freshly slain carcasses—i.e., a home base.

The behavioral descendants of both a home base living structure and food sharing can be readily perceived in the contemporary human foraging societies, where there is extensive sharing of meat.[2] Additionally, all human societies engage in one form of social exchange or another, "as would be expected if it were an ancient and central part of human social life" (Cosmides and Tooby 1992: 164). Or, contrastingly, we might look for the contemporary analogue of meat sharing in all forms of human kindness and generosity—indeed all generally moral behavior—which fulfills the same sexually attractive function now that it did when it evolved during millions of years ago on the African savannah (Miller 2000b: 320-340). For example, Malcolm X's moral behaviors

> happened to attract a beautiful young woman named Betty Shabazz[3] to become his wife, as they had evolved to do through sexual selection. Likewise for Martin Luther, whose Protestant vision attracted the ex-nun Katharine von Bora to marry him and raise six children (*ibid.*: 320).

Other specific claims about the behavior and social structure of early hominins describe them as having the following attributes:

✓ long periods of biparental investment in offspring
✓ enduring male-female mateships
✓ living in small, nomadic, kin-based bands often of 20 to 100

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[2] See Hawkes *et al.* (2001) for a critical discussion of a number of meat-sharing explanations.

[3] In point of fact, she did not adopt the name "Shabazz" until *after* she was married to Malcom X, who also adopted that name, at the same time as his wife.

√ would rarely (if ever) have seen more than 1,000 people at one time
√ had only modest opportunities to store provisions for the future
√ engaged in cooperative hunting, defense, and aggressive coalitions
√ engaged in extensive amounts of cooperative reciprocation
(Tooby and Cosmides 2005: 24).

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To the extent that the majority of these historical claims are based on the supposition that our earliest hominin ancestors were routine hunters, the foundation for evolutionary psychologists' adaptive thinking is largely illusory. This is because of the fact (undisputed within paleoanthropology) that there is no clear evidence that these early populations did much hunting or procured sizable quantities of meat. The lack of evidence to support this view extends even to the oft-cited work of Glynn Isaac (1978), whose "home base" model of hominin social life has long since been abandoned. As recently as 2005, Cosmides and Tooby have claimed that

> evidence supports the view that social exchange is at least as old as the genus *Homo* and possibly far older than that. Paleoanthropological evidence indicates that before anatomically modern humans evolved, hominids engaged in social exchange (see, e.g., Isaac, 1978) (Cosmides and Tooby 2005: 589).

This is simply false. The so-called "support" for Isaac's view disappeared decades ago, as is well-known by all paleoanthropologists working on these problems. What were thought to be indications of social exchange in 1978 are no longer considered as such. It is not a live hypothesis outside of evolutionary psychology. Through a discussion of paleoanthropological methodology, I in-tend to reveal the means by which evolutionary psychologists' core historical commitments have been eroded.

There is widespread agreement among paleoanthropologists that fossil evidence is the most reliable and important source of information concerning what our earliest hominin ancestors were like (e.g., Blumenschine *et al.* 1994; Lewin and Foley 2004), and "the only factual basis for prehistoric hominid behavioral ecology" (Blumenschine *et al.* 1994: 199. See also Foley 1999: 363). There are obvious reasons for this consensus, most notably that fossil evidence associated with prehistoric hominins (e.g., bones and stone tools) is our most direct connection with their behavior because of the direct causal relationship that these fossils bear to individual hominins. Because of its direct association with the most commonly discovered fossils—jaws and teeth—information regarding the diet is among that which has the highest likelihood of being preserved. Furthermore, as is well-appreciated by evolutionary psychologists, the diet serves as the sturdiest available foundation for behavioral ecological inference (Lewin and Foley 2004: 184). From the perspective of contemporary paleoanthropology, we are what we—or, more specifically, our ancestors—ate.

The preservation of diet-related fossils represents a potential windfall for ecological inference. An organism's diet is fundamental to its ecological milieu. Facts about what the organism ate lead to hypotheses regarding what varieties of biota were extant during the relevant period, how that food could possibly have been procured, what different procurement activities (or strategies) might have meant for an organism's physical, technological, and cognitive capacities, and what sorts of activities might have been afforded by the diet's nutritional quality. Conversely, facts about these capacities can help to narrow the space of hypotheses concerning what the organism could possibly have eaten. Thus the early hominin diet is the door behind which lies a potentially large corpus of knowledge about the human past, and fossil evidence is the key to that door. Indeed, Rick Potts, director of the Human Origins Program at the Smithsonian and Curator of Anthropology at the National Museum of Natural History, has remarked that "[e]arly hominid diets and foraging can be studied *only to the extent that data from the fossil record actually refer to hominid activities*" (Potts 1984: 138, my emphasis).

4.2. Accumulation, Alteration, and Acquisition

Scattered across the savannas of eastern Africa are several sites containing conspicuous accumulations of bones and/or stone tools and fragments (hereafter "accumulations"). Some of the bone surfaces have been altered by teeth, and a small percentage are variously speckled with striae. For anyone interested in questions related to the early hominin diet, these accumulations are thought to hold many of the answers.

What sorts of things do accumulations and their contents tell us about the diet? Unfortunately, there is almost nothing that can be immediately inferred from the existence of a particular accumulation and the alteration of bones therein, for there are a number of explanations which could account for these facts. Here I present rival explanations with respect to three categories associated with accumulations: (1) explanations of the accumulations themselves, (2) explanations of the alteration of bones (specifically striae), and (3) explanations of the method of acquisition of the carcasses formerly composed by these bones. I then discuss the ways in which the different explanations in a given category might be discriminated.

Accumulations were the original impetus for Glynn Isaac's "home base" model of hominin evolution, in which meat procurers were depicted as having transported their meat back to a semi-permanent dwelling for defleshing and apportioning (Isaac 1978).[4] Although this model was seen initially as highly intuitive, it has since been appreciated that there are a variety of reasons for why bones accumulate, and that it is often unclear what has caused accumulation at a particular site. For example, accumulations may occur because of non-hominin carnivores (hereafter "carnivores"), or for reasons having nothing to do with animal activity. It often happens (i.e., often enough) that streams will "pick up" causally unrelated bones from several different sites and deposit them together, giving the *prima facie* appearance of animal influence. Indeed many putative living sites have been shown through taphonomic analysis to be nothing more than "hydrological jumbles" (Lewin and Foley 2004: 96). Uncovering the cause of a particular accumulation thus requires us to make to distinguish between three potential etiologies: water, carnivore and hominin.

Determining the source of bone alteration is equally challenging and may require tests independent from those necessary to determine the reasons for ac-

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[4] The fate of Isaac's model and its implications for evolutionary psychological conceptions of the past and present are discussed below.

cumulation. The kinds of modification in which paleoanthropologists are interested are striae produced by stone tools, the implication being that these were left by hominins engaged in cutting flesh from animal carcasses. Difficulties arise in connection with bone striae because of the significant number of factors known to cause marks which are superficially (and in some cases, microscopically) similar. Researchers must contend with no less than five rival explanations for these markings: (1) carnivore and rodent toothmarks, (2) root etching, (3) sediment scratching, (4) archaeologists' accidental scratching, and (5) faunal trampling are all superficially indistinguishable from hominin cutmarks (Behrensmeyer *et al.* 1986; Potts and Shipman 1981: 577).

Last but not least is the controversy surrounding how, and how frequently and reliably, hominins acquired the types of carcasses on which they left cutmarks. Here there are three candidate explanations. The first and most well-known is hunting, represented in evolutionary psychology (and popular thought generally) as being the predominate method of acquisition among hominins. Next there is "active"/"early"/"aggressive" scavenging, which consists hominins forcibly confronting predatory carnivores and, somehow, wrestling the fresh kill away from its killer. Finally, there is "passive"/"late" scavenging, in which hominins are thought to have made use of whatever nutritional scraps were left over after being tossed aside by the initial predator. The debate over methods of carcass acquisition is particularly spirited, in part due to the perceived implications for hominin social interactions and for human nature itself.

TABLE 4.1

Rival Account Phenomenon	**Natural**	**Non-hominin animal**	**Hominin**
Accumulation	• water flow	• kill site • dwelling	• kill site • central foraging place • home base
Alteration	• root etching • sediment	• rodent/carnivore • trampling	• stone tools • archaeological preparation
Acquisition	N/A		• hunting • aggressive scavenging • passive scavenging

4.2.1. Accounting for Accumulation

Different methods can be used to distinguish hydrological influence from that of hominin activity with respect to bone accumulation. One such method involves analyzing the size and spatial distribution of stone fragments found at a site. Experimental modeling of stone tool manufacture suggests that the size of stone fragments produced during tool manufacture fits a predictable distribution pattern. Where the fragments are predominately small flakes of stone, it is likely that the site where these were discovered was used by hominins for manufacturing tools (Schick 1991: 80). Such an analysis would, ideally, involve sifting the site sediment through a 2-5mm mesh (*ibid.*: 88).

If employed in isolation, however, this sort of analysis is itself vulnerable to corruption by the effects of water flow and thus unreliable (larger fragments tend to filter out the further down stream one looks, thus creating an accumulation of small fragments for reasons unrelated to tool manufacture). Now, the way in which fragments tend to land during the manufacture of certain tools also follows a predictable pattern. Thus conformity of the spatial arrangement of fragments to a predetermined distribution template can help to further discriminate between the effects of water and those of tool manufacturers (*ibid.*: 80). Alternatively, researchers can attempt to literally *rebuild* a chunk of stone (a "core") thought to have been transformed through manufacture into a hominin tool. Should we find that a significant number of pieces originating from the same chunk lie in close proximity to one another, we can reliably conclude that hominins were responsible for their accumulation (*ibid.*: 93).

A related method for ruling out the influence of water is evaluating the degree of fit between patterns of bone composition at a given site with accumulations known to have been the result of carnivore activity. The bone refuse produced by carnivore consumption often embodies distinctive patterns. We are even able to make reliable projections about which subcategories of carnivores (hunters vs. scavengers, for example) may have been involved, depending on factors such as distributional biases towards particular body parts (Bunn 2001; Speth and Tchernov 1998). As in the case of stone fragments, bone accumulations matching a carnivorous template militate against fluvial influence.

We can, in addition, conduct tests for specific effects of water flow. The flow of water over a stationary object (usually a larger stone artifact or bone) across substantial periods of time has a tendency to produce a conspicuous inclination. The flow of water can be discerned where there is a trend of objects in an area to incline in particular direction. Similarly, a pattern in which the long axes of objects are oriented in one direction might suggest the influence of water flow (*ibid*.: 89-91). In sum, the discovery of stone flakes or bones alone is not enough to conclude that the accumulation in which they are discovered is explained by the presence of either hominins or carnivores there. Additional measures must be employed to separate their influence from potentially confounding fluvial effects.

4.2.2. Accounting for Alteration

Because there are relatively few confirmed cases of correctly identified hominin cutmarks (CM), explaining the origin of bone alterations is a particular important task, one for which misidentification holds serious implications. If proper care is not taken to rule out alternative hypotheses, the multitude of factors known to mimic CM could cause gross exaggerations in our estimates of the frequency of CM and, consequently, of the frequency with which hominins were engaged in, *inter alia*, meat consumption (Behrensmeyer *et al.* 1986: 770).

How do we differentiate bone striae produced by hominin tools from striae unassociated with hominin activity? As mentioned briefly above, there are several causes of striae that cannot be distinguished from each other through the use of human vision alone. Fortunately most causes leave distinctive effects at the microscopic level ($\leq$ 400x). Behrensmeyer *et al*. (1986) argue that even at extremely powerful magnification, however, striae resulting from faunal trampling look identical to those resulting from stone knives (cf. Olsen and Shipman 1988).[5]

As is the case elsewhere, discriminating between hominin and non-hominin alteration involves looking for the kind of evidence which would normally obtain if hominins were responsible for striae but which is unlikely to obtain where hominins are not involved (or conversely). Here the discriminating factor is the known tendency of trampling striae to occur in clusters, contrasted with the tendency of CM *not* to exhibit this property. Behrensmeyer *et al.* argue that without these additional, independent pieces of evidence indicating hominin activity (or lack thereof), trampling striae *cannot* be differentiated from CM.

4.2.3. Accounting for Acquisition

As indicated by the discussion above, the work involved in reliably identifying hominin activity is considerable and will nearly always require experiment or painstaking observational analysis to rule out the plethora of alternative hypotheses which are capable of accounting for the *prima facie* evidence. As contentious as these judgments can be, the debate surrounding them pales in comparison to that associated with determining the overall *significance* of CM. For the presence of CM does not by itself tell us *how* hominins came in to possession of the bones on which they are found, and it is this "how" that contains the

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[5] See Haslam (2006) for a related problem concerning the potential indistinguishability of certain kinds of artifact residues even at the microscopic level.

information which is most important to our understanding of the diet and, consequently, the parameters of hominin sociality.

Of course, determining how carcasses were acquired goes beyond determining whether it was by hunting, aggressive, or passive scavenging. What is of even potentially greater importance is the frequency with which each individual method was applied, and, moreover, the frequency of *successful* application of methods. For example, the discovery that hominins hunted a lot but were rarely successful holds potentially far different implications from the discovery that hominins rarely hunted but were nearly always successful. Similar considerations apply to the discovery that different modes of acquisition had very different success rates. Thus the *pattern* of acquisition stands to provide information whose significance is on par with what we can learn from the *method* of acquisition.

Numerous forms of arguments have been deployed in an effort to discern the method by which carcasses were obtained. Evolutionary psychologists argue in favor of the importance of hunting by citing certain features of contemporary human sociality. Other researchers attempt to extract information regarding prehistoric acquisition techniques from the subsistence behavior of modern human hunter-gatherers, whereas others turn to contemporary nonhuman primates. The most entrenched debate surrounding this issue, however, focuses on different aspects of CM and the information contained therein. Here I review the details of each of these argument forms, showing which ones are reliable and why.

4.2.4. The Diet in the Details: Correlating Cutmarks With Consumption

The potential of CM (and toothmarks [TM]) to tell us things about the early hominin diet hinges in large part on the extent to which CM reveal the order in which consumers had access to a particular carcass. Arguments suggesting that CM and TM could support inferences concerning the order of consumer access first appeared in the mid-1980s and have since multiplied (Lupo and O'Connell 2002: 102). In their strongest form, these arguments give us good *a priori* reasons to believe that CM and TM are a reliable guide to determining hominin methods of carcass acquisition.

The most prominent argument begins from the assumption that frequency of CM should vary positively with the amount of flesh on the carcass when it was acquired. Thus, carcasses that were killed by hominins through hunting or wrestled away by hominins immediately after they were killed by other predators should show a high frequency of CM because they were fully or almost fully intact when hominins acquired them, requiring an extensive amount of hacking to remove flesh. These carcasses should similarly show relatively few TM, assuming that early and efficient hominin access would have rendered a carcass to be of little interest to scavenging carnivores. Correspondingly, carcasses that were killed and consumed mainly by carnivores should show a high frequency of carnivore TM and a correspondingly low number of CM, the assumption being that the carcasses would have offered little to hominins who found them too late or were unable to wrestle them away from carnivores.

Determining whether CM/TM actually are a reliable guide to order of consumer access requires that we demonstrate the causal covariation on which the above *a priori* argument rests. Various researchers have used data derived from the Hadza, a small group of contemporary human foragers located in Tanzania, to investigate the relationship between CM/TM and access order. These studies are generally concerned with determining whether certain CM/TM patterns bear a unique relationship to a particular method of carcass acquisition. This has been achieved by tallying the CM on carcasses for which the order of access is known and then attempting to discern some statistical correlation between particular ranges of CM frequencies and particular methods of acquisition. Although some researchers have independently found evidence of a correlation, when combined their results do not suggest a unique or nearly unique pattern of marking. Firstly, in cases where the order of consumer access is held constant there is no consistent pattern of either CM or TM frequency. Secondly, marking patterns tend not to vary depending on whether humans or carnivores had first crack at carcasses (*ibid.*: 103).

There are at least two potential reasons why there has been no correlation found between CM and TM and order of consumer access. One reason is, obviously, that there *is* no such correlation. As compelling as the argument for why CM and TM should covary with order of consumer access, CM and TM, in fact, do not covary with order of consumer access. Another reason which potentially explains the absence of a correlation is the possibility that differences in the ways researchers define and/or measure CM and TM have obfuscated real correlations. At Olduvai site FLK Zinj, for example, several different teams of investigators have tallied conflicting CM and TM counts, which might be taken to support the notion that the confounding factor is conflicting definitions after all (*ibid.*: 100). Or perhaps it is a mixture of both: there is an actual but weak correlation which has been obliterated by inconsistent measurement approaches.

Whatever the explanation is, the fact that attempts to confirm any link between CM/TM frequency and order of consumer access have failed thus far militates rather harshly against the advisability of using CM and TM tallies as a guide to inference about methods of early hominin carcass acquisition. If we cannot confirm such a relationship when the values of both variables (CM/TM count and order of access) are *known*, the prospects for CM and TM counts to lead to reliable conclusions about the methods of carcass acquisition of our ancestors seem dismal at present. Reliability is further undermined by the serious possibility that whatever real link there is between CM and TM frequencies, on the one hand, and order of consumer access, on the other, may differ between modern hunter-gatherers and Pleistocene foragers.[6]

Setting aside for the moment questions of whether there is such a proposed link, this method of inference has two serious limitations for teaching us how early hominins lived. For one, even if inferring order of consumer access from CM/TM frequencies gave us insight into modes of carcass acquisition, it does not permit inference concerning the *patterns* of acquisition. In other words, it cannot (or, at least, has not been shown to be able to, even in principle) tell us

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[6] This latter concern will be the focus of the following section.

what, if any, *strategy* hominins followed—e.g., whether they hunted exclusively, or scavenged exclusively, or some mixture of the two. Secondly—and perhaps most importantly—the CM/TM method has not been shown to be capable of telling us whether meat acquisition was consistent enough for hominins to have been able to rely on it or for it to have played a major adaptive role (*ibid.*: 103). Thus most of what is significant with respect to the behavioral ecology of the hominin diet would still be shrouded in mystery even if this way of investigating access order were reliable.

4.3. The Diet in Analogical Focus

The preceding discussion suggests a more general way in which we might assess the dietary ecology of our earliest hominin ancestors. The use of data gathered from the Hadza to determine the relationship between CM/TM and order of consumer access characteristic of early *Homo* presupposes that said relationship with respect to the Hadza (or modern hunter-gatherers generally) is qualitatively *analogous* to the same relationship with respect to early *Homo*. Analogies between contemporary foragers and early hominin foragers represent the second method by which paleoanthropologists attempt to distinguish between alternative accounts of the early hominin diet.

We can use the last couple of decades of work done on Tanzania's Hadza as exemplary of observational studies of contemporary human foragers. One of anthropologist Henry Bunn's (Bunn 2001) studies investigated the correspondence between various measures associated with CM produced by Hadza, on the one hand, and order of consumer access to carcasses, on the other. Bunn begins by establishing the causal relevance of order of consumer access to a number of properties of CM distribution. For example, particular defleshing activities performed by the Hadza produce characteristic patterns of CM found on humeri. These defleshing activities, in turn, causally covary with the amount of meat on a carcass, which itself depends on whether Hadza had early access (hunting or aggressive scavenging) or late access (passive scavenging) to the carcass. So there is a consistent causal relationship connecting order of consumer access to distinctive CM patterns.

The next step in the argument is to compare the CM patterns produced by Hadza butchers with those found on bones at FLK Zinj. Bunn found "broad similarities" between the two samples, and, consequently, inferred that the hominins responsible for the bone assemblages at FLK Zinj had the same order of access to carcasses which is indicated by similar patterns of Hadza butchery.

Abstracting from Bunn's analogy, we can characterize the structure of analogy as an inference in which some object's possession of a property is inferred on the basis that that object is known to share properties with some other object. Formally[7]:

1. O_1 possesses properties $P_1 \ldots P_n$
2. O_2 possesses properties $P'_1 \ldots P'_{n-1}$
3. $P_1 \ldots P_{n-1}$ are similar to $P'_1 \ldots P'_{n-1}$

Therefore, O_2 possesses property P'_n.

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[7] I borrow this formulation from Salmon (1982), with two differences ([1] differentiating the properties of O_1 from those of O_2; and [2] the inclusion of premise 3) which seem necessary for proper characterization of the argument's structure. Salmon portrays O_1 and O_2 as both having properties $P_1 \ldots P_{n-1}$—i.e., the *same* properties. This seems too strong to me, since it seems appropriate to ask of putatively analogous objects, "*Are* the properties mentioned, in fact, similar?" Of course, Salmon might reply that, in her formulation, *that* question comes in at premise 2, where her version of the argument portrays O_2 as having the same properties mentioned in the first premise in conjunction with O_1. However, this would place a general requirement on analogical arguments such that, for an argument to go through, the putative analogues must possess the same properties. But that seems wrong. It seems sufficient that the properties merely be similar.

In Bunn's analogy, Hadza butchery (= O_1) is characterized by a consistent relationship between carcass acquisition (= $P_1 \ldots P_{n-1}$) and CM patterns (= P_n). Additionally, we know that prehistoric butchery (= O_2) embodies patterns (= P'_n) which are "broadly similar" to those produced by Hadza. However, unlike our Hadza data, we have no direct knowledge of the patterns of carcass acquisition characteristic of early *Homo* (= $P'_1 \ldots P'_{n-1}$). The analogy is the means by which we infer the prehistoric access order.

To judge whether or not the analogy confers warrant upon the inference we must take a closer look at the sources from which analogies derive their strength. First, there needs to be a relation of dependence between $P_1 \ldots P_{n-1}$ and P_n, the relation normally picked out by the word "relevance." Hence to say that $P_1 \ldots P_{n-1}$ are relevant to P_n is simply to say that there is a relation of dependence between $P_1 \ldots P_{n-1}$ and P_n. Second, where P_n is dependent upon $P_1 \ldots P_{n-1}$, the set $P_1 \ldots P_{n-1}$ should contain as many elements as are relevant to P_n. Third, $P_1 \ldots P_{n-1}$ should be similar to $P'_1 \ldots P'_{n-1}$ in the ways which account for the relevance of $P_1 \ldots P_{n-1}$ to P_n. That is, the existence of the relation of dependence between $P_1 \ldots P_{n-1}$ and P_n should be explainable by roughly the same set of facts as the existence of a relation of dependence between $P'_1 \ldots P'_{n-1}$ and P'_n. For example, the reason we can make an inference *from* the fact that a Honda accelerates when one pushes the gas pedal *to* the conclusion that a Toyota will accelerate when one pushes the gas pedal is because Honda gas pedals are connected to an engine in roughly the same way that Toyota gas pedals are connected to an engine. The reliability of this inference does *not* rely on the fact that the Honda and Toyota gas pedals have, say, similar shapes.

These strength-conferring properties can be recast in the form of three questions which we can use to evaluate analogies:

(a) Are the properties $P_1 \ldots P_{n-1}$ relevant to P_n?

(b) Are there any properties relevant to P_n which are not contained in the set $P_1 \ldots P_{n-1}$?

(c) Are properties $P_1 \ldots P_{n-1}$ similar to $P'_1 \ldots P'_{n-1}$ in the ways which account for the relevance of $P_1 \ldots P_{n-1}$ to P_n?

Asking these questions of Bunn's analogical argument allows us to see precisely where it is strong and where it may be weak. Bunn's data suggest that he has passed what is perhaps the most important test—viz., an empirically based answer to the question of whether CM patterns are relevant to the order of consumer access. But, as we saw in the previous section, the balance of independent measurements of this relationship does not support Bunn's conclusion. At best, then, we should suspend judgment as to whether Bunn's analogy derives strength from successful performance on (a).

An affirmative answer to question (b) is a potentially strong analogy breaker, and the reader's sense is that Bunn is acutely sensitive to this possibility. He mentions briefly that, were it the case that CM were produced in cases where foragers were doing something other than defleshing or disarticulating a carcass, CM would dramatically decrease in their reliability as an indicator of order of consumer access. He dismisses this idea, however, suggesting "[b]utchers do not intentionally slice directly into visible bone surfaces. CM are mistakes;

they are accidental miscalculations of the precise location of the bone surface when muscle masses obscure it" (Bunn 2001: 207). However, it's not clear that Bunn has any evidence to support this assertion other than his assumption that

> butchers with any interest in preserving the sharpness of their knife blades are not going to repeatedly hack into the visible bone surfaces when the adhering meat can be shaved free without hitting the bone directly enough to produce CM (207).

But even supposing this is true, it certainly does not follow that hominins would have taken knives to bones for no reason other than to remove meat. Indeed, we know that they *did* hack into bones for other reasons, based sheerly upon the fact that several of the Olduvai bones with CM are non-meat bearing bones such as metapodials and phalanges (Potts 1984: 141-142. See also Lupo and O'Connell 2002). Furthermore, things like carrying bags and other artifacts can be fashioned from the non-edible tissues found on bones, and extraction of these tissues is known to produce CM (Potts 1984: 141). Presumably CM produced from attempts to extract non-edible tissues would not be a reliable guide to order of consumer access.[8]

Bunn's remarks with respect question (c) are instructive. He points out that Hadza butchery is conducted with steel knives whereas this would not have been the case with early hominins. However, he argues that, while this certainly

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[8] Additionally, baboons have been observed to take an interest in entirely defleshed and demarrowed bones, suggesting that TM frequencies have the potential to mislead researchers as well, for, at least in the baboons' case, high TM frequency does not imply early carnivore access. This fact alone would seem to recommend rather strongly against the *a priori* argument used to establish a link between CM/TM and consumer access. Our assumptions concerning what animals or hominins are likely to do are simply not borne out. Note Lupo and O'Connell, "It is hard to see why baboons should have had much interest in stripped and marrow-cracked mid-shafts, but the TM values reported clearly indicate that they did" (Lupo and O'Connell 2002: 96

represents a dissimilarity between the Hadza and prehistoric foragers with respect to butcher, the "general relationships between cutmark locations and butchery tasks should apply regardless of the type of hand-held knife being used, at least in terms of the location if not the quantity of CM" (Bunn 2001: 209). In other words, although there is a dissimilarity between the Hadza and early *Homo*, it is an *irrelevant* dissimilarity—irrelevant in the sense that the difference between knives does not give rise to a corresponding difference in CM distribution.

The difficulties which arise for Bunn in his analogical efforts to distinguish between early and late hominin access bear instructive resemblance to those arising for analogies involving Hadza hunting and power scavenging success. O'Connell *et al.* (2002) note the Hadza's remarkable ability to take over carnivore kills in the initial stages of consumption. Hadza have a near-perfect successes/ attempts ratio, due mostly to their use of long-range bows which can kill or critically disable carnivore predators from up to 40m (O'Connell *et al.* 2002: 855). The Hadza depend on these bows for their success, and without them it is doubtful that they would be able to interfere at all with carnivore kills. This expectation is supported by the comparatively poor scavenging abilities and high fatality rate of Ugandan Bushmen, whose bows are much lighter and provide far less interference to hungry carnivore predators. Thus, where "P_n" in the first premise of the analogy is "scavenging success," the Hadza bow is bearing the brunt of the causal responsibility. There were, of course, no implements possessed by early hominins which were similar to the Hadza bow in the respects relevant to their scavenging success. This important determinant of Hadza scavenging success is, curiously, not mentioned by Bunn, and only serves to further establish the disanalogy between the modern Hadza and prehistoric *Homo* with respect to carcass acquisition ability.

In describing the study mentioned above, Bunn takes the anthropological community to task for "blanket dismissals" of analogies with modern foragers, stating that, while there are "kinds of information that are inappropriate for use in prehistoric analogues," based on

> the results of this study, it is clear that for some specific and significant kinds of information, modern foragers such as the Hadza provide a very appropriate and revealing source of information as analogues for clarifying some of the foraging adaptations of prehistoric foragers, including early *Homo* (Bunn 2001: 212).

But if the worries I've raised for Bunn's analogy are legitimate, the kind of information he provides seems no more appropriate than that which forms the foundation of many of the more vulgar hunter-gatherer analogies which were abandoned in the mid-20th century.[9]

What is most unsettling about the weakness of Bunn's analogy is the fact that he relies primarily on uncontroversial assumptions about mechanical processes (e.g., the assumption that fleshier carcasses will experience more knife hacks, leaving more CM) and avoids controversial assumptions about human nature. It would be easy to understand why an analogy would be poised to fail

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[9] Wylie (2002, chapter 9) provides a superb review of both the history and formal properties of analogy in the context of archaeological research.

where its strength depended upon the assumption that human beings enjoy Seinfeld-esque humor. But aside from the assertion that butchers do not intentionally hack into bone, his argument is for the most part free of references to typical human behavior. Yet it still fails to be convincing.

The soft underbelly of Bunn's argument is, in my estimation, the fact that we just don't have enough information on what sorts of early hominin activities produced CM (in abstract form, we don't know all things which might give rise to P_n). Studies embodying the form of Bunn's Hadza observations are likely to share this vulnerability for reasons I shall now attempt to illustrate. The point of these studies is to gather information concerning the possible relations of dependence between a variety of variables (e.g., social, environmental, technological, and subsistence conditions) with an eye towards understanding the values of and relations of dependence among those variables in the lives of early hominins. Analogical inferences about early hominins based on observations of modern hunter-gatherers normally take one of two forms. In this first case, early hominins are concluded to have engaged in a certain behavior because they are known to have possessed features which are similar to the causal determinants of an analogous behavior found in modern foragers (call these "Type 1"). In the second case, hominins are concluded to have possessed particular causal determinants of a certain behavior because (i) they are known to have engaged in that behavior, and (ii) the analogous behavior in modern foragers is produced by similar particular causal determinants ("Type 2"). Bunn's study falls into this latter category.

The problems raised for Bunn are symptoms of a disease which plagues Type 2 inferences in general—namely, that the reliability of conclusions about particular causal determinants possessed by early hominins in general will need to confront serious concerns raised by the fact that the same behavior might be caused by a wide range of antecedent conditions which bear very little resemblance to one another (call this the "Problem of Multiple Realizations," or MR for short). Thus, modern foragers and early hominins may have behaved in superficially similar ways which were the results of drastically different antecedent conditions, giving the appearance of striking continuity between some component of prehistoric and modern hunter-gatherer life when in fact their lives may have been very different in that respect.

4.4. Experimenting with the Diet

There is yet a third method by which we can discriminate among prehistoric dietary hypotheses—viz., experimental modeling. The structure of inference through experimental modeling is isomorphic to that of analogy; their differences lie in the tenor of their conclusions. Whereas analogies generally seek to establish the truth of some hypothesis, the point of experimental modeling is to get a sense of which hypotheses are within the space of possibility.

Anthropologist Martha Tappen's (2001) model of passive scavenging nicely illustrates the essential features of experiment modeling. Tappen and colleagues attempted to measure the efficiency (a proxy for likelihood) of passive scavenging by doing just that—roaming the Serengeti, recording the times and places at which they encountered abandoned carcasses. Discovering that passive scavenging opportunities were both rare and unpredictable,[10] Tappen and her colleagues concluded that passive scavenging opportunities would be

> impossible to strategically exploit without very high search costs or sprouting wings for soaring [cite]. Strategic scavenging is unlikely because given such high search time, such scavenging opportunities are unlikely to be a highly ranked food item (Tappen 2001: 27).

From the perspective of Tappen and colleagues, the unreliability of passive scavenging indicates that the chances of it being used as a method of subsistence for early hominin foragers are fairly low.

The broadly analogical structure of experimental modeling allows us to pose the same questions for Tappen's model which were used to illuminate some of the problematic features of Bunn's study. In particular, it is worth investigating whether there are any properties relevant to one's success as a passive scavenger which may be missing from Tappen's experiment. For example, are faunal conditions such as they were in the past? Are scavenging opportunities affected by searching in a Land Rover (Tappen's preferred mode of transportation) rather than on foot? Did early hominins possess useful knowledge (say, of routine carnivore kill sites) which would have facilitated passive scavenging to a degree not seen by her team? The extent to which Tappen's experimental model is similar in relevant respects to the behavior of early hominins will depend, in part, on whether or how accurately the model incorporates those factors (such as kill site knowledge) which are relevant to scavenging success.

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[10] The rarity and unpredictability of passive scavenging opportunities is supported by data on Hadza foragers (Lupo and O'Connell 2002: 104).

Tappen acknowledges that her team did not have knowledge of routine carnivore kill sites, and this is potentially relevant to scavenging success. It's worth thinking about just *how* important this kind of knowledge would have been. Tappen concluded on the basis the of amount of salvageable food found in the time spent searching that the payoff did not justify the time spent. But imagine being a Pleistocene hominin with intimate knowledge of spots where prey are routinely taken down. You may even have indications of the time frame in which those kills occurred, perhaps through the behavior of other scavengers which are more acutely attuned to acts of predation (e.g., the circling of vultures). It is easy to see in this scenario how the time spent in search of discarded remnants might quickly have dropped to a nearly negligible rate (Hungry? Just walk over to the ol' kill site and see if anything is lying around). Thus the picture of the passive scavenger shifts from the gaunt, hobbling hominin desperately searching for a few precious morsels to the adept and cunning hominin for whom trips to the kill site may have been as routine as kills themselves. Knowledge of kill sites could have transformed passive scavenging from a low-yield high-cost activity to one upon which early hominins could have relied as part of a balanced diet. Whether or not early hominins actually possessed this kind of knowledge, the plausibility that they did combined with the significant impact that knowledge might have had on scavenging success suggests that Tappen's experimental model may not be appropriately analogous to Pleistocene life in the ways necessary to rule out passive scavenging as a subsistence strategy.

Taking Stock

As the reader will have by now come to appreciate, there is a substantial array of plausible alternative hypotheses among which researchers will need to discriminate *empirically* if any sorts of reliable conclusions are going to be in the offing regarding the early hominin diet. This situation is by no means unique to paleoanthropology; it is constitutive of science itself and of what makes science challenging.

One thing which historical sciences like paleoanthropology do *not* share with all other sciences is a lack of direct access to the object of study. As is the case with other species, much of the data we would need to trace several aspects of human evolutionary history are lost forever. The task then becomes that of finding reliable methods of indirect access to history. It is here that the analogies to which paleoanthropologists avail themselves become central.

The methodology of historical analogy involves two basic components: (1) empirical confirmation of a relation of dependence between two variables, (2) a wager that the relation of dependence is unique and has remained invariant at least since the relevant historical period. This second component—the Analogist's Wager—can be more or less risky depending on what the variables are (e.g., protons and electrons probably behave the same way they did 2 million years ago, but a preference for Seinfeld-esque humor is probably not widespread) and what information the analogist already has (e.g., she might already have ruled out potential alternative realizations). The cases reviewed above highlighted ways in which problems can arise for each of these components.

More importantly, we were able to see how researchers are sensitive to these problems and attempt to deal with them in an appropriately rigorous way.

4.5. Evolutionary Psychology and Historical Inference

> *To understand the mind's evolution, it is probably best to forget everything one knows about human history and human civilization.*—Geoffrey Miller, *The Mating Mind* (20).

Evolutionary psychologists have largely ignored the ways in which paleoanthropologists have gone about gathering evidence for and testing hypotheses about the lives of early hominins, as well as the conclusions reached by those methods. This failure to engage either the findings or methods of paleoanthropology has occupied every position on the spectrum, ranging from exclusive focus on severely outdated material (e.g. Lee and Devore 1969), to no attention to any sort of work in paleoanthropology, culminating in outright rejection of the study of the past via direct archaeological evidence. This last manifestation has seen its most explicit formulation in the work of Geoffrey Miller, who has stated that fossil and archaeological evidence "has not proven terribly useful in explaining why we have the mental adaptations that we have—and in some cases it can be misleading" (Miller 2000: 22).

Although Miller offers no examples of where archaeological evidence has misled us concerning why we have a certain mental adaptation (a claim which, of course, implies that we actually do know why we have some mental adaptation and that we can point to where archaeological evidence suggests conflicting—and incorrect—reasons), he does point out that "[e]very year brings new bones or stones that necessitate a major rethinking about the times, places, and products associated with human origins" (23) and that often what we thought was true about some period of human evolution is shown to be false. "The result" of relying on archeological evidence, he continues,

> is often theories as transient as the evidence they cite. Most human evolution theories of twenty or fifty years ago are barely worth reading now because, by tying themselves too closely to the physical evidence then available, they aimed too much for empirical respectability at the expense of theoretical coherence (23).

The upshot: "Physical evidence about human origins seems the most secure place to begin in theorizing about human evolution, but this security is largely illusory" (23).

Miller is certainly correct in suggesting that theories based on existing evidence are vulnerable to falsification, but it's not at all clear that falsifiability is a *bad* thing for a theory to have. Lots of people think that being able to tell whether a theory is wrong is a very useful thing to be able to do. But perhaps this is, as Miller says, to unduly emphasize "empirical respectability at the expense of theoretical coherence." Arguably, what we should be focusing on is an *a priori* theory that avoids confrontation with empirical findings. A move away from the "special reverence for archeological evidence which is out of all proportion to what it can tell us about mental evolution" (24) will achieve the twin goals of (1) decreasing our chances of coming up with a false theory, and (2) freeing us from the constraining effects of trying to formulate a theory which is consistent with the existing evidence.

While other evolutionary psychologists may not consciously share Miller's distaste for archaeological data (although, their failure to engage the data suggests that they may), it has nevertheless been a fundamental assumption of that research program that theories about human evolution can only proceed via an analysis of *current* behavior interpreted within the framework of evolutionary theoretic principles—in particular, the principle that phenotypes are adapted to ancestral environments.

A survey of the literature suggests that there are two methods by which they have attempted to acquire this information. The first is to infer through *a priori* reasoning that early hominins must have faced some particular problem. The premises from which these inferences derive are *a priori* judgments about what sorts of factors would have been relevant to reproductive success in our ancestors' environment (call this the "reproductive relevance" method, or "RR"). The second is to infer the selective importance of some environmental factor based on the existence of a feature which seems ideally suited for the purposes of dealing with that aspect of the environment—the method introduced in chapter 2 as "reverse engineering" (RE).[11]

While RR and RE each have their own problems, there is a particularly prominent worry which arises for both of them. This is the by now familiar problem of multiple realizations of a given effect. In addition to discussing specific

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[11] For the entertaining nuts and bolts of reverse engineering, there is no better source than Dennett (1995).

concerns for each method, the objective of this section will be to demonstrate the debilitating effect of the prospect of multiple realizations for both RR and RE. I then critically assess the manner in which evolutionary psychologists have endeavored to resolve with these problems.

4.5.1. The Reproductive Relevance Method

Let us first introduce RR by way of an example extracted from the evolutionary psychological literature. Consider David Buss's claim that "[p]eople who failed to prevent infidelity in a mate had less reproductive success" than those that were able to prevent infidelity (Buss 2003: 10). Buss arrives at this conclusion via the following inference procedure. The first step is to establish the reproductive relevance of preventing infidelity. For men, he says, being "indifferent to the sexual infidelities of their mates risked compromising their paternity. They risked investing time, energy, and effort in children who were not their own" (*ibid.*: 10), the implication being that one man's reproductive success is lowered relative to that of another man if, *ceteris paribus*, the former raises the children of the latter. Preventing infidelity is thus judged to be relevant to reproductive success because of its role in avoiding investment in the offspring of others, also assumed to be relevant to reproductive success.

To establish empirically the relevance of infidelity prevention, Buss notes the tendency of *Plecia nearctica*, the male lovebug, to hold on to his mate in a copulatory embrace for up to three days, "[p]erhaps because other males continue to attempt to mate with her" (*ibid.*: 10).[12]

> The prolonged copulation itself functions as a way of guarding the mate. By remaining attached to the female until she is ready to deposit her eggs, the male lovebug prevents other males from fertilizing her eggs (*ibid.*: 10).

For Buss, the fact that men generally exhibit "mate guarding" behaviors (in the form of jealousy. See chapter 2) suggests human males were subject to the same selection pressures which give rise to mate guarding behavior in other species.

Like the other historical inference patterns analyzed above, RR has an analogical structure. It thus allows us to evaluate particular instances of RR via the principles for evaluating analogies developed above. First, then, does Buss establish the relevance of infidelity prevention to reproductive success? The answer here has to be "No," for at least two reasons. For one, as we learned from *a priori* arguments which attempted to associate CM patterns with order of consumer access to carcasses, Buss's *a priori* linkage of infidelity prevention and reproductive success is, however intuitive, without merit. Nor does his attempt to provide an empirical foundation for this link via the reference to lovebugs succeed, for he gives us no evidence that lovebugs' prolonged copulation was selected for the task of mate guarding.

The second evaluative question seeks to discern whether there is anything other than or in addition to selection for mate guarding which could account for

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[12] The uncertainty denoted by the "perhaps" in this sentence is eliminated in Buss (2000: 14).

prolonged copulation in lovebugs. One need not look far to find alternative explanations here. The prolonged copulation could have evolved to signal the male's endurance (and thus "good genes"), or to ensure as copious of an ejaculate as possible, for example. Additionally, there are presumably non-selectionist hypotheses which could explain the behavior. So there is little reason in Buss's account to suppose that prolonged copulation could only result under pressure of selection for mate guarding. More likely it has potentially multiple realizations.

Thirdly, in order to ensure that the analogy is apt we want to know whether our ancestors were subject to environmental forces similar to those which explain the evolution of prolonged copulation in lovebugs. This last evaluative measure makes the poverty of RR particularly stark. For, as a method for uncovering the selective forces which shaped human nature, the reasoning is patently question-begging. Like other analogies (discussed above), analogies between species contain as one of their premises the proposition that there is a similarity between the putative analogues—in this case, an *environmental* similarity between species being compared (see 2.2.3). The empirical fact that the two species evolved in equivalent habitats is supposed to warrant the inference that the (unknown) function of one species' behavior (here, human male jealousy) is the same as the (known) function of the other species behavior (here, the mate guarding function of lovebugs' copulatory embrace). Given that the inclusion of environmental similarity in the premises is a prerequisite for an analogy between species, then, one cannot *infer* the existence of some feature of the hominin ancestral environment on the basis that similar environmental features are selectively important for other species. In any case, as was stated above, we have no evidence that Buss's hypothesis for the function of prolonged copulation is correct.

One rather unpromising way around the both the objection that Buss has not established the reproductive relevance of infidelity prevention *and* the objection that we do not have the historical data on selection pressures required to known whether human jealousy and lovebug copulatory embrace are functionally analogous is to claim that there are certain adaptive problems which any possible organism would have to evolve strategies for solving (e.g., Tooby and DeVore's (1987) "principles that shape species"). Take Buss's example of avoiding investment in the offspring of others. This is certainly not a global problem, as males in many taxa do not even *provide* parental care (including, incidentally, male lovebugs [Shuster and Wade 2003: 305]). This strategy becomes more feasible when one restricts the analysis to particular classes of organisms, but in the end we run into familiar problems—viz., that we need to have independent information about the early hominin environment before we can make any inferences regarding selection pressures. This problem generalizes even to comparisons with contemporary hunter-gatherers. Assuming we know which factors are relevant to modern hunter-gatherer reproductive success, unless we know that early hominins shared with them the suite of environmental variables which form the basis for the reproductive relevance of these factors, we are barred from making inferences about ancestral selection pressures here as well.[13]

The use of RR (and its accompanying problems) can be discerned wherever evolutionary psychologists endeavor to support an hypothesis regarding the function of a given human trait via reference to the behavior of some nonhuman species. RR's analogical structure requires that researchers know at least three things in advance: (1) the environmental factors which gave rise to the nonhuman trait, (2) the function of the nonhuman trait, and (3) *either* that early hominins faced similar environmental factors *or* the function of the human trait. Evolutionary psychologists consistently fail to provide evidence of any probative value for any of these components. Instead the reader is treated to case after case of casual comparison between what nonhumans do and what humans do. Buss (2003: 7) warns against the use of casual comparisons between humans and nonhumans.

4.5.2. Reverse Engineering

RE is the most widely employed method of historical inference in evolutionary psychology. RE is formally similar to RR and other analogies, but its major premise calls for a special type of proposition. Whereas the analogies mentioned thus far have taken as their first premise an empirical claim about a relation of dependence between two states of affairs, the major premise of RE is a categorical statement about what must be true of a trait for it to have been ca-

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[13] See 2.2.3 for a more robust description of the problems involved here.

pable of meeting a particular historical selective challenge. The minor premise is a claim that a given trait has the aforementioned properties, and the resulting inference is the double conclusion that the trait's function and selective history are such as is indicated in the major premise.

The essence of RE is to think about what a trait must be like if it is to be good for doing a particular task, and then check to see whether the trait in question is like that. In this paper I argue that RE, particularly as it is used in evolutionary psychology, is apt to direct us away from knowledge of the selective history of an organism, rather than to lead us toward it. The research tenets of RE have perverted evolutionary psychologists' (and others') sense of what kind of evidence is probative when considering the plausibility of a hypothesis which suggests that some property of an organism is an adaptation.

How do we uncover an organism's selective history? In evolutionary psychologist Randy Thornhill's words, we need to

> hypothesize about the selection that made an adaptation, and then test predictions derived from the hypothesis [cite]. The predictions are about what must be true of the design of an adaptation if the hypothetical historical selective force was, in fact, causal (Thornhill 1997: 6).

This passage is excerpted from the clearest explication of RE of which I am aware, Randy Thornhill's (1997), "The Concept of an Evolved Adaptation." In this essay Thornhill defends the view that RE is the *only* way of knowing which adaptive problems were faced by our ancestors, which he believes follows from the idea that "adaptations are the biologist's sole source of information about the forces of selection that were actually effective in designing organisms during the evolutionary history of life" (*ibid*: 5).

The argument behind Thornhill's view that adaptations are our only source of information about the effects of selection is fairly straightforward. First, the necessary and sufficient conditions for some factor *F* to be a force of selection are that *F* causes type *A* organisms to be better equipped to reproduce than type *B* organisms, and that *A*s actually do outreproduce *B*s. Whichever property *P* differentiates *A*s from *B*s with respect to *F* is an adaptation. Notice that whether *F* qualifies as a force of selection depends on whether *A*s outreproduce *B*s, *not* the other way around (i.e., rather than *A*s outreproducing *B*s depending on whether *F* qualifies as a force of selection). Now, because *P* is the only existing record that *A*s once outreproduced *B*s, *P* is the only source of information we have for knowing whether some factor once qualified as force of selection.

RE capitalizes on the specialness of *P* as our link to the past by devising ways of uncovering what kind of a force would have caused *P* to spread through the population; in essence, trying to discover an evolutionary question to which *P* is the answer. The general approach is, as Thornhill says, to try to imagine what *must* be true of a hypothetical adaptation in order for it to have been a successful way of dealing with some hypothetical selective force (call this the "design question"), and then determine whether that which must be true of a hypothetical adaptation *is* true of some organismal feature. If we find a property which meets these criteria, we can infer that the property evolved to deal with the hypothetical selective force, which of course entails that the hypothetical selective force was actualized during the relevant period (Thornhill draft; Tooby and Cosmides 1992, 2005; Williams 1966, 1992).

4.5.2.1. Reversing RE: General Objections

There are a number of objections we can raise against the idea that RE is likely to lead to reliable conclusions about evolutionary history. First, RE's focus on the final product of an evolutionary process as the best source of information about that process runs a grave risk of being undercut by the problem of multiple realizations—specifically, the possibility that selection for different types of functions could give rise to the same form. For, if what must be true of an adaptation to *F* (which *ex hypothesi* humans encountered) might also be true of an adaptation to *G* (which *ex hypothesi* humans did not encounter), then the fulfillment of those criteria does not by itself allow us to discriminate between traits that are adaptations to *F* and those that are adaptations to *G*. Since RE does not incorporate any other means of discriminating between rival hypotheses regarding historical selection pressures, the success of RE as a strategy for reconstructing human evolutionary history is entirely dependent upon our ability to correctly guess which historical environmental factors had a selective influence on our ancestors.

How likely is it that we will be able to do this? We do not have the luxury of inferring our selective history by direct comparison with other taxa without already having lots of relevant historical information (which we do not have). Nor can we appeal to selection pressures which *all* possible organisms will face, because there is nothing to suggest that there are any such non-trivial selection pressures. We could try a slightly watered-down version of this appeal, though. We could argue, for example, that our chances of correctly guessing which selection pressures were faced by our ancestors are pretty good because all possible organisms will face certain *categories* of selection pressures. Thus, we do not need any specific information about the early hominin selective environment. We can simply apply the "principles that shape species" to our own, and this will furnish us with knowledge of which selection pressures produced our adaptations.

There is a part of this suggestion which, I think, is basically right. All possible organisms *will* encounter many of the same categories of selection pressures, and the more narrowly one restricts his attention to the tree of life, the more likely organisms are to share categories. Survival and reproduction are obvious ones, and there are even subcategories which we can identify for lots of families of organisms. Many organisms will face foraging problems, or mating problems, for example. Where the appeal to shared categories of problems breaks down, however, is when we try to extend that principle to the level of individual problems within a category. The specific problems for a particular category encountered by different populations are likely to be both novel and highly idiosyncratic in many cases, such that they may never have arisen before and may never arise again.

Consider the role of sensory bias in mate choice discussed in chapter 3. Here it was shown that the selective effects of sensory bias have serious potential to be both pervasive and very powerful. One thing that work on sensory bias has revealed is that the biases of different taxa do not follow any sort of predictable pattern, that they will tend not to resemble each other, and that they do not bear any lawful or principled relation to the environment in which they arise. These are all properties one would expect from the accidental effects of neural organization, which is where sensory biases reside. Moreover, the ubiquity of adaptations of one sex to the sensory biases of the other suggests that this spectre is not a remote logical possibility, but is in fact very common across taxa. Nor are the adaptations to sensory biases trivial aesthetic modifications of the organism. Often they have harsh consequences for survival, as is suggested by the backlash effect found in instances of Fisherian runaway. So it won't due to reply that adaptations to sensory biases are marginal in terms of their impact on the evolution of the species; they are not. The prospect of idiosyncratic selection pressures like sensory bias presents a fundamental obstacle to our hopes of guessing which selection pressures early hominins were likely to have faced.

Research on the genus *Xiophophorus* represents a telling example of how the application of so-called "principles that shape species" can mislead. One "principle" to which evolutionary psychologists have been partial is the idea that females will be selected to prefer the fittest males. The alleged principle would have been of no use (or worse) in determining the origin of the female swordtail (*X. helleri*) preference for males with longer swords (a part of the tail). Whereas the application of "fundamental evolutionary laws" (Tooby and Devore 1987:

189) might have easily led to the idea that female swordtails evolved to prefer longer swords because longer swords indicate "good genes," it turns out that the female preference for longer swords evolved *prior* to swords themselves. This was determined by demonstrating that females from evolutionarily prior taxa in which swords did not exist *also* prefer males with longer swords. The RE approach suggests that we could have discovered the evolutionary origin of female swordtails' mate preferences by simply reflecting on the ecological reasons for why preferences might evolve. But the principles of mating ecology cannot tell us anything about the reasons for the female swordtails' preference, because those principles were not, so it appears, interestingly involved in determining that feature of female swordtails (Sinervo and Basolo 1996: 174-175).

The fact that sensory biases are both idiosyncratic and important means that there is a least one category of adaptive problems for which our ability to correctly guess the specific instances across large swaths of evolutionary time is basically non-existent. Unlike the common response to adaptationism which appeals to idiosyncratic *solutions* to problems (see below), there is no refuge for the adaptationist in the face of novel selective *problems*. As we said above, the success of RE is entirely dependent on our ability to guess which selective problems were faced by our ancestors. The existence of novel, short-lived, and idiosyncratic problems suggests that this ability is woefully deficient—certainly deficient enough to warrant abandoning any research strategy which depends upon it.[14, 15]

A related difficulty for RE concerns its ability to discriminate between properties that are adaptations *per se* and properties that are not. In the same way that what *must* be true of any adaptation in order for it to successfully deal with *F* may also be true of an adaptation designed to deal with *G*, it is also plausible to think that what must be true of adaptations to *F* may also be true of properties of organisms that are not adaptations at all. RE's failure to discriminate between adaptations and non-adaptations is rooted in the same feature which is responsible for its failure to discriminate between different kinds of adaptations—i.e., the fact that something could fulfill the design criteria for adaptations to *F* and yet fail to be an adaptation to *F*.

Lewens (2002) recognizes the inability of the design question to pick out *only* adaptations to *F*. He states that "for the inference to be watertight" would require that some adaptive solution *S* "is adopted when and only when" *F* is a genuine selection pressure (Lewens 2002: fn10) . Lewens's suggestion implies that the failure of the design question to pick out *only* adaptations to *F* is due to the fact that it leaves the door open for adaptations which satisfy the design criteria delineated for *F* but which are in fact adaptations to some other selection

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[14] There is much to recommend the appeal to novel adaptive *problems* as a general worry for adaptationism. Anti-adaptationists would do well to focus on developing arguments geared towards categories in which it is known that adaptive problems tend to take on very unique forms.

[15] Interestingly, the father of modern RE, George C. Williams, has commented that "[e]very organism will show a long list of characters that make no adaptive sense but record past adaptations" (1992: 76). This is essentially the point I have been making, and it is rather difficult to see how this fact can be reconciled with the alleged reliability of RE.

pressure *G*. Although this is true, it is too restrictive. The problem with Lewens's recommendation is that, while it shores up the design question's ability to differentiate adaptations to *F* from those that are not, it still will not allow us to distinguish between adaptations which match the necessary design criteria from suites of properties which also match the design criteria but which are not themselves adaptations.

This is not a minor quibble. Indeed, the problem I attribute to Lewens's formulation lies at the very heart of complaints surrounding adaptationism. RE allegedly has the ability to simultaneously demonstrate both the *presence of* and *reasons for* selection. Lewens's comment suggests that the problem with RE is that it has the potential only to confuse the reasons for selection, while leaving intact RE's ability to correctly identify the presence of selection. Lurking behind his formulation is that idea that looking for conformity to *a priori* design criteria is a good way to identify adaptations *per se*, it's just not a very good way to know *why* a population "adopted" a particular "solution." But in its canonical form, RE is no better at picking out the presence of selection than it is the reasons for selection. In order to be "watertight," the inference from the presence of properties which conform to *a priori* design criteria to the conclusion that the organism has an adaptation to *F* requires not merely that a population *adopt* solution *S* when and only when faced with *F*, but that properties which conform to *a priori* design criteria *appear* when and only when a population is faced with *F*. Where the latter biconditional holds, embodying design criteria could, in principle, sanction inferences concerning the presence of and reasons for selection.

A third, more fundamental objection to RE is to raise questions concerning the very idea of design *criteria*. Some authors have criticized RE on the basis that the same adaptive problem "can be solved in several different ways" (Griffiths 1996: 517-519). Although Griffiths is lamentably unclear on how this suggests problems for RE, one might guess from his example (alligators and anacondas are very differently adapted fresh water predators) that he imagines that the often very different solutions to the same adaptive problem may lead researchers to mistakenly rule out some trait as an adaptation to selection pressure *F* when in fact it *is*. But while it is undoubtedly important to point out that there are many ways to solve an adaptive problem, as a response to RE this is somewhat wide of the mark. For, evolutionary psychologists (and any other adaptationists) can simply reply (and, indeed, have replied) that different local solutions do not negate the fact that "at some level" these seemingly different solutions can be characterized using the same functional description, and it is at that level that we should be looking (e.g., Tooby and Cosmides 1992).

Here is an alternate approach. Stated another way, the design question ("what must be true of an adaptation designed to deal with selective force *F*") asks "what do all possible adaptations caused by selective force *F* have in common?" The appropriate response here seems to me to be that it is possible that the answer to this question is "Nothing." The design question assumes that, no matter *which* way an organism adapts to *F*, and no matter what its phylogenetic history and constraints are, there will be some non-trivial level at which the organism's adaptation to *F* is similar to all other adaptations to *F*, whether these organisms evolved on our planet or in some other space-time dimension. But what reason do we have to believe this? Of course, it *might* be true. Whether it is or not, if RE is going to be able recommend itself as a research strategy, it *has* to give a positive reason for why we should expect that all possible adaptations designed to solve adaptive problem *F* will have *something*—let alone *many* things—in common. The mere presence of functional similarities among distantly related organisms living in equivalent habitats (aka "convergence") is not sufficient to infer that, for any given selection pressure, all possible organisms will have some design features in common.

We do not as of yet have any reason to think that all possible adaptations caused by a certain environmental factor will *ipso facto* share a suite of properties. Thus, the identification of conformity to certain design criteria is, for all we know, not necessary for identifying adaptations for that feature of the environment. Furthermore, it is plausible to suppose that adaptations for different types of problems could all call for the same criteria to be fulfilled, so identification of conformity to design criteria is not sufficient for identifying adaptations caused by a particular environmental factor. Since RE is neither necessary nor sufficient for demonstrating adaptation, it is *a fortiori* incapable of revealing a trait's selective history.

The final blow to RE is delivered in the context of its proponents' assertions that conformity to design criteria is stronger evidence for selection than reproductive success differentials. Thornhill (1997; draft) argues for the proposition that "[t]he only way you could be sure that you had identified an EEA feature that mattered in terms of generating reproductive success differentials is to find evidence for its existence in the design of the adaptation" (Thornhill 1997: 15). In this regard he explicitly juxtaposes the significance of conformity to design criteria with the *insignificance* of measures of the contribution of a trait to current reproductive success as evidence for selection, a view in which he is joined by the majority of evolutionary psychologists (Cosmides and Tooby 1987; Tooby and Cosmides 1990a; Williams 1992: 40).

There are two serious problems for the juxtaposition of the usefulness of conformity to design criteria with the uselessness of current contributions to reproductive success. First, it may be true that whether an historical environmental force *F* was selective depends solely on whether there are (or were) adaptations for it. However, it is quite another thing to say that the design of extant adaptations (or, more accurately, properties which conform to design criteria) are the "only evidence that support...hypotheses" concerning *F*'s selective efficacy (Thornhill 1997: 15). Second, the problems which Thornhill and others have raised for measures of current reproductive success apply equally to perceptions of conformity to design criteria.

Lots of biologists take demonstrations of selection in the form of current differential contributions to reproductive success as very good evidence for selection, and I presume Thornhill would agree with them (see Endler [1986] for review). But the value of these kinds of demonstrations can go beyond what they tell us about current reproductive success. There are also very good evidence for what *would* happen in an historical population where the relevant parameters were instantiated. It is easy to interpret Endler's (1980) study on guppies within this framework. Endler demonstrated experimentally via reproductive success differentials that one color of guppies will outreproduce another under certain predatory conditions (specifically, conditions similar to those of their native habitat). This experiment is rightly interpreted as supportive of the hypothesis that an adaptive relation between coloring and predation explains the native trait frequency distributions, because it shows us what *would* happen given native conditions and thus, what *might plausibly* have produced the native distributions. Scores of similar experiments attest to the widely held view that these kinds of tests are good for establishing rules of inference, and the reasoning linking the structure and results of these experiments to hypothetical historical states of affairs suggests that these kinds of tests actually *are* good at underwriting certain rules of inference.[16]

Evolutionary psychologists have attacked the use of (or insistence that they themselves provide [Thornhill (draft): 8]) data on current reproductive success as being insignificant to whether some organismal property *P* is an adaptation to an historical environmental factor *F* because of the fact that *P* could be an adaptation to *F* without *P* contributing positively to current reproductive success. It is undoubtedly correct that current reproductive success is conceptually distinct from the historical facts about selection, due primarily to the possibility of environmental differences between the past and present. But it is *equally* true that

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[16] And it doesn't stop there. There are many other categories of evidence which can be and are routinely brought to bear on selectionist hypotheses. We can, for instance, have independent evidence that genetic drift or pleiotropy played a minor or insignificant role in the fixation of a trait (Abrams 2001: 292).

whether something conforms to *a priori* design specifications is conceptually distinct from the historical facts about selection. If, as Thornhill says, "[a] scientific prediction is one that must be true if the hypothesis generating it is true," then a hypothesis of conformity to *a priori* design criteria, "improbable functionality," "complexity," or any other heuristic in the evolutionary psychological arsenal, is no more "scientific" than hypotheses concerning current contributions to reproductive success. Arguably, data on current contributions to reproductive success are a far better source of evidence about selection—past or present—than conformity to design criteria, if for no other reason than the fact that the former are not reliant upon the researcher's intuitions to the extent of the latter (Williams 1992: 41). Furthermore, we have a rich empirical and theoretical tradition informing our use of reproductive success to learn about selection. There are no corresponding credentials for *a priori* design criteria.

The preceding discussion has been aimed at establishing the unreliability of RE as a method for learning about the historical selection pressures faced by our ancestors. The reliability of RE consists of the conjunction of our ability to accurately specify *a priori* what must be true of an adaptation if it evolved in response to a particular selective challenge, combined with our ability to correctly guess which selective challenges may have been faced by a species in the past. The first conjunct is undermined by the fact that there may be no properties which are shared by all possible solutions to a particular adaptive problem. The second is undermined by the fact that our ability to correctly guess historical adaptive problems may be irremediably poor, owing to the often random, idiosyncratic nature of these problems. Thus, I think RE can be rejected on purely theoretical grounds.

4.5.3. Reversing RE: Case Studies

Theoretical objections notwithstanding, I will now go on to assess the performance of RE (assuming its reliability) in the context of specific studies conducted by evolutionary psychologists. I argue that there are special problems in this context which contribute to the overall uselessness of RE.

The structure of studies conducted by evolutionary psychologists in which RE is employed is essentially a type of optimality analysis (Parker and Maynard Smith 1990: 29). According to some proponents, optimality analysis "has allowed biologists to move from merely describing patterns or mechanisms to being able to predict, from first principles, how organisms should be designed" (Sutherland 2005: 569). Optimality models provide a platform upon which we can make predictions about which form and value a behavior would be likely to take in the case where it is an adaptation designed by a specific selective force. If we find that the behavior conforms to our predictions, optimality theorists believe we are warranted in inferring that the behavior was selected for its performance with respect to the hypothesized selective force.

We can divide optimality models into roughly two types—those that make quantitative predictions and those whose predictions are qualitative. Quantitative predictions offer the opportunity for a clear test of the accuracy of the model; we simply see whether the observed numerical values match the predicted values within a suitable confidence interval. A sterling example of the quantitative sort is Parker's predictions for copulation duration in male dung flies. Incorporating a variety of parameters, Parker predicted that if males were optimally designed in this respect, then copulation would last 41 minutes.[17]

Models making qualitative predictions are far more common, for obvious reasons. The object here is to predict that data will show a general trend and then look for evidence of that trend in the phenomena. Qualitative models have been widely criticized for their potential to mislead and the general tendency to evaluate the fit of data to the model without "a prior expectation as to what constitutes an unacceptable match between theory and data" (Orzack and Sober 1994: 367). Furthermore, because of the lack of precision endemic to qualitative predictions, it is (or at least, *ought* to be) more difficult to generate confidence in their probative value. To be sure, qualitative predictions do not immediately spell "doom" for a model, so long as the predictions would, if true, be "sufficiently striking" (Parker and Maynard Smith 1990: 31). Alternatively, researchers can make several independent qualitative predictions. In this case, the probative value of the model increases with each independently confirmed prediction (Brown 2001: 151).[18]

Whether quantitative or qualitative, the power of optimality models to provide evidence for adaptation is dependent upon two factors: (1) the fine-grainedness of the predictions derived from the model; and (2) the uniqueness of those pre-

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[17] The observed mean value was actually 36 minutes. Kitcher (1985: 138-141) discusses different approaches to resolving the discrepancy between observed and predicted values.

[18] See Earman (1992)for a Bayesian explanation of the ability of several independent predictions to raise the posterior probability of a hypothesis.

dictions. The prediction that dung fly copulation should be designed to last for 41 minutes is more precise than one which stated that copulation should last from 15-45 minutes, which is in turn more precise than if we were to predict that it should last for more than 5 minutes. The more precise or fine-grained our predictions are, the more likely our model is to be true if it is supported by our observations. This is due simply to the fact that, *ceteris paribus,* the prior probability that the observed value will fall into a given range varies inversely with the size of that range. The smaller the range, the less likely it is that chance could be responsible for the observed value falling somewhere within that range. When the range is reduced to only one number (e.g., 41 minutes), our confidence in the correctness of our model given a tight match between theory and data should be at its highest (Kitcher 2001: 179-180). Of course, even with precise quantitative predictions our confidence can always be undermined. This might be the case when the predictions derived from our model are not unique to that model. If the implications of our favored model could have been similarly derived from other candidate models, "no progress can be made until some way is established for differentiating between them" (Parker and Maynard Smith 1990: 31), due to the problem of multiple realizations. In these cases, the fine-grainedness of our prediction won't be of much use to us. It should, however, be pointed out that the more finely grained our predictions are, the more likely they are to be unique to that model—although there is nothing in principle wrong with the idea that the same hyper-precise prediction(s) could be made by two radically divergent models.

When it comes to the testing of evolutionary psychological models, both fine-grainedness and uniqueness are absent. For starters, the predictions *never* move beyond the general, qualitative sort mentioned above. Secondly, rather than surprising us, the predictions of evolutionary psychological models typically border on common sense. Researchers pick out some already widely held belief *B* and claim that their theory "predicts" *B*. Needless to say that the probability that the explanations offered in these cases are true is not raised by the "discovery" of *B*. Third, rarely do we find that the predictions of the model could, if true, distinguish it from other potential explanations.

Below I describe two studies which attempt to use *a priori* design specifications to uncover the selective history of a particular feature of some species. This first is an investigation into the design of the sex ratio responses in several species of wasps. The second is a study of the relationship between certain features of women's mate preferences and men's developmental stability. The two studies are structurally similar and so make for a good comparison. The differences are instructive.

4.5.3.1. Case Study: Sex Ratios Across Fig Wasp Species

It is surprisingly ordinary to find that the ratio of males to females in a given population is 1:1, or very nearly so. Ronald Fisher, through characteristically clever reasoning, was the first to explain why (Fisher 1958), and his account is now treated as gospel. The argument is roughly this: imagine a population in which there are more females born than males. Males in this population will have better chances of mating (owing to the abundance of females relative to males) and can be predicted to have higher mean reproductive success than females. The result is that members of the population who are genetically predisposed to produce males will, because of male mating advantage, have more grandoffspring than average. The offspring of male-producing members of the population inherit the tendency to produce males, as do their progeny, and so on and so forth. At some point, the sex ratio will approach 1:1, and males will no longer enjoy a relative mating advantage (*mutatis mutandis* for females).

As W.D. Hamilton pointed out, however, in some species sex ratios are "extraordinary" (Hamilton 1967). In particular, local mate competition theory (LMC) predicts that when mating occurs among the offspring of *N* females before daughters disperse, there will be selection for female-biased sex ratios such that the optimal proportion of males (*p*) is given by

$$p = \frac{N-1}{2N}$$

When there is inbreeding in the population, the degree of relatedness between mothers and offspring increases. In haplodiploid species (e.g., bees and wasps), inbreeding will cause mother-daughter relatedness to increase relative to mother-son relatedness (Herre *et al.* 2001: 194-195; Shuker *et al.* 2004: 473-474). The addition of the inbreeding parameter *S* (the average number of sib-matings) predicts that the optimal portion of males will be given by

$$p = \frac{N-1}{N}\left(\frac{2S-1}{4S-1}\right)$$

Herre *et al.* investigated the actual sex ratio responses of 15 species of fig wasp to different selective factors as compared with the predictions of LMC. Female fig wasps ("foundresses") lay their eggs inside the fruit of fig trees and subsequently die there, with the normal number of foundresses per fruit (1-3) differing across species. Based on figures derived from the above equations, Herre *et al*. made two predictions: (1) that decreases in the number of foundresses per fruit will be associated with increases in the degree of female bias in the sex ratio; and (2) that for a given number of foundresses, more inbred species will be associated with increases in a brood's female-bias (Herre *et al.* 2001: 197). In this case we can obtain numerical predictions simply by substituting the number of foundresses (or average number of sib-matings) into the above equations.

The results: "there is qualitative and in some cases quantitative agreement between theoretical predictions and the sex ratio response of the fig wasps" (*ibid*: 208). Not only are the basic qualitative trends confirmed, but in some cases the actual sex ratios correspond precisely to the numerical values predicted by the theory. This is indeed impressive, but it's unclear whether we ought to consider the case closed—the wasps really *are* optimally designed in the manner predicted by LMC—or press Herre *et al.* to give some account for the quantitative deviations.

To some extent, the authors have made up our minds for us. They're sensitive to the quantitative failure and devote considerable discussion as to how to resolve the matter. Their preliminary solution is to subsume the deviations under the original theory in the following manner. Species vary with respect to how many foundresses typically occupy an individual fruit. As we move away from the conditions with which a species is most familiar, the observed sex ratios begin to deviate from the 95% confidence interval. Thus, the observed values are closest to the predictions in the situations (in terms of number of foundresses) encountered most often by a given species of wasp, which is what we would expect to be the case if a species is optimally designed for its native environment (*ibid*: 203). Rather than being satisfied with the general qualitative fit of the data to LMC, then, Herre *et al.* use theoretical considerations associated with LMC to explain the cases in which quantitative fit breaks down.

4.5.3.2. Case Study: Extrapair Copulation and Fluctuating Asymmetry

What follows is an analysis of a well-regarded ongoing project directed by Thornhill and his colleague Steve Gangestad. This example is ideally suited for our purposes in that, in addition to the structural congruence with the fig wasp study, it embodies the typical form of evolutionary psychological studies and is considered an exemplary piece of work in evolutionary psychology.

Let's begin with a little background. An extrapair copulation (EPC) is defined as copulation with any partner other than one's current long-term mate, with the term length required for sexual partners to qualify as a "pair" differing depending on the species. EPCs are often characterized by short-term sexual encounters with little or no material or parental investment on the part of the male. For this reason among others, the function of EPCs has been a source of considerable debate in behavioral ecology. For if the female is not receiving any material or parental benefit in exchange for access to her reproductive capacities, why grant the male access at all? One popular explanation suggests that the benefits received by the female come in the form of "good genes" for her offspring. The EPC male's high genetic quality is thus thought to explain why the female consents to a copulation in the absence of material or parental investment.

The second bit of background concerns the term "fluctuating asymmetry" (FA), which is used to describe "a random non-directional departure from perfect bilateral symmetry" (Maynard Smith and Harper 2003: 4). One line of thought in evolutionary biology holds that the degree of bilateral symmetry exhibited by an organism can provide indirect evidence of that organism's genetic quality. The extent to which an organism's left and right halves are symmetrical is thought to vary directly with the degree of stability of the organism's developmental processes. Developmental stability is in turn thought to be partly determined by genetic quality, with high genetic quality resulting in developmental processes that are highly stable and low genetic quality resulting in relatively unstable processes. On this view, then, a low degree of bilateral asymmetry should indicate high genetic quality, or "good genes."

Based on the theoretical considerations involving EPC and FA, Gangestad and Thornhill made two predictions about EPCs among humans: first, that "men's number of EPCs would correlate negatively with their fluctuating asymmetry;" and second, that "men's number of times having been an EPC partner of a woman would negatively correlate with their fluctuating asymmetry" (Gangestad and Thornhill 1997: 69). Both predictions are derived by conjoining the proposition that (a) females engage in EPC in order to receive good genes for their offspring, with the proposition that (b) the lower a male's FA is, the better his genes are. It follows from (a) and (b) that the strength of females' preferences for a particular male should vary inversely with his degree of FA. Thus, the lower a man's FA is, the more often he is likely to be preferred by females as an EPC partner.

4.5.4. Assessment

First , the authors' choice to limit their predictions to the qualitative sort might be taken as suggestive, given that quantitative predictions could have been made. For example, they could have specified a value or range of values of FA corresponding to a man's number of times having EPCs and having been an EPC partner. This would have given us a clear idea of what to expect if natural selection was to have played a dominant or important role in shaping women's preference for EPCs and a clear idea of what constitutes, in Orzack and Sober's words, "an unacceptable match between theory and data." Testing those predictions would have been easy (after all, FA measurements *were* quantitative), and a good fit would have been impressive. Moreover, as in the wasp study, any trend in deviations from the quantitative predictions could have potentially shed light upon why we failed to see an exact match.

Unfortunately, since the predictions of the model are not quantitative, we are forced to assess how surprising it would be if they turned out to be true, given common sense. Here, as in the majority of evolutionary psychological models, we find that the predictions fail to rise above the platitudinous. If symmetrical faces are considered to be more attractive than asymmetrical ones, then it would seem to follow plainly from common sense that men with low FA will be preferred over men with high FA for the obvious reason that more attractive men should be expected to be preferred over less attractive men. The idea that women prefer attractive men over unattractive men is hardly surprising, and certainly not the kind of prediction which, if true, should inspire confidence that our model is correct.

A possible reply on behalf of evolutionary psychologists would be to suggest that a general preference for symmetry might itself have an adaptive explanation behind it. That's true enough, but it is similarly true that a preference for symmetry can be explained by the fact that a wide range of taxa are attracted to environmental novelty and that symmetry is relatively novel in natural environments (Enquist and Arak 1994). It is simply not possible to distinguish between these two hypotheses using the evolutionary psychology methodology.

This brings us to the second evaluative question—viz., are the predictions of the model unique? The predictions certainly appear to be "consistent with the notion that 'good genes' sexual selection has partly forged the design of human psychological adaptations that underlie mating" (Gangestad and Thornhill 1997: 84). Unfortunately, the authors fail to make the obligatory distinction between being *consistent* with a model and providing *support* for that model. By themselves, the predictions, if true, would not allow us to distinguish between a selective process which has designed females to prefer men with "good genes" versus general sensory bias in favor of symmetry. If women prefer symmetry regardless of which object they are perceiving, they will naturally tend to prefer symmetrical men over asymmetrical ones. In fairness to the authors, they do acknowledge that their "research cannot rule out all other explanations" (Gangestad and Thornhill 1997: 84). But they do not attempt to provide a basis for why *their* model should be preferred over *any* alternative, and the reader is left wondering what other than mere consistency with their own model is motivating the authors' belief that the model has been supported by their findings. Simply recasting commonsense observations in terms of fuzzy, poorly supported evolutionary principles does nothing to increase the model's probative strength. In addition, the only alternative model they are even willing to recognize is one which emphasizes the adaptive significance of the finding that "low FA men are seen as more able to provide physical protection to their partners than high FA men" (*ibid*: 84), a minor variation on their own genetic benefits model.

At any rate, Gangestad and Thornhill found qualitative agreement with their predictions: men with relatively low FA—in their words, "men who show evidence of developmental stability" (*ibid:* 83)—were more likely to have sex with people other than their long-term mate, and they were more likely to be the person with whom women had extra-pair sex. Again, there's no surprise here, and no light is shed on the underlying reasons for women's preference for men with low FA by wheeling out some fuzzy associations with evolutionary theory. What *is* surprising is the casualness with which the authors convert "men with relatively low FA" to "men who show evidence of developmental stability." Aside from the questionable association between FA and developmental stability (see below), the authors provide no basis for thinking that men who show evidence of developmental stability *per se* are more likely to engage in and be sought out for EPCs. Even if FA *were* a reliable indicator of developmental stability, it is an entirely open question whether, in general, men who show evidence of developmental stability exhibit the predicted associations with EPCs. There is no mention of other potential proxies for developmental stability and their associations with EPCs. In this context, to say that "men who show evidence of developmental stability" are more likely to have EPCs and be EPC partners is a bit like saying that men who show evidence of being wealthy tend to get a lot of traffic tickets, after demonstrating a positive association between driving a Ferrari and being cited for speeding. Even assuming that driving a Ferrari is a good indicator of being wealthy, there are lots of other ways of evincing one's wealth that will show no association with getting lots of speeding citations. Similarly, there may be a variety of types of evidence for developmental stability. In order to provide foundation for the claim that there is a general tendency for men who show evidence of developmental stability to seek and be sought out for EPCs, Gangestad and Thornhill need to present more than one type of association between a developmental stability proxy and EPCs.

4.5.5. Assessing Assumptions: The Link Between Developmental Stability and Fluctuating Asymmetry

The preceding discussion of FA points to another component of optimality models which is often overlooked in evolutionary psychological practice—the truth of assumptions. Evolutionary psychologists often place lots of eggs into baskets woven from assumptions for which they have no empirical support (e.g., the assumption that adaptation is revealed by conformity to *a priori* design criteria). But correspondence between observations and predictions will be of little matter unless the assumptions from which our predictions are derived are themselves true (Herre *et al.* 2001: 212). For, when our observations confirm the predictions derived from our model, the model can only be seen as having been supported by those observations *given the truth of the model's assumptions*. In the Gangestad and Thornhill model, the predictions are derived from a few primary assumptions, many of which are not made explicit. Here I will discuss what I take to be the most important assumption of their model—viz., that developmental quality is accurately represented by FA.

Let me first briefly outline the argument for the idea that an organism's FA is a cue to its developmental quality. Because bilaterally symmetrical traits (e.g. ears) are likely to be controlled by the same gene or gene complex, under perfect developmental conditions the left and right halves should be perfectly symmetrical, having received the same set of developmental inputs. When there is some developmentally relevant perturbation, left and right halves should deviate from perfect symmetry to the extent that their developmental inputs differ.

Many biologists' interest in FA lies in the belief that it is an indicator of the organism's ability to withstand developmental perturbation, an ability which is determined by their genetic quality. It is assumed that the degree of symmetry exhibited between the organism's left and right halves is representative of the degree of fidelity maintained by the organism's developmental processes in the face of "developmental perturbations" such as pathogens, mutations, and environmentally induced stress factors like temperature shifts (Gangestad and Thornhill 1997: 72; Kruuk *et al.* 2003).

There are a number of phenomena we should expect to see if FA is truly representative of high genetic quality (which is usually understood in terms of viability). First, FA

> should reflect environmental stress, such that it increases when environmental conditions are harsh either during the development of the trait or during early development of the individual (Kruuk *et al.* 2003: 102).

Second, FA should be negatively associated with the degree of multilocus heterozygosity, on the assumption that heterozygosity, *ceteris paribus*, provides for better phenotypic condition than does homozygosity. (Plainly, inbred individuals are characteristically of lower phenotypic quality, which is a function of the increased homozygosity of their genotype due to inbreeding).[19] Third, the FA of a given trait thought to be subject to sexual selection should be heritable. This

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[19] Lewontin (1974)

follows directly from the notion that differences in FA are caused by genetically based differences in developmental stability (Kruuk *et al.* 2003: 102).[20]

Gangestad and Thornhill take all of this and more on board in their study of EPCs. Whether the truth of their predictions provide support for the idea that women have been directly selected to prefer men whom they perceive to have good genes depends on the truth of the above assumptions (as well as a host of others discussed in chapter 3 in connection with indicator models). So then, *are* the above assumptions true?

A recent review of the few experiments which have actually tested for associations between FA and various stresses in a number of species found there to be no consistent relationship between FA and developmental perturbations (Bjorksten *et al.* 2000). In addition, a formidable study on FA in the antlers of red deer *Cervus elaphus* found no evidence to support the idea that there is an association between FA and factors known to affect the fitness of *C. elaphus* (Kruuk *et al.* 2003). Most importantly, concerning what we should expect to see if low FA is associated with high genetic quality (see above), the study demonstrated each of the predictions to be false (i.e., no consistent relation to developmental perturbations, no consistent relation to inbreeding, and "no evidence of additive genetic variation [i.e., heritability: CH] underlying FA" [*ibid*: 111]) Thus they concluded that there was "no evidence to suggest" that FA is "useful as *any* sort of indicator...and so is presumably a poor indicator of developmental stability" (*ibid*: 111, my emphasis).

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[20] See Kruuk (2003: 102) for additional phenomena to be expected from the assumed relationship between FA and genetic quality.

Now, Kruuk *et al.* *did* find that FA in antler length was negatively related to breeding success. And, perhaps interestingly, the only empirical support Gangestad and Thornhill provide for the idea that FA is indicative of developmental quality is reference to a number of studies which show a negative association of FA with mating success (a principal determinant of reproductive success). But where Gangestad and Thornhill use this correlation as evidence for an association between low FA and individual condition, Kruuk *et al.* concluded that "FA in antler length" may "be important because of the function of antlers, rather than because it reflects individual condition" (Kruuk *et al.* 2003: 110) specifically *because* they could not find a consistent relationship between FA and either condition itself or known determinants of condition in red deer. Kruuk's *et al.* inability to find direct evidence for FA as an indicator of condition led them to believe that the negative association between FA and breeding success which they had found—and which had similarly been found by others (see Gangestad and Thornhill 1997: 72)—was just an epiphenomenal effect of some other causal process (e.g., that more symmetrical antlers, for mechanical reasons, give red deer an advantage in antler-locking contests which bear a direct causal relation to mating opportunities [Kruuk *et al.* 2003: 110]). In this case, direct tests of the argument for why low FA indicates developmental stability—the major assumption of the Gangestad and Thornhill study—showed that argument to be unsupported by the actual evidence.

Conclusion

These remarks, I think, go a long way in undermining the view that there is any support for the hypothesis that women's EPC preferences for men with low FA evolved because of the genetic benefit that accrued to our ancestors' offspring. Let's look again briefly at the major weaknesses. The first weakness is the long, fragile, and questionable causal chain putatively linking the selection of women's mate preferences to Gangestad and Thornhill's evidence: relatively low FA is a proxy for high developmental stability, which is in turn a proxy for "good genes." Whether these are legitimate proxies is an entirely open question. The second weakness is the lack of probative value of the predictions towards establishing the truth of the hypotheses, due to the fact that the predictions themselves do nothing to rule out rival explanations and follow from common sense.

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The foregoing discussion has revealed that, considered as the science by which we can learn about the history of human psychological evolution, evolutionary psychology is in a lot of trouble. The major parameters of evolutionary psychologists' adaptive thinking—hunting and the home base social structure—were uncovered as either outright falsehoods or, at best, unsupported. Their situation in this respect is reminiscent of the unhealthy distance (discussed in chapter 3) between evolutionary psychology and current theoretical and empirical work on sexual selection and mate choice. Accordingly, either evolutionary psychologists are unaware of the last few decades of paleoanthropological research or they have chosen to adopt discarded models of human evolution for ideological reasons. Whichever disjunct turns out to be true, it raises serious questions about their accounts of human evolutionary history.

In their defense, evolutionary psychologists might reply that neither of these disjuncts is true; they have arrived at their beliefs about the human past via reverse engineering. This response would, if true, explain why they have not entertained rival accounts of selection pressures and adaptive functions. For, the use of reverse engineering precludes any chance of alternative explanations showing up on the reverse engineer's radar. But as we have seen, it is this feature of reverse engineering which makes it useless for understanding history. Neither it, nor the reproductive relevance method can serve as shortcuts around the arduous road back to our beginning.

5. "Grace" Under Fire: On Being Consistent With Evolutionary Theory

One popular method for supporting the claim that some evolutionary psychological account is the best explanation for a putative component of human nature is to rule out all other explanations on the grounds that their manifest inconsistency with evolutionary theory implies that they could not possibly be true. Since the evolutionary psychological explanation is the only remaining account (because it is consistent with evolutionary theory virtually by definition), it warrants our acceptance.

The whipping boy for this strategy has been social science. Evolutionary psychologists have claimed that social science must "accept with grace the...tenet of mutual consistency among disciplines" in order to "move away from its present fragmented and insular form" (Cosmides *et al.* 1992: 12-13). In this chapter I examine evolutionary psychologists' concept of consistency as well as the tenet of mutual consistency itself and argue that neither can bear the load required by the arguments against social science found in the evolutionary psychological literature.

Many evolutionary psychologists have criticized social scientists for paying insufficient attention to making their theories of human behavior "consistent with what is known in the natural sciences" (Cosmides *et al.* 1992: 4), in particular, evolutionary biology. Social science, they claim, has been conducted in an environment largely devoid of evolutionary considerations. By not taking into account the fact that our species evolved just like any other species, researchers have ignored natural selection, a causal process "known to govern all life" (Buss 1991: 461). A lack of proper concern for the forces of evolution would put any account of human psychology in jeopardy, for the simple reason that psychological theories "inconsistent with evolutionary theory stand little chance of being correct" (Buss 1991: 461). In the succinct language of leading evolutionary psychologists Daly and Wilson, "[m]any...theories that are still debated by social scientists implicitly deny the action of natural selection, and are therefore surely wrong" (Daly and Wilson 1988: 7).

In stark contrast to the evolutionarily uninformed social sciences stands evolutionary psychology, a research program whose results are derived from, and thus assumed to be consistent with, the "strong deductive framework" of evolutionary theory (Tooby and Devore 1987: 189). Because of its strong emphasis on the centrality of evolution to any plausible theory of human psychology, evolutionary psychology avoids the risky business of theorizing about human nature which might turn out to be incompatible with what we've learned from evolutionary biology.

5.1. Examples of Evolutionary Inconsistency in Social Science

Domain-Generality

The most egregious violation of evolutionary theory perpetrated by social scientists is the assertion that the human mind consists primarily or solely of "general-purpose, content-independent, or content-free mechanisms" (Tooby and Cosmides 1992: 34). Mental mechanisms given free reign over what inputs to focus on and what behaviors to produce would allow for an unwieldy variety of behavioral plasticity, in which the organism will rarely if ever provide the appropriate behavioral response to an environmental challenge.

> Accordingly, to be endowed with broad behavioral plasticity unconnected to adaptive targets or environmental conditions is an evolutionary death sentence, guaranteeing that the design that generates it will be removed from the population (Tooby and Cosmides 1992: 101).

The unerring eye of natural selection will weed such mechanisms out because "the property of freely varying behavior in all dimensions independent of conditions is not advantageous: It is evolutionarily and individually ruinous" (Tooby and Cosmides 1992: 101).

Passive Reception of Information

Another psychological property which social scientists have proposed is the "passive reception" of sociocultural norms, in which individuals learn appropriate behavior by imitating other members of their social group. Here, as in the case of domain-generality, social scientists have taken a "conceptual wrong turn" (Cosmides *et al.* 1992: 13) because of their evolutionary ignorance.

> Evolution could not have produced a psyche that functioned as the passive receptacle of information transmitted from the social group, because (among other reasons) many members of the social group have antagonistic interests (Tooby and Cosmides 1990a: 44).

The idea here is simple: the interest of other members of one's social group will often be at odds with one's own interests. Anyone who merely imitated the behavior of others would either be exploited or, at a minimum, behave in a way that didn't necessarily cohere with his ultimate reproductive interests. Instead, evolution would had to have produced an "individually tailored adaptive system" (Tooby and Cosmides 1990a: 44) which generated behavior appropriate to the individual's specific adaptive predicament.

Unreliable "Status-Striving" Mechanisms

During a discussion of the evolutionary dynamics of psychological mechanisms, David Buss asserts that the evolution of psychological mechanisms which created a desire to climb the social ladder would be impossible "unless they reliably produced classes of acts that actually led to the increase or maintenance of positions within social hierarchies" (Buss 1991: 464). According to Buss, given that "[p]sychological mechanisms evolve because they have behavioral consequences," such mechanisms could only evolve in the instance where they faithfully caused a certain (presumably adaptive) behavioral output.

Family Violence and "Easy Striking Distance"

In their Lakatosian defense of evolutionary psychology, Ketelaar and Ellis assert that the psychological mechanism(s) for violence cannot be victim-general because this would undermine the "basic metatheoretical assumption of evolutionary theory...that natural selection favors nepotism." If violence mechanisms did not discriminate between family members and non-family members, then genetic relatives would, *ceteris paribus*, be just as likely to be attacked as would non-relatives. This kind of mechanism would be less adaptive than one which discouraged violence against family members. According to Ketelaar and Ellis, for such a mechanism to have evolved would be inconsistent with evolutionary theory and "would require a reformulation of the basic assumptions" of that theory (Ketelaar and Ellis 2000: 5). Thus, we can rule out the possibility that violence mechanisms are victim-general, i.e., assuming that natural selection favors nepotism.

5.2. What's Supposed to be Inconsistent?

Uniting these claims of inconsistency is the notion of negative effects on fitness. In the case of domain-general mechanisms, evolutionary psychologists argue that such mechanisms would reduce the pace of cognition to a debilitating rate, and that behavioral responses will more often than not be contextually inappropriate, both of which are assumed to adversely affect the reproductive success of the organism. For passive receivers of information, their lack of consideration for their particular adaptive situation will result in behavior which goes against their evolutionary interests. Victim-general violence is assumed to lower inclusive fitness. And status-striving mechanisms which did not reliably produce an elevation in social status would not have been adaptive enough to evolve. The essence of the objection is best stated by Tooby and Cosmides themselves:

> Adaptive tracking must, of course, have characterized the psychological mechanisms...during the Pleistocene, or

> such mechanisms could never have evolved (Tooby and Cosmides 1989: 35)

and elsewhere:

> ...a psyche that contained nothing but general-purpose information-processing procedures could not, in principle, generate adaptive behavior, and therefore is an evolutionary impossibility" (Tooby and Cosmides 1990: 27).

Now, this specific reference is to mechanisms "governing culture," but the message is general: *that which is not adaptive cannot evolve*. When a proposed behavior or morphological trait is perceived *a priori* to most likely have negative effects on the fitness of its bearer, it is determined that that behavior could not have evolved. To propose the existence of a trait that could not evolve is to be inconsistent with evolutionary theory. Therefore, to claim that we have some trait that is perceived to be the kind of thing that would have negative effects on fitness is to make a claim which contradicts evolutionary theory, a claim which has little chance of being correct.

5.2.1. *A Priori Judgment of Negative Effects on Fitness*

There are at least three serious problems with these claims of inconsistency. The first has to do with how we can know the effects of a given trait on an organism's fitness. The second has to do with domains of fitness. The third has to do with the notion of what could possibly evolve.

With the exception of a trait whose inability to evolve was logically necessary, there is no reason to think that we should be able to tell *a priori* that a particular trait would have negative effects on the fitness of *any* organism which possessed it. An *a priori* evaluation of a trait's evolutionary trajectory requires that the very concept of the trait entails either that it (a) cannot evolve, or (b) cannot *but* evolve. This is because, in the absence of a logically necessary trajectory, we cannot know in advance of the actual expression of the trait precisely how it is going to fit into the organism's overall phenotypic economy. Moreover, we certainly cannot know whether a trait would have had negative effects on fitness without knowing the actual historical conditions in which it arose—i.e., without knowing which alternative morphs were available or what kinds of selection pressures the population encountered. This is why, for example, Kingsolver and Koehl label their own study (which is incomparably superior to the *a priori* functional comparisons provided by evolutionary psychologists) as "speculative." But evolutionary psychologists' charges of *inconsistency* presuppose that we can *and do* have this knowledge. The widespread pronouncement that domain-general cognitive structures could not possibly make up a significant portion of an organism's cognitive architecture because no such structures could have evolved implies that there are no possible phenotypic or ecological conditions under which domain-generality could have any effect on fitness other than an overwhelmingly negative, "ruinous" one. But whether this is the case is an entirely *a posteriori* matter which cannot be judged in any way other than experiment and observation—i.e., the way biologists usually determine what kinds of fitness effects a trait has. "[I]maginations informed by evolutionary theory" (Daly and Wilson 1988: 13), no matter how fertile, cannot furnish us with answers to questions about fitness in advance of the actual performance data.

It is likely that there will be some resistance to the notion that, except for the case in which there is no possible world in which the trait could evolve, we cannot determine the evolutionary trajectory of a trait *a priori*, but examples can be adduced at will to allay any such fear. Here are just a few. Sterility immediately suggests itself, but quickly retreats owing to the preponderance of insect species where sterile males have been around for a long time. Traits which are extremely physiologically debilitating may also seem like attractive candidates. Again, however, we find these all over the place, from frog chucks to peacock trains. In fact, theories like Fisher's "runaway" model and Zahavi's "handicap mechanism" are virtual recipes for turning seemingly maladaptive traits into adaptive ones. Any *a priori* proposal for a trait's evolutionary trajectory would have to incorporate some way of circumventing this recipe. None of the "impossible" traits on offer in the field of evolutionary psychology provide a way of doing this.

5.2.2. *Fitness Domains*

This brings us to the second general problem. When we want to assess the fitness value of a trait, often what we must do is measure the performance of that trait with respect to a particular task. Good performance can provide some indirect evidence that the trait was selected to perform that task. Poor performance can provide indirect evidence that the trait was not selected to perform that task, but it *cannot* provide evidence—direct or indirect—that the trait was not selected to perform *any* task. Poor performance at a particular task may just indicate that we are assessing the value of the trait relative to the wrong task, a task for which it was not selected. This idea forms the foundation of methodological adaptationism, practitioners of which believe that moving on to another task analysis when the trait is shown to have failed at the original task is just how science gets done (Beatty 1987; Mayr 1983; Parker and Maynard Smith 1990).

For example, suppose we suspect a certain local species of bird to be a Batesian mimic based on the fact that it has colored spots similar to some sympatric unpalatable species of butterfly. If the bird is this sort of mimic, its viability should be increased by causing predatory species to avoid it as they avoid the local butterfly. To test our hypothesis, we paint the colored spots of half the members of this bird species so that their coloring is homogeneous. The other half we leave as they are. If our hypothesis is correct, the viability of the painted group should decrease as a result of having lost its ability to mimic the unpalatable butterflies. But lo, we find that viability in the homogeneously colored group actually *increases*. This could indicate that the colored spots were not selected for their positive effects on viability, contrary to our hypothesis. But it does not show that the spots are not an adaptation. In fact, a subsequent experiment shows that females prefer to mate with males with colored spots. Colored spots have positive effects on fitness through sexual selection and thus may still be an adaptation, even though they negatively impact survival.

What this example shows is that the domain in which we judge the value of a trait for reproductive success may just be the wrong domain in which to judge the value of that trait. So, even if evolutionary psychologists are capable of demonstrating that domain-general cognitive structures in any organism in any environment are, say, very slow, they still have a long way to go in showing that domain generality could not be an adaptation. Perhaps cognition actually *slowed down* in the transition from chimpanzees to humans in order to allow us to deal with a greater variety of information, or to expand the range of inferences of which we're capable. Perhaps some accidental property of the early female hominin brain produced a sensory bias which caused them to prefer slow thinkers. Of course, all of these alternatives are, like the charge of cognitive sloth, pure fantasy until the appropriate tests are carried out. The point is merely that even if we consider evolutionary psychologists to have had the last word on the issue of computational speed, there are many other domains in which the fitness value of domain generality needs to be assessed. A simple glance at our own anatomy should suffice to drive the argument home. Our relatively large brains made us, *ceteris paribus*, heavier than our smaller-brained ancestors. But it would be a serious error to suggest that larger brains couldn't have been selected for because of the negative effects on speed or balance created by the added brain mass.

This objection highlights a confusing irony in much of the evolutionary psychological literature aimed at critiquing social scientific models of human psychology. If what makes it permissible for adaptationists to retain their belief that a particular trait is an adaptation after a given function hypothesis has failed is the fact the trait might have *some other function*, then evolutionary psychologists *qua* adaptationists cannot turn around and reject a theory of human psychology or behavior on the grounds that the theory implies negative fitness consequences when measured against the demands of a particular task. If it were reasonable to conclude that some trait "could not evolve" because it would perform poorly on a given task, then adaptationists would never be justified in retaining their belief that a particular trait is an adaptation after the failure of an explanation of that putative adaptation's function. Therefore, in order to retain their right to employ adaptationism, evolutionary psychologists must refrain from condemning a trait to the evolutionary dustbin simply because that trait does poorly in a given domain.

5.2.3. *Other Ways of Evolving*

Let's suppose that evolutionary psychologists accept our challenge of testing the performance of a trait for each task for which it could reasonably be thought to have been selected and find that the performance is in every domain poor relative to other variants that probably existed when the trait was evolving.[1] If there are no domains in which the trait could have outperformed contemporaneous variants, then we are justified in concluding that it is not an adaptation. It

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[1] This brings us back to the problem of *a priori* biology. It's customary to measure performance relative to some variant which we know to exist or to have existed. But we have no clue whether the domain-specific cognitive architecture posited by evolutionary psychologists was extant at the time we were evolving. Obviously, if it wasn't around, it doesn't matter how poor domain-general mechanisms perform. They win by default.

is quite another thing, however, to show that the trait could not *exist*—that, for example, domain-general cognition is "an impossible psychology" (Tooby and Cosmides 1992: 34).

One rather obvious way in which uniformly maladaptive traits can evolve is through genetic or functional correlation with other, adaptive traits (Price and Langen 1992: 309-310). Experiments with artificial selection have demonstrated a variety of correlated responses to selection for a specific trait. Selection for tameness in foxes, for instance, brought along with it several "juvenile-like characteristics which... appeared as a side effect of changing hormone concentrations" (*ibid*: 309). Similarly, selection for certain life-history traits can cause the persistence of traits that are severely maladaptive. A negative *genetic* correlation between traits that are positively *functionally* correlated (such as life-history traits) will cause tradeoffs between trait values when there is selection for one but not the other (Charlesworth 1990). Conversely, single genes may produce multiple traits (i.e., traits with a perfect genetic correlation), some of which are adaptive, some of which are maladaptive. Where the positive effects outweigh the negative, maladaptive traits can persist. Let it suffice to say that when there is the right kind of correlation between traits, maladaptive traits can and indeed *do* evolve. Thus there is nothing "impossible" about the evolution of a psychology that might have been slower than other variants, or a personality type that learned behavior through socialization rather than adaptive planning.

Living in a post-Spandrel world, evolutionary psychologists are presumably acutely aware of evolutionary avenues that do not strictly follow the path of natural selection. Indeed, one can find exhortations to that effect across the literature. However, given the continual *a priori* evaluation of traits and references to things which "could not evolve" or are "impossible," I see no reason to think that the professed sensitivity to modes of evolutionary change other than natural selection is anything other than lip service. Gould and Lewontin (1979) made the point almost thirty years ago that, in Kitcher's words, "what is preached as possible on the holy days is often dismissed from consideration in the workaday world" (Kitcher 2004: 6). If evolutionary psychologists took seriously forces like drift and character correlation, there would be no rationale for them to claim that, for example, domain-general cognitive architectures could not evolve, due to their possible negative effects on fitness.

5.3. Real Inconsistency

We have seen that claims of inconsistency on the part of evolutionary psychologists fail to *show* inconsistency, due to a mistaken conception of what it means to be "inconsistent with evolutionary theory." If evolutionary psychologists have painted an inaccurate picture of inconsistency, then what is the right picture?

In order to actually be inconsistent or incompatible with evolutionary theory (by which evolutionary psychologists typically mean natural selection) an hypothesis would have to entail that the proposed trait was selected for *because* *of* its negative effects on reproductive success.[2] This is something that Darwin's theory of natural selection cannot sustain logically. To make this condition clearer, consider what might (or might not) have caused the widespread existence of human noses. If we wanted to explain the existence of human noses in a manner consistent with evolutionary theory, then we could not, for example, assert that noses caused the people who had them to have less children, and that those children (who acquired noses through genetic inheritance) also ended up having less children because of their noses. The reason that this explanation would be inconsistent with evolutionary theory is this: evolutionary theory entails that a property cannot be selected for *because of* its negative effects on fitness, and our explanation of the evolution of noses asserts that the nose was selected for because of its negative effects on fitness. Evolutionary theory says "p," and our theory says "$\neg p$."

Of course, as I have already argued in detail, this does not mean that noses could not have evolved unless their fitness effects were non-negative. For noses to have negative effects on fitness and still evolve is perfectly consistent with Darwin's theory of evolution. Suppose the current version of the human nose N_c was caused by the same mutation which gave us the opposable thumb, and suppose that N_c worked much more poorly than the previous version of the

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[2] Since evolutionary psychologists use "evolutionary theory" to mean the principle of natural selection, this is accurate for the purposes of the discussion—but not as a general principle. Inconsistency with evolutionary theory is going to depend on what one takes to be the axioms (along with their logical entailments) of that theory. It is not always clear what these axioms are, such there be. Natural selection is surely one. Genetic drift is probably another. Ironically, then, evolutionary psychologists claims about inconsistency are *themselves* inconsistent with evolutionary theory. For, as the examples in 7.1 show, they often effectively propose that a trait cannot evolve other than by direct selection, which is something which the axiom of genetic drift contradicts.

nose, N_p. Even though the fitness effects of N_c relative to N_p were negative, the overwhelmingly positive effects of the opposable thumb allowed the inferior N_c to spread through the population. Now, even though this example is strictly fiction, it nonetheless remains a fact that the ability of properties with negative fitness effects to become widespread is a phenomenon the possibility of which is not in serious doubt.

5.3.1. *Social Science and Real Consistency*

Although it may not be rare for social scientists to offer some casual remarks on why a particular mode of human behavior might have evolved, I know of no explanation proffered by a social scientist which takes the form of the human nose explanation outlined above—i.e., an account which attempts to explain the existence of a behavior by way of reference to its negative effects on fitness. The closest thing we see to such an explanation comes from evolutionarily-minded anthropologists who argue that certain behaviors evolved via the handicap mechanism, where the high viability costs of a behavior (e.g., hunting) signal that the person performing it must have "good genes" (Hawkes and Bird 2002). In this case, the negative fitness effects (in the domain of viability) of hunting are in a sense causally related to its evolution, but the reason hunting is *adaptive* is because of the preferential treatment received by men who hunt, *not* the viability-reducing effects. The fitness advantage caused by the preferential treatment outweighs the disadvantage incurred by the behavior itself.

The work of Hawkes and other evolution-savvy social scientists, while interesting and important, stands at the margin of social science. The vast majority of claims made by social scientists are completely divorced from evolutionary considerations. But if we *do* consider it important for social scientists to make their theories consistent with evolutionary theory, we are presented with a puzzle: How do we determine whether a social scientific claim (SSC) is consistent with evolutionary theory when that claim does not mention evolution?

Above we saw the evolutionary psychological attempt to solve this puzzle—viz., to judge the potential fitness consequences of a behavior and see whether, given those consequences, it could have evolved. This strategy turned out to be a chimera for two reasons: (1) we cannot judge *a priori* the fitness consequences of a behavior, and (2) fitness consequences alone cannot tell us whether a trait could have evolved. However, the strategy itself is suggestive of the kind of approach we must take. If indeed we are to check SSCs against evolutionary theory, we will need some way of rephrasing or translating them into the predicates of evolutionary biology. Unfortunately, we have not yet been able to accomplish this.

What can we say in general about the compatibility (by which I mean something like "mutual realizability of all statements") of two theories in advance of the requisite translation? If we have independent reasons to believe that each theory is true, we could infer that the theories are compatible from the fact that no two statements can be true and contradict each other. This kind of reasoning might be behind Cosmides' *et al.* assertion that "the theory of natural selection cannot, even in principle, be expressed solely in terms of the laws of physics and chemistry, yet it is compatible with those laws" (Cosmides *et al.* 1992: 4).[3] In the absence of shared predicates, this appears to be the only option we have available to us.[4] Accordingly, we should apply the same rule when we find we are unable to translate the predicates of SSCs into the predicates of evolutionary biology. Where an SSC appears to be well-grounded independently of its relationship to evolutionary theory, we might properly conclude that it is compatible with evolutionary theory.

Contrastingly, Harman Holcomb III has suggested that the very fact that SSCs are formed in a semantics different from that of evolutionary biology is itself reason enough to suspect that SSCs are inconsistent with evolutionary theory.

> "If social scientists are free to describe and explain behavior in ways that need not take into account biological evolution, then it is likely that their descriptions and explanations of human behavior will often be irrelevant to or inconsistent with evolutionary theory" (Holcomb Iii 1993: 122).

I find the source of Holcomb's skepticism elusive. Why assume that social scientists are likely to make claims inconsistent with evolutionary theory if they do not use it as a guiding principle? A SSC that is internally consistent and well-supported should inspire us to give credence to it, irrespective of whether it is formulated in evolutionary semantics. Of course, given the lack of a common

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[3] In fact, it is entirely unclear why Cosmides *et. al.* think that the theory of natural selection is compatible with the laws of physics and chemistry. Nor is it clear how they were able to determine that the theory of natural selection cannot be expressed solely in terms of the laws of physics and chemistry.

[4] I am grateful to Frank Thompson for helpful discussion on this point.

semantics between the social and evolutionary sciences, it's certainly *possible* that most SSCs could turn out to be inconsistent. But to predict in advance of the translation of one into the other (or both into a third language) that

> it would be a miracle if a social science unguided by evolutionary considerations would on its own describe and explain human behavior in a way directly subsumable under evolutionary theory (Holcomb lii 1993: 123)

strikes me as unreasonable. Given that we are admittedly incapable at present of judging the compatibility of SSCs and claims made in evolutionary biology, it's unclear upon what Holcomb's pessimistic stance could be founded. If we have yet to determine the compatibility with evolutionary theory of even a single SSC, we could have no basis for thinking that their consistency with evolutionary theory would be unlikely or miraculous.

5.3.2. *Is Consistency Important?*

Quite apart from evolutionary psychology's misconceptions regarding what consistency with evolutionary theory *is* or whether we can determine whether some SSC achieves it, we should ask whether they're right to insist that social scientists' claims be consistent with evolutionary theory (along with the rest of the natural sciences). The fact that evolutionary psychologists are wrong about whether social scientists' claims and the claims of natural scientists are mutually consistent does not immediately let social scientists off the consistency hook. We still need to assess the requirement of consistency in and of itself.

There's a clear sense in which the demand of mutual consistency is, as Cosmides, Tooby and Barkow have emphasized, "absolute" and "incumbent upon all valid scientific knowledge" (Cosmides *et al.* 1992: 12). If statements in the natural sciences are true, social scientists' claims cannot both be true *and* contradict those statements. But the mutual consistency of true statements isn't a requirement restricted merely to the natural and social sciences. *No two statements—be they within the same discipline, between disciplines, or beyond any discipline—can both (1) be true and (2) contradict one another.* Thus, the requirement of consistency extends not just from, for example, evolutionary biology to the social sciences, but even from evolutionary biology to the library sciences. Normally, though, evolutionary psychologists are not emphatic that statements about, say, microfiche and statements in evolutionary theory be consistent with one another. Yet, the burden of consistency with evolutionary biology weighs no less heavily on the library sciences than it does on the social sciences. Why, then, we might ask, are evolutionary psychologists so insistent that the social sciences observe the consistency requirement, while the library sciences receive no mention at all?

The asymmetry with which evolutionary psychologists treat the social sciences, on the one hand, and the library (as well as all other) sciences suggests that their demands for consistency come not from the *logical necessity* that all truths must be mutually consistent, but rather from the *methodological assumption* that evolutionary theory—specifically, the theory of adaptation through natural selection—and theories of human psychology and behavior should have a lot to do with each other. If the real motivation was the general requirement of mutual consistency then we should expect to see articles lambasting the library sciences for ignoring the principles of quantum mechanics and organic chemistry. But we have no such expectation, and with good reason.

As evidence for the existence of the assumption that the theory of adaptation through natural selection and theories of human psychology and behavior must bear upon one another, consider the claim by Donald Symons that "there is no known scientific alternative to the theory that human nature is the product of natural selection" (Symons 1992: 147). Concerning the properties of organisms in general, even within evolutionary biology itself there are at least two "scientific alternatives" to the theory that those properties are the products of natural selection—viz., genetic drift and character correlation. For example, the notion that some mammalian tooth characters are the product of genetic drift rather than natural selection is an alternative to the theory that those characters are the product of natural selection (Lande 1976), and it's difficult to see precisely what about that alternative could be characterized as "unscientific." What would undoubtedly be unscientific would be to rule out *a priori* the possibility that mammalian dentition is the product of genetic drift. Lande notes,

> If the hypothesis of evolution by random genetic drift cannot be consistently ruled out from fossil evidence, there would be no basis for supposing that the phenotypic evolution is purely a result of natural selection, and random genetic drift would emerge as a potentially significant motive force in evolution (1976: 321).

The same presumably is true for the aggregate property "human nature," whose name refers to the bundle of psychological and behavioral properties that are common to all humans in virtue of their shared genetic inheritance. For each property, there will be a variety of "scientific alternatives" to a selectionist account, many of which will come from *outside* evolutionary biology. As evolutionary psychological folk hero George C. Williams warned us many years ago,

> This biological principle [i.e., adaptation through natural selection: CH] should be used only as a last resort. It should not be invoked when less onerous principles, such as those of physics and chemistry or that of unspecific cause and effect, are sufficient for a complete explanation (Williams 1966: 11).

Each of these alternatives will need to be entertained in a systematic, empirical way in order for our explanations of the focal properties to demand any sort of confidence.

Further evidence for the existence of an assumption that theories of human psychology and behavior need always to intersect with the theory of natural selection is provided by the assertion that there is an "irrefutable" logical progression from the premise that physiological properties are generally adaptive to the conclusion that "human nature, including human psychology, must have...an adaptive logic" (Daly *et al.* 1982: 23). Generally speaking, it does not follow that some biological property (e.g., our psychology) is an adaptation from the fact that another property (e.g., our physiology) is plausibly an adaptation. This inference procedure would effectively license us to conclude that all of our properties are adaptations in the case where we found that *one* of them was. Whether or not two organismal traits have similar evolutionary histories (specifically in the respects relevant to determining whether they are adaptations) is going to depend on the particular historical facts of each trait considered separately, not on the supposed existence of a logical progression which dictates that a commitment to adaptation *somewhere* is a commitment to adaptation *everywhere*.

The assumption that theories of human behavior and the theory of natural selection have a lot to do with each other is based on the view that it is true *a priori* that the theory of natural selection, in Jerry Fodor's words, "importantly constrains" theories of human psychology and behavior (Fodor 2000: 83). But the theory of natural selection can only constrain theories of human psychological and behavioral traits in the cases where those traits were actually selected for. And while it may be true in some cases—even every case—that a particular trait's evolutionary history suggests that it is the product of direct selection, it is not true *a priori*. For, as we have seen, even functional traits may arise through evolutionary means other than natural selection. Thus, whether the theory of natural selection and theories of human psychology and behavior should have a lot to do with each other is not an *a priori* truth but will instead depend on the particular psychological or behavioral trait in which we are interested. So evolutionary psychologists are not justified in their use of the theory of natural selection as a logical constraint on the social sciences.[5]

Now although it is not an *a priori* truth that evolutionary theory and theories of human behavior should have a lot to do with each other, that such a relation-

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[5] Thanks to Rachana Kamtekar for helpful discussion on this point.

ship exists between them may be a *reasonable* methodological assumption. There doesn't seem to be anything in principle *wrong* with adopting it as a methodological assumption and then going on to see whether work done under that assumption bears any fruit, in the same way there should not be anything in principle wrong with adopting adaptationism as a methodological assumption. But there *is* something in principle wrong with demanding that *anyone* who endeavors to study human behavior adopt that assumption, in the same way it would be wrong and scientifically ridiculous to demand that every evolutionary biologist adopt adaptationism as a methodological assumption. We know that many important properties of organisms are not adaptations, and to push on as though they were would certainly not help to expand the breadth of biological knowledge.[6]

Conclusion

The arguments in this chapter have aimed at establishing three general claims. First, evolutionary psychologists are typically mistaken in their beliefs about what kinds of phenotypic properties are inconsistent with evolutionary theory, a mistake which derives from a general misconception regarding what consistency with evolutionary theory actually is. Second, given the correct conception of consistency there is no clearly understood method for determining whether claims in the social sciences are consistent with evolutionary theory. Hence, there is no firm basis for the skepticism on the part of many evolutionary

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[6] See Fodor (2000: 80-84) for related comments on the consistency requirement.

psychologists with respect to whether social scientific claims are consistent with evolutionary theory. And third, evolutionary psychologists' insistence that social scientific claims be consistent with evolutionary theory derives not from a principled commitment to the mutual consistency of scientific truths, as is usually claimed, but rather from an *a priori* assumption that the principles of evolutionary theory are necessary for understanding human psychology and behavior. While such an assumption may be methodologically justifiable, it is not a logically necessary constraint on our ability to understand human psychology and behavior.

6. Adaptation and Explanation

Several authors (e.g., Holcomb III 1996, 1998; Ketelaar and Ellis 2000) have argued that the fact that evolutionary psychological hypotheses are consistent with evolutionary theory contributes to the overall goodness of those explanations—indeed, making them the best explanations of human behavior available.

Inference to the best explanation is the process by which we accept an hypothesis based on our appraisal of it as superior to that of any rival hypothesis. As controversial as inference to the best explanation has been (due in no small measure to conflict over the meaning of "best"), one element that has remained relatively uncontroversial as a description of our inference practices is the notion that we characteristically *adjudicate* between rival hypotheses when deciding what to believe (or what would be best to believe)—rather than, say, picking one at random. I call this process of adjudication "explanatory competition."

In the same way in which Olympic athletes must participate in the same event in order to compete against each other, I argue here that whether certain accounts can compete against each other in an explanatory competition, whether they are true rivals, depends on whether they are the same kind of account (in the sense explicated below). I then make some specific remarks about explanatory competition as it pertains to the explanation of certain aspects of evolutionary adaptation.

6.1. Explanatory Competition

Let us say that, in general, an explanation *E* of phenomenon *P* is the kind of account which, if true, *would* explain *P* (Lipton 2004). Depending on the nature of *P*, there might be a variety of different kinds of candidate explanations, each invoking the laws or principles of different fields—e.g., explanations invoking the principles of physics, or of sociology, or of geology. For any *E*, then, if *E* is the kind of account which, if true, would explain *P*, *E* must possess all of the elements required by its field to explain *P*. From *modus tollens* it follows that if *E* does not possess all the necessary explanatory elements, then it is not the kind of account which, if true, would explain *P*—which means that *E* is not an explanation of *P*. And if *E* is not an explanation of *P,* then *E* cannot participate in a competition to explain *P*.

With this in place, consider the kinds of accounts which, if true, would explain why a certain organism has a certain property (call these "property-accounts"). When a property-account aims to show that the property was *selected for*, Brandon (1990) gives us five criteria required to make the case: (1) evidence *that* selection for that trait has occurred; (2) evidence for *why* selection for that trait has occurred; (3) evidence for the heritability of the trait in question; (4) information about the "patterns of gene flow and patterns of selective environments" for the relevant population; and (5) "phylogenetic information concerning what has evolved from what" (Brandon 1990: 165). He refers to such accounts as "adaptation explanations" (I follow his usage here). Of course, property-accounts *needn't* invoke natural selection. The claim is simply that, *if* a property-account invokes natural selection—i.e., if an account purports to be an adaptation explanation—that account could only qualify as an explanation if it provided us with the five kinds of information.

We can imagine lots of instances in which rival property-accounts compete to explain the same organismal property. Some of them might be adaptation explanations, but there can be other kinds of property-accounts. Some, for example, might be sociological, or physical or chemical accounts (Williams 1966: 11). The requirements for what qualifies as a property-account will differ depending on what kind of property-account is being given—i.e., on the field from which the laws and principles mentioned in the purported property-account come. There will not be any obligation on the part of a physical property-account to provide information about gene flow patterns in a population, for instance. This kind of information is not part of the structure of a physical explanation, although it is part of the structure of an adaptation explanation. The physical property-account may need only to invoke some established law of form in order to qualify as a physical explanation.

6.1.1. Explanatory Competition Between Property-Accounts

Now, it follows from the argument given at the beginning of section 6.1 that explanatory competition between property-accounts can only take place when the competitors possess all of the explanatory components called for by their respective fields. Accounts which lack some explanatory components are *ipso facto* not the kinds of accounts which, if true, could explain the fact that a certain organism has a certain property, and are therefore not property-accounts. To illustrate this, suppose we have two accounts of a property, one of which fulfills all the requirements called for by a physical explanation and the other of which fulfills only three out of the five requirements called for by an adaptation explanation. The account which fulfills three out of the five requirements for an adaptation explanation does not qualify as a property-account because it is not the kind of thing which, if true, could explain the fact that a certain organism has a certain property. It could possibly explain certain *aspects* of that fact, but it will necessarily fall short of the mark. Here there can be no competition between property-accounts because only one of these accounts *qualifies* as a property-account—viz., the one which fulfills all the requirements called for by a physical explanation. In this case, the physical property-account may warrant our acceptance because it is the only available account which could explain the organism's having that property.

If, however, none of the available accounts provides all the information required by a complete explanation in their respective fields, we are not warranted in accepting *any* account. If all of the candidate accounts are incomplete, the fact that account *E* is by some measure the best among them does not entail that we are warranted in accepting *E*. Inference to the best explanation can only be reliable if the rivals vying for explanatory victory actually qualify as explanations. Without this prior constraint, there could be cases in which employing inference to the best explanation would commit us to accepting an account that admittedly could not explain the phenomenon we are trying to explain. But it seems right to say that there are no conditions under which we would be warranted in accepting an account which we believed to be incapable of explaining the phenomenon.

6.2. Function-Accounts

Now consider the kinds of accounts which, if true, would explain why a certain trait is (or was)[1] *adaptive* (call these "function-accounts"). The first thing to note about function-accounts is that they are *not* property-accounts, i.e., they are not the kinds of accounts that, if true, would explain the fact that a certain organism has a certain property. Corresponding to Brandon's criterion (2), a function-account is a *part of*, and thus not identical to, a property-account which invokes natural selection as the *raison d'etre* of some organismal property. Since Brandon's criteria are criteria for *qualifying* as an adaptation explanation, a function-account cannot itself *be* an adaptation explanation. The most we can gain from a function-account is, in Brandon's words, "an ecological explanation of why some types are better adapted than others" (Brandon 1990: 165). I devote the remainder of the chapter to an explication of the scope and limits of the ability of function accounts to enhance our understanding of evolutionary history.

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[1] For brevity's sake, I will not include the parenthetical "or was" in my explications of function-accounts, but it is nonetheless implied.

6.2.1. Explanatory Competition Between Function-Accounts

Can there be competition between function-accounts? Yes. Consider, for example, the aforementioned study by Kingsolver and Koehl (1985) in which they consider two rival function-accounts regarding the reasons for which winged insects might have outreproduced wingless insects: (1) reproductive benefits derived from thermoregulation, or (2) reproductive benefits derived from aerodynamic effects. Through a series of ingenious experiments investigating the impact of a number of ecological variables, they determined that at

> any body size, there is a relative wing length below which there are significant thermal effects, and above which there are significant aerodynamic effects due to increasing wing length (Kingsolver and Koehl 1985: 499).

The competition between function-accounts produces the following results. Assuming that shorter wings phylogenetically preceded larger ones, we know that the initial ability of winged insects to outreproduce wingless insects cannot be explained by the aerodynamic advantage which wings conferred upon insects because that advantage would have been insignificant until a fairly late stage in wing development. However, these early, flightless versions of the insect wing would have had rather immediate and significant positive thermoregulatory effects. Thus, where the explanandum is the ecological reason for the initial adaptiveness of wings, thermoregulation survives the explanatory competition while aerodynamic effect does not. While aerodynamic effect is certainly the *kind* of account which, if true, would explain why winged insects initially outreproduced wingless ones, it turns out not to be true. Aerodynamic effect does not explain why winged insects initially outreproduced wingless insects.

In terms of the ecological reasons for the *extension* and *persistence* of insect wings, we get the opposite result. These features of the wing's evolutionary history are not explained by thermoregulation, because longer wings contribute no more to thermoregulation than do wings below a length of 1.0cm (Kingsolver and Koehl 1985: 495). However, *aerodynamic* effects were observed to be significant *only* for longer wings. In the case of extension and persistence, then, thermoregulation does not survive the explanatory competition. While it is the *kind* of account which, if true, would explain the ability of insects with longer wings to outreproduce contemporaneous variants, it turns out not to be true.

Kingsolver and Koehl add a bit of caution to their report:

> ...our results illustrate that one cannot predict *a priori* the functional consequences of small changes in character. Changes in wing length may have large or insignificant effects on thermoregulation and aerodynamics, depending on body size and wing length. It is in exploring the functional consequences of such structural changes that engineering analyses can play a useful role (Kingsolver and Koehl 1985: 504).

This is perhaps the central lesson which any judgment regarding the merits of competing function-accounts needs to take into consideration. For example, that thermoregulation better explains why, initially, winged insects were able to outreproduce wingless ones is not something which could have been decided by judging *a priori* which account was the most plausible. Plausibility lies in the empirical details of the account. The fact that wing lengths below a certain value have no significant aerodynamic effects is what makes thermoregulation a more plausible explanation than the available alternatives. Without this kind of analysis, we can't say much in favor of an account other than that it is logically consistent with what we currently know. Logical consistency comes cheap; plausibility of the Kingsolver and Koehl variety comes only with honest toil.

A further note of caution: While they have made important empirical advances on the issue of what might explain the evolution of insect wings, the authors are careful to point out that there "are no fossils representing transitional stages between wingless and flying insects" and thus

> any understanding of selective factors operating during this crucial period in insect evolution must be *speculative*. At best, we can eliminate certain hypotheses as untenable and document other hypotheses as at least plausible (Kingsolver and Koehl 1985: 500).

Even though, for instance, thermoregulatory effects emerge as the best currently available explanation for the early evolution of the insect wing, that these effects were responsible for the early selection of the wing is pure speculation. As the authors note, we *can* believe with confidence that aerodynamic effects were not responsible for the initial reproductive benefits conferred upon winged insects relative to wingless types because we were able to rule out that option experimentally. This, however, does not license us to infer that better thermoregulation was responsible for the increased reproductive success of winged insects. Other alternatives remain to be tested. We know nothing about the role played by mate preferences or by size exaggeration, for example. To be sure, Kingsolver and Koehl have given us good evidence of a certain kind that could help support a thermoregulatory explanation. Until more is known about the transitional forms, and patterns of gene flow and selective environment, we cannot say with confidence whether thermoregulation was even *involved in*, let alone *responsible for*, the early adaptive value of insect wings (Kingsolver and Koehl 1985: 503).

Yet, even if we *were* able to conclude from Kingsolver and Koehl's work that enhanced thermoregulatory capacity explains why short-winged flightless insects would have been able to outreproduce wingless ones—i.e., even if they have given us a *correct* function-account—they still would not have shown that nature selected for short-winged insects. Assuming their account is true, the idea that there was selection for short-winged insects could be undermined by, for example, demonstrating through mathematical modeling that random genetic drift could have caused wings to evolve. Alternatively, advances in insect phylogeny may completely overturn the notion that there ever *were* insects with short wings, although this latter prospect seems rather unlikely.

One such case where a selection hypothesis derived from a function-account *has* been overturned by phylogenetic data comes from Coddington's work on spiders. Whereas it had been believed for roughly a century that selection for orb webs over cob webs was explained by the superior ability of orb webs to catch flying prey, Coddington's re-analysis of the phylogeny of cob- and orb-web spiders demonstrated this to be impossible, as orb web spiders had evolutionarily *preceded* cob web spiders (Coddington 1988: 9-10). Thus, even if orb webs can be demonstrated *a la* Kingsolver and Koehl to be significantly better than cob webs at catching flying prey, the phylogenetic priority of orb webs shows that selection for orb webs over cob webs did not occur for this reason because it shows that selection for orb webs over cob webs did not occur at all. All that true function-accounts can do is explain selection *if* there is any selection to be explained, a fact which would have to be determined independently of any function-account. This point is especially important when considered in context of evolutionary psychology's brand of reverse engineering, which attempts to raise the probability of an adaptation explanation up by tugging on its functional-account bootstraps. No function-account, no matter how intuitively persuasive or manifestly true, can provide evidence that selection has taken place. It is simply not that kind of account.[2]

6.2.2. *Explanatory Competition Between Function-Accounts Which Lack Empirical Support*

Setting cladistic concerns aside, let us confine our discussion strictly to matters internal to function-accounts. Suppose we had conducted the explanatory competition (thermoregulation vs. aerodynamics) prior to any kind of functional analysis and based primarily on intuitive judgments of plausibility. We might have attempted to argue along *a priori* lines similar to the traditional stepwise argument for the evolution of the eye, e.g.:

> While it would conflict with what we know about genetics and development to propose that insects went from having no wings at all to having the wings they have today in

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[2] Notice that this point extends to optimality models (chapter 4) insofar as they are considered function accounts. See Brandon and Rausher (1996) for comments.

> a single macromutation, we *can* tell an evolutionary story about increasing aerodynamic effect that is more gradualist in nature. For instance, it seems plausible to suppose that even though short wings do not afford the *same* aerodynamic capacities as do larger wings, they offer *enough* of an aerodynamic benefit to favor types with short wings over types without short wings. Thus, aerodynamic effect *can* explain the early evolution of the insect wing.

This example highlights the ways in which conclusions about evolutionary history (among other things) based on intuitive plausibility can lead to serious errors that could easily be avoided with a little (or a lot of) careful experimental work. Our judgments of plausibility would have lead us to conclude something which functional analysis ended up showing to be impossible.

Furthermore, when we allow our intuitions rather than functional analysis to judge between rival function-accounts, we are not able to derive the kind of evidence which in the Kingsolver and Koehl study licensed us to confidently rule out a particular candidate. Their demonstration unveils the implausibility of the function-account which invokes aerodynamic effect to explain why winged insects were initially better adapted than wingless ones, and we no longer need to consider it as a possible explanation. By contrast, the explanatory competition between different *a priori* function-accounts of the wing which settled for appeals to intuitive plausibility might easily have concealed the implausibility of the aerodynamic effect account, preserving the actual loser in the competition as a less viable candidate, though still "plausible."

6.3. Making the Best of a Bad Explanation: The Value of Function-Accounts Which Lack Empirical Support

Despite the unfortunate conclusions to which we might be led by basing our inferences on judgments of the relative plausibility of certain function-accounts, there still might be some utility to function-accounts which lack empirical support. To show where the value of empirically vapid function-accounts lies, I will divide this part of the discussion into cases in which selection for the trait in question has already been demonstrated and cases in which selection has not been demonstrated.

6.3.1. *Value where selection has been demonstrated*

For many studies which successfully demonstrate selection for a particular trait, the reasons why some types are better adapted than others are either questionable or completely unknown (Endler 1986). What role can unsupported function-accounts play for these kinds of studies? At best, the principal value of unsupported function-accounts in these cases would be to enumerate the possible reasons for selection that do not obviously conflict with what is currently known. These are accounts "based on generalizations or laws we have good reason to believe are true, but whose initial conditions are speculative" (Brandon 1990: 179). A list of possible reasons for selection gives us some idea of the kinds of tests we need to design in order to rule out rival hypotheses. It is doubtful that we would, in the absence of such tests, be warranted in accepting any one of these function-accounts, however. The only conceivable case in which simple enumeration of possible reasons for selection could warrant us favoring one particular function-account would be when all the candidates except one conflict with current knowledge. In this case, the function-account which does not conflict with current knowledge wins the explanatory competition by default, as it were. Where we know (1) that selection for a trait has occurred, and (2) that there is only one function-account for that trait which does not conflict with current knowledge, it seems that we would be warranted in our acceptance of that function-account.

A less cautious opponent might reply that part of our current knowledge is knowledge of what is likely to be the case. Thus, we can rule out certain function-accounts based on our knowledge of what is likely and what is unlikely (e.g., Cosmides and Tooby 1995: 21). Whomever favors this objection will have to tell us how knowledge of what is likely or unlikely could have helped us to judge *a priori* between thermoregulation and aerodynamic effect as the best available explanation for why the insect wing was initially selected. As I argued above, subjective judgments as to which alternative account is more likely could have led to a conclusion which functional analysis demonstrated to be impossible just as easily as it could have led to one which functional analysis demonstrated to be possible. This, I would submit, is a wholly unsatisfactory epistemic situation—one that could be avoided by doing the kind of analysis performed by Kingsolver and Koehl, as well as a vast number of other researchers.

6.3.2. Value where selection has not been demonstrated

It's not clear to me why anyone would bother offering a function-account where selection has not been demonstrated. Any such account would obviously beg the question, "but *was* the trait selected for?" The hope on behalf of those who offer unsupported function-accounts where selection has not been demonstrated seems to be that by telling a plausible-sounding story about why the trait in question might be adaptive, somehow they will have provided evidence both for why a trait was selected for and for *whether* a trait was selected for. But this is simply a fantasy. It should be clear from the preceding remarks that this sort of strategy is not going to work even in cases where the possible adaptive virtues of the trait in question have been firmly established by functional analysis. *A fortiori*, then, it cannot reasonably be expected to work when we have *no* evidence pointing to why a trait might be adaptive apart from a few clever stories.

Our less cautious opponent might rightly press us on the value of unsupported function-accounts in cases where there is a *strong suspicion* of selection, though no demonstration. To resist the notion that function-accounts have value even where selection is only strongly suspected, I will appeal to a lovely example derived from Richard Lewontin (1998). Universality of a trait is often used as evidence enough to strongly suspect selection, if not to demonstrate it outright (Kitcher 1985). Suppose that thousands of years from now humans have become extinct and aliens land on Earth hoping to piece together our natural history. They will probably notice that the ability to read and write had achieved fixation or near-fixation near the end of the species' existence. The aliens will rightly suggest that reading and writing had many virtues which might have favored types who could read over types that could not read, and thus they form a strong suspicion of selection for ability to read and write. Different camps of alien scientists might offer competing unsupported function-accounts for the adaptive value of reading and writing. Some camps may establish empirically the impossibility of certain accounts and the possibility of others. The cleverest of them may even empirically rule out all but one function-account.

Has the alien race thereby demonstrated selection for reading and writing and its accompanying adaptive value? No. We know that they have not because we know that reading and writing is not something that was selected for. It is certainly a *useful* thing to be able to do, but unfortunately perceived or demonstrated usefulness is not sufficient grounds for inferring selection.

Can anything of value be salvaged from unsupported function-accounts where selection has not been demonstrated? As Brandon points out, Darwin himself used this kind of account to counter charges of impossibility when it came to the evolution of a certain trait. Certainly, Darwin could never have provided an adaptation explanation conforming to Brandon's criteria. But this was not Darwin's aim. He was concerned with preserving the viability of the theory of natural selection, which, in its early stages, would have required him to provide "how-possibly" explanations for how "organs of extreme perfection" such as the eye could possibly have evolved (Brandon 1990: 177-178).

Today the viability of the theory natural selection is not in serious doubt. We might ask then, are unsupported function-accounts still needed to combat charges of impossibility? Arguably, yes, but not in order to maintain the viability of the theory of natural selection. Even those who readily accept Neo-Dariwinian theory may balk at the notion that some properties of some organisms were selected for. Unsupported function-accounts may serve to undermine this skepticism. Unsupported function-accounts, however, should not be taken as a demonstration of either selection for the trait in question or the reasons for selection, and neither should their well-supported brethren.

Conclusion

The preceding discussion has important implications for, among other things, the study of human nature. Brandon (1990: 167) points out that much of the thrust of Gould and Lewontin's (1979) celebrated critique of adaptationism was to show that "'just-so stories' often substitute for difficult ecological analyses." This is a keen and unfortunately still under-appreciated insight, and in this chapter I have tried to provide a philosophical analysis of why it is simply poor epistemic practice to use empirically unsupported accounts of why some type in a population was able to reproduce more than another type in order to adjudicate between rival ecological hypotheses. But the true value of Gould and Lewontin's critique, I think, transcends the particular value attributed to it by Brandon. What is perhaps most regrettable about function-accounts of the variety discussed by Gould and Lewontin, and in this chapter, is not that they often substitute for ecological analyses, but that they substitute for *entire adaptation explanations*. As we have seen, this mistake is particularly common in evolutionary psychology. One does not have to look far to find a case in which the mere prevalence of some behavior inspires the researcher to create "how-possibly" explanation of the behavior which is then used to infer not only that it (a) increased relative reproductive success at some point in the past, but also that it (b) increased reproductive success for the reasons outlined by the researcher *and* (c) was selected for those reasons (which, of course, assumes (d) heritability of the behavior at the historical point in question). As I have tried to make clear, even evidence derived from rigorous functional analysis cannot license inferences regarding (a), (b), (c), or (d). Where the "functional analysis" is nothing more than the intuitions of the researcher (Williams 1992: 41), our epistemic situation with respect to (a), (b), (c), and (d) is even more dire. This should not be seen as skepticism concerning our ability to know things about evolutionary history. Rather, the point is that certain kinds of tests are only good for uncovering certain features of the world—and intuitions are rarely, if ever, good for uncovering *any* feature of the world.

7. Carving Culture at the Joints: The Evolutionary Psychological Approach to Domain Specificity

More than anything, evolutionary psychology portrays itself as the key to unlocking the form and content of our cognitive architecture. This architecture, it is argued, contains a massive array of functionally specialized computational mechanisms—"modules"—each dedicated to a specific domain of representational content. These mechanisms determine the way we process information and, in turn, are responsible for the behavioral outputs produced by that information. The ways in which we process information in the present are the result of the enduring adaptive problems faced by our species during the EEA.

In this chapter I look at a few of the methods employed by evolutionary psychologists (in particular, Cosmides and Tooby) to discover our evolved cognitive architecture. Continuing in the tradition of previous chapters, I argue that these methods do not seem well-equipped for yielding reliable results. I conclude with some worries about the "cheater detection module" allegedly discovered by Cosmides and Tooby.

7.1. An Argument for Species-Wide Domain-Specific Cognitive Mechanisms

The principal argument for why our cognitive architecture is composed predominately of domain-specific mechanisms proceeds along lines which have been made familiar by the preceding chapters. The purpose of outlining this argument is to provide a backdrop to subsequent discussion of the method by which domain-specific mechanisms can be discovered.

The argument begins with the uncontroversial notion that natural selection causes populations to evolve *adaptations*: traits which were at one time rare but allowed their possessors to reproduce more successfully than other members of the population and which consequently spread. Natural selection will operate on any feature of the organism which is relevant to reproductive success. Now, "[h]ow an organism processes information can have an enormous impact on its reproduction" (Tooby and Cosmides 1992: 64). Thus, in the same way that natural selection modifies the gross morphology of organisms—be it in the form of copulatory mechanisms, lactation mechanisms, or locomotive mechanisms—so too will it modify the mechanisms responsible for producing behavior—i.e., information-processing mechanisms.

Second, we noted in chapter 2 that any trait that is an adaptation is necessarily an adaptation for performing a particular task. The need to perform this task is created by some feature of the environment in which the organism resides, and the adaptation reflects (in some sense, one which evolutionary psychologists think is obvious) the demands posed by that environmental feature. "Like a key in a lock, adaptations and particular features of the world fit together tightly, to promote functional ends" (Tooby and Cosmides 1992: 69). Parallel to morphological adaptations, then, adaptations for processing information evolved "to solve the *specific problems* posed by the regularities of the physical, chemical, developmental, ecological, demographic, social, and informational environments encountered by ancestral populations during the course of a species' or population's evolution" (Tooby and Cosmides 1992: 62, my emphasis). Because information-processing adaptations are problem-specific, they are expected to process only informational inputs which are relevant to a certain problem and produce behavioral outputs which are relevant to solving that problem (Cosmides and Tooby 1995: 54). Thirdly, adaptations are "species-typical": there is a negligible amount of qualitative variation within a species with respect to all adaptations (Tooby and Cosmides 1990b; Tooby and Cosmides 1992: 78-79). Therefore, information-processing adaptations will be shared by all members of a given species.

7.2. E Pluribus Unum: How to Uncover Domain Specificity

From the perspective of evolutionary psychology, the fact that our cognitive adaptations are uniform across the entire human species suggests that there will be a "single human metaculture," a set of "universally recurring relationships" between features of the human environment which were relevant to reproductive success during the Pleistocene (Tooby and Cosmides 1992: 91). The idea here is that informational inputs of a given category *C* are processed by whichever cognitive adaptation(s) evolved to solve the problem(s) posed by *C* (e.g., "physical, chemical, developmental, ecological, demographic, social, and informational" problems). Similarly, the cognitive adaptations which evolved in response to *C*-type problems will produce behavioral outputs which would have been adaptive responses to *C*-type problems during our ancestral environment.

Since cognitive adaptations are shared by every member of the species, the ways in which our cognitive mechanisms structure the relationships between information and behavior for *C* will be uniform across the species, and therefore across what we call "cultures." Quoting from Tooby and Cosmides' (1992) manifesto:

> Our immensely elaborate species-typical physiological and psychological architectures not only constitute regularities in themselves but they impose within and across cultures all kinds of regularities on human life, as do the common features of the environments we inhabit (Tooby and Cosmides 1992: 89).

All of this is, of course, not to deny the enormous amount of behavioral variation across cultures and individuals. Indeed, the variation is precisely what we would expect from cognitive mechanisms which are designed to respond in different ways to different token inputs, "but these [different behaviors: CH] are all expressions of" the same metaculture. (*ibid*: 91), variations on the same universal theme. Thus, in order to correctly classify behavior, we must redescribe behavioral variation across culture in such a way that apparent variations are just different manifestations of the same domain-specific cognitive programs. Since we know that the relationships between a given type of information and the appropriate behavioral response will be uniform in all human societies,

> one needs a language that can describe what is invariant across individuals and generations. *This process of description is key*: By choosing the wrong descriptive categories, everything about an organism can seem variable and transitory to the extent that 'plasticity' or 'behavioral variability' can seem the single dominant property of an organism. In contrast, well-chosen categories can bring

> out the hidden organization that reappears from individual to individual and that, consequently, allows psychological phenomena to be described both economically and precisely (Cosmides and Tooby 1995: 24; Tooby and Cosmides 1992: 64, my emphasis).

Once we have successfully redescribed the cross-culturally "phenotypically variable and the transitory in terms of the recurrent and the stable," we will have literally discovered which human psychological adaptations there are.

> Discovering the underlying recurrent characteristics that generate the surface phenotypic variability is essential to the discovery of adaptations. To recover adaptive design out of behavioral or morphological observations, one needs to determine what is variable and what is invariant across individuals (Cosmides and Tooby 1995: 23-24).

I am interested in two aspects of this approach to discovering human psychological adaptations. The first concerns the relationship between our ability to *describe* two things as being in the same category, on the one hand, and whether those two things *actually are* members of the same category, on the other. The second concerns the likelihood of this approach to lead to true conclusions about the history of selection.

7.2.1. Discovery through Description?

It might be true, as Tooby and Cosmides point out, that

> [s]ciences prosper when researchers discover the level of analysis appropriate for describing and investigating their particular subject: when researchers discover the level where invariance emerges, the level of underlying order (Cosmides and Tooby 1995: 63; Tooby and Cosmides 1992: 14).

However, it is equally true that sciences often flounder when researchers are overzealous in the pursuit of "the level where invariance emerges, the level of underlying order." There are many examples of this as well, some of the most stellar coming from the field of psychology (e.g., female "hysterics" of the late 19th century, as well as various "syndromes" which no longer exist).

If description is going to be a reliable guide to truth, then there must be something about our ability to describe things that makes it particularly apt for capturing the actual structure of the world. With respect to Tooby and Cosmides' suggestion that we use our powers of description to uncover the different modules in our domain-specific cognitive architecture, our ability to discover a given module is contingent upon our ability to accurately describe the specific domain for which that module processes information. In turn, whether we can accurately describe a specific domain depends on our ability to accurately *re*describe seemingly different types of behaviors as token behaviors of a single type (the type corresponding to the category of problems which the module was selected to solve).

7.2.2. *General Worries About Description and Kind Membership*

There are serious questions about why we should rely on our ability to classify distinct objects as falling in a given category as a reliable guide to what kind of things those objects are. The most general question concerns a potential divide between our and nature's perceptions of similarity. We seem to have a reflexive tendency to perceive similarity between objects (Quine 1969). What is more, individuals routinely differ as to which things we take to be similar to which (You and I order the same sandwich at lunch. After our first bite, I remark how the sandwich tastes like chicken. "No it doesn't," you reply, "it tastes like albacore"). The history of medicine is replete with examples of how bad we are at correctly placing objects in their natural category; either that, or there are just far fewer hysterics and demonic possessions than there used to be.

Our dismal record of accurate classification is matched only by our superb ability to lasso apparently disparate objects as part of the same gerrymandered category. Some readers may recall an episode of the sit-com *Cheers* in which postal worker and trivia buff Cliff Clavin appears on *Jeopardy*. In response to the Final Jeopardy clue: "Archibald Leach, Bernard Schwartz and Lucille LeSueur," Cliff answers, "Who are three people who have not been in my kitchen?" Now, of course, Cliff doesn't give the "right" answer.[1] But it would be rather difficult to show where Cliff was *wrong*. After all, he *has* found something that is "invariant across individuals"—namely, that none of them has ever been in his kitchen. In fact, Cliff has discovered a property which is in all probability less variant across individuals than any putative cognitive adaptation. People are routinely born without traits which might be regarded as "species-typical." In contrast, no person, living or dead, has ever been in Cliff's (fictional) kitchen.

There are plenty of similar examples of this phenomenon in the real world. In fact, I'd wager to say that for *any* group of objects, we could find some (non-trivial) property which they all share, and thus some (non-trivial) category into

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[1] Answer: What are the real names of Cary Grant, Tony Curtis and Joan Crawford.

which they all fit. All of the objects on Earth are members of the category of things that are smaller than Mars. This is not a matter of logic, it is a contingent fact about how the world is.

None of this is new, however. Nor is it, I suppose, new (if we follow a recent trend in the philosophy of science) to say that all categories—even the gerrymandered ones—are equally real (Dupré 1993; Kitcher 2001a).. It might be, as Dupré says, that "there are countless legitimate, objectively grounded ways of classifying objects in the world" (Dupré 1993: 18). But it is one thing to believe in ontological pluralism (roughly, the view that for every type of invariance that we can describe there is a thoroughly natural kind corresponding to that invariance-type), and quite another thing to hold that mere description can pick out a *privileged* invariance-type (e.g., the category whose members have structurally similar selective histories).[2] If anything, ontological pluralism, while granting some reality-conferring powers to our descriptive practices, would weigh entirely *against* the idea that those same descriptive practices are capable of revealing something more significant about a category beyond the fact that it is real. Now, ontological *monism* would certainly afford us this capability. That is, having discovered a group of objects that share some property, we could infer that there was something significant about that fact (e.g., that objects of that kind occupy some pivotal role in the causal structure of the world). Of course, if we accept monism we would have to give up the reality-conferring power of de-

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[2] This was the principal thrust of Goodman's (1955) point about *projectible predicates* (what I am calling—for the sake of continuity of evolutionary psychological terminology—*privileged invariances-types*).

scription. Tooby and Cosmides's innovation is the notion that we can simultaneously enjoy the privilege of description and the description of privilege.

7.2.3. Specific Worries about Description and Kind Membership: Adaptation

My first specific worry about Tooby and Cosmides's approach to discovering human psychological adaptations has already been outlined in rough detail. The major objection here is that humans share an enormous, even infinite, number of properties. Hence, looking for adaptations—psychological or other— in properties that are "invariant across individuals" is going to lead researchers to absurd conclusions about which of our properties have been selected for. Even if we restrict the class of properties to only behavioral and morphological properties (Cosmides and Tooby 1995: 24), many, if not most, human universals will obviously not be adaptations.

The other worry derives from one of the problems faced by researchers engaged in reverse engineering (see chapter 4). The other hidden assumption behind discovery through description (i.e., other than the assumption of privileged invariance-types) is the idea that all tokens of the same functional type will share some properties other than the trivial property of being a member of that functional type. The notion that all tokens of this type share some properties is what enables us to use the coincidence of those properties to infer function (recall the design question: what *must* be true of an adaptation if it is designed to solve environmental problem *F*?).

The view that invariances reveal adaptations is a descendant of this assumption. Redescribing "surface phenotypic variability" in terms of functional invariances can only reliably identify adaptations to F in the case that any possible adaptation to F possesses some property or suite of properties relevant to dealing with F, some *a priori* specifiable "design criteria." It is these putative design criteria which will be "invariant across individuals." But as our discussion in chapter 4 revealed, it is possible that the answer to the question of which invariances there are will be, "None." If in some cases it is true that there are no invariances at the functional level, then in those cases we will end up thinking either that (1) humans do not have an adaptation for F when, in fact, they do (because we have incorrectly formulated the design criteria along monistic lines), or that (2) humans have an adaptation for F when, in fact, they do not (because we have monistically, but incorrectly, captured behavioral variation). As we noted in chapter 4, the mere presence of convergence is not sufficient to establish the proposition that no entity could perform a given function unless it has a specific suite of properties.[3] As in other problem areas in evolutionary psychology, these difficulties could be avoided if evolutionary psychologists would think of the concept of *function* in terms of a trait's selective history rather than its extant features.

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[3] Indeed, there is a sense in which the fact of convergence and the existence of invariance at the functional level (i.e., the design question) are not even related. The former is, as far as we know, a contingent fact about *our* world (and it's not even clear that it *is* a fact, insofar as convergence is supposed to indicate functional invariances). The latter is a claim about all possible worlds.

7.3. From Any, One

A sizeable portion of the criticism of evolutionary psychology has been directed towards the potential problem of incorrectly labeling seemingly disparate behaviors as different manifestations of the same domain-specific cognitive apparatus. This problem is perhaps described more intuitively as wrongly reducing cultural variation to instances of some component of "human nature." The thrust of the principal complaint (closely resembling early criticisms of human sociobiology, esp. Gould and Lewontin 1979) has been that any possible evidence could be made consistent with some evolutionary psychological hypothesis. The focus on description as a method for discovering adaptations brings this objection into sharp relief. If researchers begin with the assumption that there is an adaptation to *F* held by every past, present and future member of the species (a "reliably developing" cognitive mechanism, for example), it is thereby a researcher's theoretical *obligation* to keep redescribing variation until she has found a "level of description" which captures all variation in functional terms.

One possible reply here is to say, as did early defenders of the "adaptationist programme," that this is just "how science works" (Mayr 1983; also Parker and Maynard Smith 1990)—we test a hypothesis; if it appears false we move on to another hypothesis. Likewise, when one level of description fails to capture all the cultural variation, we try out another level of description to see if *it* can capture the variation under one functional umbrella.

As a reply to criticisms of the adaptationist approach, I think this is fairly successful. Traits can be directly selected for any number of reasons (which, as we saw in chapter 5, is why evolutionary psychologists charges of inconsistency with evolutionary theory often fail). If one hypothesis concerning the function of a trait turns out to be false, exploring other function hypotheses certainly does not seem like irresponsible science.[4] But it seems far too generous to label simple redescription as the exploration of another hypothesis.

First, unlike the cases of adaptationist hypothesis testing, it's not even clear *what* "trait" is being examined in the redescription approach. Suppose we know of only two cultures, one with custom *X* and the other with custom *Y*, both of which *appear* radically divergent. Suppose we believe that *X* is produced by a cognitive mechanism that at one time increased reproductive success. After a sufficient amount of time in the armchair, we come up with a way of redescribing *X* and *Y* so that, in the terms of our redescription, *X* has all of the properties of *Y*. We've thereby discovered a cognitive adaptation *A*, the behavioral manifestations of which are *X* in one culture and *Y* in the other.

But wait! We subsequently discover conspicuous custom *Z* in a third culture. We redescribe *X* and *Y* again, this time along with *Z*, so that now each of *X*, *Y*, and *Z* has all the same properties as the others. We've thereby discovered a cognitive adaptation *A*', the behavioral manifestations of which are *X* in one culture, *Y* in another, and *Z* in another.

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[4] Beatty (1987) is especially clear on this issue.

Which trait have we been testing? It can't be *A*, because we no longer believe that *A* exists. Nor can it be *A*', for we had no idea that *A*' could have existed back when we only new about customs *X* and *Y*. This situation is rather unlike the one in which the adaptationist finds himself. His function hypothesis is meaningless—*literally*—without a clear idea of the trait being tested. If his hypothesis turns out false, he moves on to a new function hypothesis regarding *the same trait*. In contrast, the redescription approach is nothing more than fishing for traits. If we haven't pulled anything out of the water yet, just cast the net a little wider, and a little wider after that, and...

Second, it seems that in the redescription approach, we're not so much testing a specific hypothesis as we are our ability to come up with clever generalizations that can adequately capture all the phenomena under one functional rubric. Inability to monistically redescribe all cultural variation just shows that we are "choosing the wrong categories." When, subsequently, our categories are "well-chosen," we will be able to "bring out the hidden organization that reappears from individual to individual." But all this shows is that we're good at (often insignificant) generalizations, something we already knew, something which bothered Quine and which he thought *frustrated*, rather than facilitated, our attempts to understand nature.

7.4. Detecting Cheaters

I now examine the evolutionary psychological approach to domain-specificity in the context of a well-publicized example—Cosmides and Tooby's work on social exchange and cheater detection. Cosmides and Tooby have accumulated a voluminous body of results in support of the hypothesis that people have a domain-specific cognitive mechanism designed for processing representations of social exchange. Much (though not all) of this support comes from the use of the Wason selection task, which asks subjects (in any variety of ways) to point out situations in which a conditional rule (of the form $p \longrightarrow q$) has been violated (i.e., instances of $p \& \neg q$). Subjects' "performance changes radically" for the better when they are reasoning about cases in which a benefit is taken without a cost being paid (Cosmides and Tooby 1992: 183).

I'm not going to question whether the reason people perform better on Wason tasks depicting social contract situations is because people actually *are* better at evaluating material conditionals when they represent contractual relationships; let's assume that they are.[5] That is, let's assume that the "content effect" with respect to social contract reasoning is real and not an artifact of some more general reasoning ability. What I am interested in, rather, is whether these results comport with what we would expect from an adaptively specialized mechanism for processing social contract content.

Cosmides and Tooby have interpreted the results of this work as evidence for a domain-specific cognitive mechanism which is designed by natural selection to perform adaptive computations on representations of social contract situations. The specific proposal is that the reason people perform better in social contract reasoning is because their brains contain a reliably developing mecha-

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[5] See Fodor (2000), Buller (2005) and Buller *et al.* (2005) for some recent challenges, and Cosmides *et al.* (2005) for reply.

nism which exists because phenotypes who had it in the past had higher reproductive success than did phenotypes who lacked it.

In this section I develop two related arguments against this proposal. The first exposes an inconsistency in the *a priori* reasoning behind the cheater detection hypothesis. The second argues that our ability to perform differentially better on social exchange conditionals no matter which objects are being exchanged or conditions being fulfilled actually *goes against* what we would expect from a mechanism which evolved to detect cheaters.

7.4.1. Adaptive Cheating Detection and Value Realism

Cosmides and Tooby characterize a cheater as "an individual who illicitly benefits himself or herself by taking a benefit without having satisfied the requirement that the other party to the contract made the provision of that benefit contingent on" (Cosmides and Tooby 1992: 180). Because cheaters take benefits ("any act, entity, or state of affairs" that "increases the inclusive fitness of that individual") without paying costs ("any act, entity, or state of affair" that "decreases the inclusive fitness of" an individual), any party who contracts with a cheater will have their fitness decreased—i.e., being cheated was *maladaptive* Thus, the reasoning goes, people should have cognitive adaptations designed to detect cheaters (*ibid*: 171).

In what sense is individual *S*'s fitness decreased by being cheated? There might be lots of ways of fleshing this out, but the sense relevant to social exchange must be that whatever is received by *S* increases her reproductive success to a lesser degree than what was given by *S* to the other party. Notice that the only circumstances under which it makes a difference in terms of selective consequences if one gets cheated in a social exchange is if the goods being exchanged affect *S*'s reproductive success. Accordingly, the *value* of a good should be understood in terms of its effect on reproductive success. For example, if widgets increase *S*'s reproductive success by 4x and blidgets increase her reproductive success by 2x, then widgets are more valuable than blidgets.

It is important here to note that where the notion of what is valuable to a person is understood in terms of the effect on her reproductive success, *value* is an objective property of the world, rather than a subjective property rooted in a person's psychological dispositions.[6] In other words, in order for the cheater mechanism to have any sort of effect (positive or negative) on reproductive success, it cannot be the case, as Fiddick, Cosmides, and Tooby have claimed, that "in social exchange, any item, action, or state can count as a benefit or cost to the interactants because values are in the eye of the holder," where value in this context is explicitly contrasted with "facts about the world—and not the desires of agents in the scenario" (Fiddick *et al.* 2000: 18). To see the authors are mistaken, consider an exchange between *S* and *T* in which *S* is trading her widgets for *T*'s blidgets. Suppose, as Fiddick, Cosmides, and Tooby suggest, that "any item...can count as a benefit...because values are in the eye of the holder." Suppose *S* just really loves blidgets and doesn't care much for widgets. If value is truly "in the eye of the holder" and not a "fact about the world," then *S* will be

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[6] Peter Railton (1986a,b) provides an intuitive framework for understanding what is valuable to a person in terms of how a thing affects her (sometimes reproductive) success.

delighted when *T* offers her three whole blidgets in exchange for just two of her widgets. More importantly, however, she will not feel *cheated*. If a cheater detection mechanism is supposed to engage whenever something of lesser value is being received in exchange for something of greater value, and if an individual's preferences are constitutive of an object's value, then *S*'s cheater detection mechanism won't engage because of the comparatively high value she assigns to blidgets. But certainly her reproductive success will have been decreased in this case, as she gave up two widgets, which increase reproductive success by 4x, for three blidgets, which only increase reproductive success by 2x—a net loss of reproductive success. In order for the cheater mechanism to be selected for, it needs to compute value in terms of facts about the world rather than desires of agents. So, no matter how much *S* loves and desires blidgets, her cheater mechanism needs to quash that desire and compel her to hold on to her widgets until she gets at least one more blidget. Widgets are more valuable than blidgets, regardless of the agent's beliefs. Let's call this view of value "value realism."

If value realism is true and the value of an object is determined by its effect on an agent's reproductive success, then some objects would have been more valuable than others during the EEA—irrespective of agents' desires—because some objects have more positive effects on reproductive success than others (e.g., widgets vs. blidgets). Now, if some objects were more valuable than others, an agent would have had to accurately appraise the value of an object in terms of reproductive success in order to avoid being cheated (Remember: in order for the cheater detection mechanism to be adaptive, it has to compute *real* differences in value). Individuals whose cheater detection mechanisms were triggered by real value differences would have been selected over those whose cheater detection mechanisms engaged when an agent received something which she merely desired less than what she traded away. Compared to the former kinds of cheater detectors (call them "realist-driven"), desire-driven cheater detectors would have had a higher propensity to engage in cases where the agent wasn't being cheated and a lower propensity to engage where the agent *was* being cheated. Realist-driven detectors would track real differences in value; desire-driven detectors would have done no better than chance.

Therefore, if cheater detection mechanisms were adaptive, then they would have engaged when something of relatively high value during the EEA (understood in terms of reproductive success) was traded away in exchange for something of relatively low value. In today's environment, then, our cheater detection mechanisms should engage only in cases where something of relatively high EEA-value is traded away in exchanged for something of relatively low EEA-value. Given that the cheater detection mechanism evolved to track real differences in the EEA-value of objects, it should only engage in exchanges in which there are real differences in the EEA-value of objects. Therefore, the content domain over which our social exchange reasoning mechanisms should operate should be restricted to goods exchanged during the EEA. This implies that our ability to evaluate conditionals in the context of social exchange situations should *not* be general. Rather, we should perform better only with respect to those objects which carried real value during the EEA.

Fiddick, Cosmides, and Tooby point out that the "evaluative strategy of attempting to falsify social contract theory through identifying social contract contents that do not elicit the [content: CH] effect has consistently failed," (*ibid*: 19) implying that no matter what the contents of the exchange are, subjects reason better in these sorts of situations than in others. But the manifest generality of our reasoning in social exchange situations would seem to *undermine*, rather than *support*, the view that we are adaptively specialized to reason in social contracts. If it were true that we were adapted in this way, we should not perform well (or better) when the objects being exchanged are assigned random values or contrived conditions for attainment. This sort of reasoning pattern would have been *mal*adaptive during the EEA, because, with respect to the real value of objects, such reasoning would be patently *indiscriminate*.

To recap, selection for cheater detection implies value realism. Value realism implies that our abilities to reason about social contracts should vary depending on the goods being exchanged. Most importantly, value realism implies that most social exchange situations we see today (in particular, those which do not depict goods which were valuable during the EEA) should *not* elicit the content effect found in Cosmides and Tooby's work. This creates a dilemma: on one horn of the dilemma, evolutionary psychologists must allow value realism in order to tell a coherent story about how cheater detection could have been adaptive; on the other horn, they must deny value realism in order to make sense of the fact that our ability to reason about social exchange does not vary depending on the goods being exchanged.

7.4.2. How Evolutionary Psychologists Might Reply

One way to reply would be to deny that our cheater detection mechanisms should be specialized towards particular kinds of representational content—viz., differences in the EEA-value of goods (again, understood in terms of reproductive success). For example, perhaps we should expect a more content-general cheater detection mechanism because the adaptive value of goods may change from person to person. Thus, it would be better to have a mechanism which processed any sort of social exchange representation.

I think the right way to respond to this argument is, first, to question the extent to which the adaptive value of goods changed from person to person during the EEA. Obviously, there are lots of empirical implications here, all of which require actual evidence in order to be substantiated. First, which sorts of things were adaptively valuable during the EEA? Second, what evidence is there that individuals differed significantly in the degree to which their reproductive success was affected by these valuable items? Since the rationale for a content-general cheater detection mechanism depends on the answers to these questions, it is appropriate for us to ask for some evidence along these lines.

Beyond empirical worries, there are reasons to question the theoretical plausibility of a content-general cheater detection mechanism. These relate back to my earlier comments about cases in which a cheater detection mechanism would be maladaptive. First, it does not follow from the idea that the adaptive value of goods changes from person to person that content-general cheater detection mechanisms would be more adaptive than content-specific cheater detection mechanisms. As long as content-general detection mechanisms fail to track the real value of goods, they will be vulnerable to being cheated. But, as Fiddick, Cosmides, and Tooby note, no one has yet found a social contract content which fails to elicit the content effect first uncovered with the Wason selection task. We can set up the exchange in terms of any two imaginary goods—goods that have never existed—and achieve the same effect. There needs to be an explanation for how a mechanism which performs equally well for all possible kinds of exchanges could possibly have been adaptive during the EEA. Value realism suggests that only highly discriminate cheater detectors which tracked the real adaptive value of EEA objects could have been adaptive.

Second, it's not clear that evolutionary psychologists even have the option of denying that cheater detection mechanisms should discriminate between goods which were valuable during the EEA and goods which were not, on pain of inconsistency with much of which they hold dear. As they routinely point out, we are adapted to the Pleistocene environment, not the modern industrialized world, and our adaptations reflect the conditions of that prehistoric environment. For example, we (allegedly) have adaptations for snake and spider avoidance because of the adaptive threat they posed during the Pleistocene. For most of the modern human population, these animals are mere pests. But when our species was evolving, they represented grave danger. Similarly, we tend to gorge ourselves on (plausibly) currently maladaptive candy bars and french fries because they contain high contents of sugar and fat which we evolved to desire when they were in short supply on the plains of Africa. By contrast, a cheater detection mechanism which is reliably triggered by objects which were useless or non-existent during the EEA does not reflect the conditions of the EEA. Our cheater detection mechanisms should be specialized for *that* environment just like all of our other (putative) adaptations.

Conclusion

As a test case for uncovering adaptive domain-specific cognitive mechanisms, the cheater detection module receives poor marks. To the extent Cosmides and Tooby have discovered something about the human mind, it appears that we have been equipped by evolution with a relatively domain-general information processing mechanism which, whatever its effects now, would (at least, according to the first principles of evolutionary psychology) have been maladaptive during the EEA. I would submit that this is indeed a rather awkward position for proponents of the cheater detection module to find themselves, having advertised it from its inception as an adaptive domain-specific mechanism *par excellence*. Where to go from here?

Can redescription save the phenomena? I argued above at length that, with respect to discovering adaptations *per se*, redescription is ill-advised. And, in any case, the generality of the behavior is not at issue. We *could* try redescribing the putative *problem* that the sort of reasoning ability described by Cosmides and Tooby was supposed to have solved for early hominins. This move is also recommended by the fact that the alleged evidence upon which their hypothesis is based, Isaac's (1978) theory that early hominins shared food at home bases, has been widely discredited and has few, if any, remaining adherents.[7]

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[7] See, for some out of many examples, the essays in Stanford and Bunn (2001).

8. Science, Selection, and Cinderella

8.1. Bully for Buller, but...

Evolutionary psychologists Martin Daly and Margo Wilson have focused much of their professional attention on the phenomenon of violent behavior in humans and its motivation in a variety of contexts. One area with which they have been especially concerned is family violence and its covariation with different forms of parent-child relationships. Using collections of data documenting child maltreatment, Daly and Wilson believe they have uncovered a trend in which children who reside with a stepparent are more likely to experience maltreatment than children who reside with genetic parents, dubbed the "Cinderella effect."

The Cinderella effect, they suggest, can be explained within the framework of kin selection theory. Proto-human parents who invested intensely in the welfare of their genetic children would have left more descendants than those who did not. Thus, the psychological mechanisms responsible for producing parental care should "be designed to allocate parental investment discriminately, in ways that will promote the individual parent's genetic posterity" (Daly and Wilson 1998: 39). While investing in the welfare of stepchildren may have had *some* positive effect on an individual parent's reproductive success (specifically by creating mating opportunities with the child's genetic parent), "a stepchild must rarely have been as valuable to a stepparent's expected fitness as a child of one's own would be" (Daly and Wilson unpublished manuscript-b). Therefore, evolution should have designed parents to feel less love for stepchildren, love being the mechanism by which nature encourages parents to invest in children.

Philosopher David Buller, in his critical study of evolutionary psychology (Buller 2005), raises a number of points aimed at calling into question the evidence for the Cinderella effect. Echoing early criticism of Daly and Wilson's evidence, Buller's primary focus concerns whether it is likely that reports of child maltreatment have, for a number of reasons, been biased in such a way as to exaggerate the likelihood of a child being abused by a stepparent relative to that of being abused by a genetic parent. He argues that there are several factors which indicate that a reporting bias in this direction has occurred, such as the demonstrated underreporting of filicides (which, contrastingly, Daly and Wilson have claimed *a priori* on a number of occasions to be so unlikely as to be unworthy of consideration) and the fact that genetic parents who might have been predisposed to maltreat unwanted children simply forestall any potential episode by *aborting* those unwanted children, whereas stepparents have children "thrust upon them" (Daly and Wilson 1985: 206).

Buller's criticisms of Daly and Wilson are carefully reasoned and his statistical analyses are truly Herculean.[1] But I think that his general strategy is misguided. Nowhere in the chapter he devotes to Daly and Wilson's work does he discuss what would appear to be the *really important issue*—viz., what *would* the Cinderella effect tell us about evolutionary history were we to find that it is real? Devoting concerted attention to the accuracy of Daly and Wilson's results

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[1] See Daly and Wilson (2005) and Daly and Wilson (unpublished manuscript-b) for replies to Buller.

is surely a laudable task, but it seems to grant tacit approval to the use of this kind of evidence for helping us understand the history of selection. It is precisely this approval which needs to be questioned.

8.2. The Prediction Confirmed by the Cinderella Effect

We begin by placing the Cinderella effect in its proper theoretical context. The "Darwinian view of parental love" outlined above suggests that parental care in humans evolved to increase the likelihood that parents' descendants will survive and reproduce. Those parents who were willing to invest in the development of their descendants ultimately had higher genetic representation in future generations than those who were not as willing. But being around kids, and especially being a parent, can be a very difficult business. For example, I, until recently, disliked the sound of a crying baby more than any other sound I've ever heard. Why do you suppose "until recently?" Daly and Wilson could probably have guessed: shortly after the birth of my first child, I no longer cringed at the sound of a baby's cry, least of all my own baby's (In fact, I think it's wonderful!). This sea change, on their account, is a manifestation of "the emotional mechanism that permits people to tolerate—even to rejoice in—those long years of expensive, unreciprocated parental investment" (Daly and Wilson 1988: 83)—an adaptation we call "parental love." Those of our ancestors who were equipped with this emotional mechanism found it tolerable—even enjoyable—to invest in the welfare of their children. Because parental love promoted parental investment, it was selected for.

In order to be adaptive, however, parental investment would had to have been *discriminatory*. Any parent who invested equally in all the children of the world would have failed to increase the chances of her descendants' survival and reproduction relative to children which were not her descendants. Thus, to ensure that an individual's investment in offspring was adaptive, parental love needed to promote discriminatory, child-specific investment. "Parental investment is a precious resource, and selection must favor those parental psyches that do not squander it on nonrelatives" (*ibid*: 83). The notion that only *discriminatory* parental solicitude was adaptive explains why modern humans are more prone to tolerate the crying, complaining, resource-consuming behavior of their own descendants than they might be to afford someone else's descendants the same courtesies.

Which brings us to

> the most obvious prediction from a Darwinian view of parental motives...: Substitute [i.e., step: CH] parents will generally tend to care less profoundly for children than natural parents, with the result that children reared by people other than their natural parents will be more often exploited and otherwise at risk (*ibid.*: 83).

Daly and Wilson's finding that children are more likely to be maltreated when living in a household where there is a stepparent present than they are in other types of households—the Cinderella effect—confirms this prediction, which, in turn, confirms their hypothesis that discriminative parental solicitude (i.e., parental love) is an adaptation.

8.3. The Confirmation of Common Sense

Legend has it that the Cinderella effect was first predicted in rough form by then-graduate student Suzanne Weghorst. As Daly and Wilson tell the story, Weghorst was struck by the idea in the midst of a seminar on E.O. Wilson's *Sociobiology*, which discusses the widespread tendency of males across taxa to kill the young of other, recently deposed males. Queried Weghorst:

> hey, what about human step-parents? Everyone knows the stereotype: they're hostile and 'wicked,' right? Well, is there any truth behind this stereotype? Are stepchildren *really* disproportionately neglected and abused? (Daly and Wilson 1998: 20).

While Weghorst may have been the first person to connect "the stereotype" about human step-parents with the child-killing behavior of males in other taxa, it was, as the quote says, something that "everyone knows." Daly and Wilson devote the first chapter of their (1998) monograph, *The Truth about Cinderella*, to showing just how universal that knowledge actually is. Cinderella is a folk character "of which there are hundreds of variants" in cultures all over the world (*ibid.*: 1-7). The fact that Cinderella-types appear cross-culturally reveals that abusive stepparent "themes have something to do with the human condition," further evidenced by the discovery that "[o]rdinary people think" that "stepparents are relatively exploitive, neglectful, and cruel" (*ibid.*: 5).

None of this, of course, is evidence for the Cinderella effect. It merely attests to the fact that prior to Daly and Wilson's research—*centuries* prior, even—the proposition that the presence of a stepparent increases a child's likelihood of being maltreated was believed by all people. This puts the prior probability of the Cinderella effect at or near "1." Given this enormously high prior probability, then, Daly and Wilson's subsequent confirmation of what everyone already believed does rather little to raise the probability of the hypothesis from which their prediction is derived. Of course, that hypothesis might be true. The point is simply that the "discovery" (Daly and Wilson unpublished manuscript-a) that the presence of a stepparent actually *does* increase a child's likelihood of being maltreated cannot do much to raise our degree of belief that their hypothesis is true, because the high prior probability of the "discovery" does not provide any confirmation of the hypothesis .[2] The fact that predictions with very high prior probabilities have no probative value means that the probability of the hypothesis from which this prediction is supposed to follow—i.e., that parental love is an adaptation—is left virtually unchanged by the truth of that prediction.

Consider the following analogy, which properly illustrates the weakness of the support lent by the discovery of the Cinderella effect. Suppose I have a theory *T* which entails that George Washington was the first president of the United States. My subsequent "discovery" that George Washington really was the first president of the United States should have very little effect on whether people believe *T*, because everyone already believes that George Washington was the first U.S. president. The prior probability that he was the first president is so high that, were I to propose a theory T^* which predicted that someone other than George Washington had been the first U.S. president, T^* would be almost

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[2] A parallel point applies to David Buss's "discoveries" concerning the "sexual strategies" of humans (Buss 2003: 5). That is, if the degree of confirmation of hypothesis *H* provided by some bit of evidence *E* is given by Pr(H/E)-Pr(H), the fact that E is roughly 1 in these cases implies that the degree of confirmation is effectively Pr(H)-Pr(H)—i.e., 0. See Earman (1992, chapter 5) for an insightful analysis of this dynamic.

instantly rejected. Were I then to actually discover that the first president was *not* George Washington, but was in fact John Adams, the truth of a prediction with such an obscenely low prior probability (i.e., the denial that Washington was the first president) would have an enormous impact on whether I should believe *T**. *Ceteris paribus*, the probative value of a true prediction varies inversely with its prior probability.

Another worry concerns the overall informativeness of the prediction that "substitute parents will generally tend to care less profoundly for children than natural parents." As described above, the prediction derives from Daly and Wilson's theory of "discriminative parental solicitude," which they argue follows from kin selection theory. Now, kin selection theory is at bottom a mathematical theory about when an organism should act so as to increase the reproductive success of another at the expense of his own — specifically, when the increase in the beneficiary's reproductive success (B), multiplied by the degree of relatedness (r), is sufficiently high so as to offset the fitness costs incurred by the benefactor (C), or $rB > C$. Thus Daly and Wilson's prediction is a special case of a more general implication of Hamilton's Rule, namely that the grade of a parent's care will vary directly with their degree of relatedness to the child (call this the "Grading effect").

Knowing whether the Grading effect is real would help towards deciding whether the Cinderella effect was the result of kin selection or some other causal factor. If it was discovered that the predicted relationship between relatedness and grade of care is violated for some degrees of relatedness (i.e., that there is no Grading effect), that would suggest that the Cinderella effect was not the result of kin selection. As things stand, however, we have no idea whether the Grading effect is real. Consequently, we have little license for inferring that the Cinderella effect is the product of kin selection in action. It would have been more compelling had Daly and Wilson confirmed the existence of the Grading effect, which in fact would, if true, explain why there is a Cinderella effect. Moreover, testing for the Grading effect would have put the investigation of human discriminative parental solicitude on the road to quantitative respectability, for it comes pre-packaged with quantitative implications (for example, that the care of a natural grandparent should be half of that of a natural parent, and *mutatis mutandis* for other relatives). It does not follow from the comparative difficulty of obtaining quantitative evidence for the Grading effect that we should suddenly lower our standards and draw inferences from far less informative evidence, i.e., the Cinderella effect.

8.4. Does the Evidence Confirm the Prediction?

Up to this point I have been speaking as though the evidence uncovered by Daly and Wilson shows that their prediction is true. I will now raise some questions which cast doubt upon the notion that their prediction is confirmed by the evidence. Here again, my approach will differ from that of Buller (2005) in that I will not be questioning whether Daly and Wilson's data are artificially biased such as to exaggerate a child's risk of maltreatment at the hands of a stepparent. My worries for Daly and Wilson are with respect to whether the kind of evidence they have gathered is what is needed to establish the truth of their prediction.

Daly and Wilson provide us with a platform for distinguishing the kind of evidence which can plausibly go towards establishing the truth of their prediction, on the one hand, from the kind of evidence they offer in support of their prediction, on the other. Consider again the prediction in full:

> Substitute parents will generally tend to care less profoundly for children than natural parents, with the result that children reared by people other than their natural parents will be more often exploited and otherwise at risk.

This, for Daly and Wilson, yields the following rule of inference:

> We can infer from the Cinderella effect that substitute parents care less profoundly for children than natural parents.

Whether this rule is reliable will depend primarily on two factors: (1) the nature of the evidence for the Cinderella effect, and (2) whether the level of substitute parents' care for children relative to natural parents can be reliably captured by (1). I will argue that we have reasons to doubt that (2) can be answered in the affirmative. Before beginning the argument, however, there needs to be some discussion of the concept of parental care as understood in evolutionary biology.

8.4.1. Parental Care

Whatever the particulars are for a given species, the concept of *parental care* must be understood in terms of effects on reproductive success. It makes sense to think of parental care as an adaptation only if we measure its effects in terms of reproductive success, or, alternatively, some demonstrated proxy of reproductive success (although the latter is less desirable).[3] Daly and Wilson seem to agree with this much, given their focus on kin selection theory. Therefore, the *costs* to individuals in connection with parental care need to be thought of as costs to an individual's reproductive success; likewise for the notion of *benefits* to an individual.

Interpreted within this framework, the Daly and Wilson prediction that stepparents will tend to care less for children than do their natural parents amounts to one of the following:

(a) holding both child and parental phenotypic quality constant, a particular child will have lower net reproductive success under the care of a stepparent than under that of a natural parent
(b) as in (a), but irrespective of parental quality
(c) as in (a), but irrespective of child quality
(d) as in (a), but irrespective of both child and parental quality
(e) holding both child and parental phenotypic quality constant, stepparents will incur fewer reproductive costs than will natural parents as a result of behaviors aimed at augmenting the child's reproductive success
(f) as in (e), but irrespective of parental quality
(g) as in (e), but irrespective of child quality
(h) as in (e), but irrespective of both child and parental quality
(i) some combination of (a)-(d) and (e)-(h) (e.g. a child will have lower reproductive success under the care of a stepparent, and a stepparent's loss in reproductive success will be lower than that of a natural parent.

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[3] The proviso that a suspected parenting behavior be demonstrated (either directly or via a suitable proxy) to affect reproductive success may sound unduly strong, but it would appear that there is sufficient variation in the forms of parenting across taxa, and in the determinants of reproductive success generally, to warrant direct demonstration (Clutton-Brock 1991: 13, 31-46); we cannot assume that a given species augments its reproductive success via a particular mode of behavior based on the knowledge that some other species does so (as discussed in chapter 4).

Whether Daly and Wilson have amassed appropriate evidence for confirming their prediction will depend, in part, on which of (a)-(i) is seen as equivalent to that prediction. However, it is evident that whichever interpretation we apply to Daly and Wilson's prediction, the evidence will have to come in the form of some kind of reproductive success differentials—either with respect to offspring fitness or parents' fitness, or both. Again, this follows plainly from the kin selection theory under which Daly and Wilson take themselves to be working.

8.4.2. *What the Cinderella Effect Is*

Setting aside the criticisms made by Buller (2005) mentioned above, Daly and Wilson have amply documented (broadly) three trends regarding stepchildhood relative to genetic childhood: (1) stepchildren are disproportionately *beaten to death*; (2) stepchildren are disproportionately abused in *forms other than fatal beatings*; (3) stepchildren receive disproportionately smaller amounts of *material support* (e.g., "higher education, routine medical and dental care, and even food"[4] (Daly and Wilson unpublished manuscript-b). While these trends are suggestive of a pattern of discrimination against stepchildren, whether this pattern is associated with one of the interpretations (a)-(i) above is entirely unclear. Let's assume for the sake of argument that the phrase "substitute parents will

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[4] These latter data, derived from Case *et al.* (2000), are subject to a variety of interpretations. First, what the data actually show is that *stepfamilies*, taken as a household, spend less on food than do biological families. On its face, this does not allow us to infer any discrimination against stepchildren. That is, it would be consistent with these data if it were the case that stepparents were starving themselves and giving all the food to the children, making stepchildren *better off* relative to genetic children.

generally tend to care less profoundly for children than natural parents" should be thought of in terms of parents' reproductive success as a function of *parents' resource expenditure* (i.e., one of (e)-(h)), with the implication being that stepparents' expend less resources on a given child—and therefore experience smaller reductions in reproductive success—than do natural parents. None of data (1)-(3) gives us any information on differences in reproductive success as a function of parents' resource expenditures. On this interpretation of "caring less," therefore, it is impossible to assess whether substitute parents provide less care than natural parents based on the data which constitute the Cinderella effect.

Alternatively, we can attempt to make use of (1)-(3) by using one of interpretations (a)-(d), i.e., by thinking of "caring less" in terms of *offspring* reproductive success. *Prima facie*, we could infer from (1) that, *ceteris paribus,* because stepchildren have higher mortality rates than genetic children, they will have lower reproductive success. Unfortunately, as Lewontin says, all other things are never equal (Lewontin 1979b: 8). We have no clue as to how being a stepchild may affect reproductive success (positively or negatively) in capacities other than mortality. However, it is interesting to note in this case that "[g]irls from step families...become sexually active sooner, and are more likely to become teen mothers than girls from families with two biological parents" (Case *et al.* 2000: 782), potentially confounding the inference from higher mortality to lower reproductive success, at least for girls (if stepdaughters are giving birth sooner than genetic daughters, the fact that stepdaughters are dying sooner may not, all things considered, affect mean reproductive success). Nor do we have any clear rationale for inferring lower reproductive success for stepchildren on the basis of (2) or (3). Briefly, Daly and Wilson give us no information regarding how the categories included under (2) or (3) influence reproductive success, and, *a fortiori*, no information on differences in reproductive success causally associated with those categories. Hence, none of the evidence offered in support of the Cinderella effect can tell us whether substitute parents care less profoundly for their children than natural parents in any sense which we can demonstrate to be relevant to natural selection. Whatever the significance of the Cinderella effect turns out to be, its relevance to anything associated with natural selection is at this point utterly mysterious.

8.4.3. How Evolutionary Psychologists Might Reply

In this section I explore to kinds of replies which Daly and Wilson (as well as other) evolutionary psychologists might offer to the criticisms just made. The first reply denies the significance of current facts about reproductive success differentials for providing us with information about adaptation. The second reply claims that we can infer on the basis of the discriminative parental solicitude in its modern-day form (i.e., the Cinderella effect) that it would have been adaptive during the Pleistocene.

When asked to provide evidence for reproductive success differentials in support of some adaptationist hypothesis, evolutionary psychologists can be expected to reply that the extent to which a trait influences reproductive success in the present is irrelevant for determining whether it is an adaptation, which depends only upon how it affected reproductive success in the past. Thus, to attack Daly and Wilson, as I have done, on the grounds that they give us no information about reproductive success differentials is a red herring. Daly and Wilson give us no information about current reproductive success differentials because current reproductive success differentials give us no information about past selection.

As far as it goes, this reply is roughly correct.[5] The extent to which discrimination against stepchildren affects anyone's current reproductive success is immaterial to whether that discrimination is the result of an adaptation for discriminative parental solicitude which evolved during the Pleistocene. However, this reply makes the sense in which we're supposed to interpret the Daly and Wilsonian notion of "caring less" either mysterious or unmotivated.

Let us discuss the mysteriousness first. While it might be true that *current* reproductive success differentials are uninformative about past selection, it does not follow that reproductive success differentials *per se* are uninformative—far from it. They are constitutive of the facts about past selection. Thus, to dismiss data on current reproductive success as irrelevant does not free researchers from the burden of measuring reproductive success during the EEA, something which is a lot harder to do than measuring it in the present. Furthermore, given that Daly and Wilson's prediction is derived *a priori* from the principles of kin selection theory, it should be just as true of EEA populations as it is of present

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[5] "Roughly" in that it's doubtful that current reproductive success differentials give us *no* information about past selection. There is a fair chance that they might preserve some information about how a trait performed in the past relative to other variants, provided there is sufficient similarity between the past and present environments. See chapter 4.

populations, making the facts about EEA reproductive success all the more relevant. If we are to abandon facts about reproductive success in favor of Daly and Wilson's alternative, we are at a minimum entitled to an argument as to why their proffered evidence is relevant to past selection—i.e., how data (1)-(3) connect with fitness differences during the Pleistocene. Daly and Wilson have attempted to connect these two notions via the concept of parental care. However, unless their sense of parental care is to be understood in terms of its effects on reproductive success, there is, effectively, no connection between their data and fitness differences during the Pleistocene. If their sense of parental care is unrelated to reproductive success, then its significance is mysterious. In this case, we can grant *arguendo* that data (1)-(3) confirm their prediction, without ascribing any probative value to that true prediction for establishing the truth of their theory of discriminative parental solicitude.

Daly and Wilson (and other evolutionary psychologists) might reply that, *pace* my allegation, there is a demonstrable connection between data (1)-(3)—the Cinderella effect—and fitness differences during the Pleistocene. The connection is that the Cinderella effect is what we would expect to see, based on *a priori* design criteria, if discriminative parental solicitude were adaptive during the Pleistocene. The idea here is that whereas in the Pleistocene parents' caring less entailed lower reproductive success for children, parents caring less in the present entails that children will be "exploited and otherwise at risk," which would have had a negative impact on children's reproductive success in the past. Daly and Wilson have provided evidence of elevated levels of exploitation and other types of risk for stepchildren. Therefore, the argument might go, they have shown that parents exhibit the kind of adjustment of parental care relative to the child being cared for which would have been adaptive for Pleistocene hominins.

I suppose all that can (or need) be said in response to this argument is that we have absolutely no reason to believe that the kind of discrimination we see against stepchildren (again, assuming Daly and Wilson's data accurately represent their situation) today would have had any sort of effect on either parents' or children's reproductive success in the past. We have nothing connecting current forms of exploitation to past reproductive success, or known determinants of past reproductive success. Without an understanding of patterns of parental care which were, in fact, adaptive for Pleistocene hominins, and without any evidence that the current Cinderella effect is structurally similar to what typically resulted from those historically adaptive patterns, on no basis should we conclude that Daly and Wilson have confirmed the prediction that stepparents will care less for a child than natural parents, or that this prediction, even if confirmed, would be of any significance for understanding our natural history. The only thing which seems to be motivating this view is the fact that there is discrimination against stepchildren in the present. As I have tried to show, this is not sufficient. So far, we have no reason to think that it is even *relevant*.

8.5. Can We Ignore Adoption?

It will undoubtedly have occurred to those who read Daly and Wilson with a skeptical eye that an apparent logical consequence of their theory is that families who adopt and who thus possess the least amount of genetic relatedness between parent and child for any form of two-parent family should show the highest rates of fatal beatings, nonfatal abuse, and material deprivation. Yet, they consistently show the lowest. Doesn't this constitute a direct falsification of their theory?

Daly and Wilson have argued in several places that people who adopt (henceforth "adopters") cannot be viewed as a representative sample of the population, for a few reasons. First, adopters are rigorously screened to detect any potential parental malfeasance, making those who end up adopting far less likely to exploit or otherwise put at risk their unrelated, adopted child (Daly and Wilson 1988: 84; Daly and Wilson 1998: 45). Second, adopters are typically more affluent than other kinds of parents, decreasing the risk of infanticide and general abuse (Daly and Wilson 1988: 84). And third, adopters have the option of returning an unsatisfactory child (*ibid*: 84). Therefore, the *prima facie* conflicting case of adopters turns out not to be a problem for Daly and Wilson's theory of discriminative parental solicitude.

Yet, although modern adopters may not represent a counterexample to the theory, it is nevertheless true that from the perspective of Daly and Wilson's theory, "care of young who are not the caretaker's own requires explanation," to wit:

> In nonhuman animals, adoption of unrelated young is usually best interpreted as a failure of discrimination...In the human case, adoption by unrelated persons is a recent cultural invention rather than a recurrent aspect of ancestral environments, and cannot have been a feature of the social milieus in which our parental psychology evolved [cite]. (Daly and Wilson 1998: 38-46; Daly and Wilson unpublished manuscript-b)

The goal of this final section will be to critically assess this explanation of adoption in the human and nonhuman cases. Here I will argue first that the assertion that adoption of unrelated young is usually best interpreted as a failure of discrimination is demonstrably false. Second, I will argue that we can construct a coherent adaptationist explanation for adoption based on the reasons that falsify Daly and Wilson's "failure of discrimination" explanation. Lastly, I will question the compatibility of "recent cultural invention" and "modern novelty" (Daly and Wilson 1998: 46) with what evolutionary psychologists think must be true of our evolved psychological mechanisms.

8.5.1. *Adoption in Nonhumans*

Hamilton's (1971) model of the "evolution of gregariousness" attempts to explain the conspicuous clustering found across a variety of taxa by showing that individuals acting selfishly to avoid predators can decrease their likelihood of being preyed upon by decreasing the space between each other. Under this model, certain forms of cooperation can be adaptive even when there is no genetic relatedness between cooperating individuals. In this connection, McKaye and McKaye (1977) have shown that parents in several species of cichlid fish will adopt orphans or literally kidnap unrelated young (including young from other species) and incorporate them into their own brood, and have offered a similar explanation to that proposed by Hamilton—viz., that parents can decrease the likelihood of child mortality by piling on additional, unrelated children (Clutton-Brock 1991: 158).

Similar examples can be found in higher taxa. For example, a number of "adoptions" have been observed on game preserves in Kenya. The most striking and recent example is that of a lioness who is known to have adopted at least five consecutive baby oryx (Figure 8.1 below). In the first case, the lioness scared off the baby's mother and then began leading the baby around, napping with it and protecting it from predators, including a pack of cheetahs. Additionally, the lioness would occasionally allow the oryx's mother to nurse the baby, shortly before chasing her away again. When the oryx was finally prevailed upon by a male lion, the lioness confronted the male and began roaring at him.[6]

It would be implausible to suggest that any of the adoptions described above are the result of a "failure of discrimination." The notion that cichlid fish exhibit systematic failure in their ability to discriminate their young from others seems an unnecessarily extreme position, especially given that Hamilton's (1971) model provides us with a parsimonious and widely applicable alternative adaptive explanation. It is much more likely that cichlid parents have been adaptively designed to incorporate other young into their brood, rather than that cichlid fish are uniformly awful at discriminating between their young and others, and that

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[6] "The Lioness and the Oryx" *BBC News*, Jan. 7, 2002.

luckily this turns out to decrease the mortality rate of their offspring. Similarly, there can be little doubt that the lioness was not mistakenly behaving as though she were the mother of the baby oryx. The fact that the lioness was not observed feeding flesh to the fledgling and would allow the natural mother to feed the baby both appear to strongly warrant the inference that she knew she was not the real mother. It is, of course, doubtful that Hamilton's gregariousness model is applicable here, however. The point is simply that the idea that adoption in nonhuman animals is "best interpreted as a failure of discrimination" is a demonstrably poor rule of inference, and would seem to have no justification beyond a myopic devotion to kin selection theory.

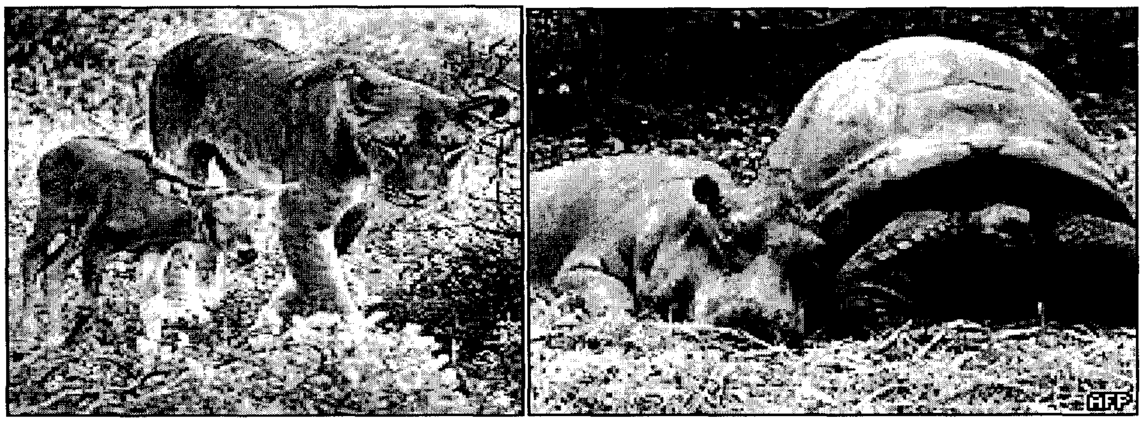

Figure 8.1 The lioness, seen above, left. There is also the case of Mzee, a 100-year old tortoise, and Owen, a one-year-old hippo, who follows Mzee around, eating and sleeping with him and licking his face. (Photos courtesy of BBC News)

8.5.2. A Dilemma

As a consequence of their conception of adoption in nonhuman animals as aberrant behavior, Daly and Wilson state that adoption of unrelated children among humans "cannot have been a feature of the social milieus in which our parental psychology evolved." Since human adoption is fairly common now, they attempt to explain its prevalence by referring to it as "a recent cultural invention," a "modern novelty" which says nothing significant about human nature.

There are at least two senses in which this way of handling human adoption is unsatisfactory. The first is that it is not clearly an explanation of "care of young who are not the caretaker's." Assuming Daly and Wilson are correct in their assertion that adoption could not have been part of the Pleistocene (an assertion for which they provide *no* evidence and which seems to be derived, again, from some perceived *a priori* implications of kin selection theory), calling it "a modern novelty" does nothing to shed light on *why* care of unrelated young occurs among humans. In order for "modern novelty" to be part of an explanation of human adoption, it needs to be shown which differences between modernity and the Pleistocene account for the allegedly recent emergence of adoption.

A slightly more adequate but equally unconvincing explanation can be found in Daly and Wilson (1995), where they add that this "novelty" is something "against which the evolved parental psyche has no specific defenses" (Daly and Wilson 1995: 1279). The argument is that because adoption did not exist during the Pleistocene, our ancestors never had to evolve adaptations for avoiding its fitness-reducing effects. Thus, because we have no adaptation to defend against adopting unrelated young, we end up adopting them in the modern environment.

Unfortunately, this move generates more questions than it answers. First, we can imagine two intuitive reasons for which adoption would have been adaptive during the Pleistocene. One reason is that it is always adaptive to outsource parental care, so long as that care is reliable. If Pleistocene parents could get others to raise their kids, why not do that? Another reason is that adoption would certainly have been adaptive for Pleistocene orphans, who would have otherwise died. In light of each of these factors, why wouldn't ancestral parents have needed to defend against adopting unrelated young? Daly and Wilson have nothing to say on this score, other than that adoption simply did not occur during the Pleistocene. But *why* did it not occur? Given the absence of any empirical evidence suggesting that adoption did not occur, the only reasonable theory as to why it didn't occur is the idea that parents were designed to avoid adopting unrelated young. But Daly and Wilson's explanation of modern adoption depends upon the premise that we don't have these adoption-avoidance adaptations.

The second question calls for an explanation of why adoption is a *modern* novelty. What reason would there be for adoption not to have emerged until recently, especially given Daly and Wilson's conjecture that "the parental psyche has no specific defenses" against it? Since Daly and Wilson's own work has shown how comparatively little risk there is to adopted children, one would think that orphans (or clever parents) would have started exploiting our lack of defenses much earlier than "recently." Why wait millions of years? One might reply that there is enormous social pressure to have kids these days which overrides the defenses we have against raising unrelated young. But this is too little too late. Is the pressure greater now than it ever was? That is presumably an empirical question. Furthermore, should not our psychological adaptations for discriminative parenting be protected from irrelevant kinds of information (such as how our peers think we should invest our parental effort), in the same way that all our other alleged psychological adaptations are *ex hypothesi* protected from irrelevant information given their domain-specificity? If not, there needs to be some explanation as to why parenting mechanisms, which are supposed to be of such enormous adaptive significance, are penetrable in ways in which, for example, our snake-avoidance mechanisms are not.

There is a final, more far-reaching worry for the suggestion that human adoption is an evolutionary novelty. This is the fact that much of the theoretical and empirical core of evolutionary psychology relies on the assumption that there generally will not *be* any novel behavior. Why? Because our psychological mechanisms only compute certain categories of informational input, and only produce certain kinds of behavioral patterns in response to those input categories. If anything is fundamental to evolutionary psychology, it is this idea. Yet, in the case of adoption, Daly and Wilson are suggesting that the modern era has modified the behavioral output of the mechanism(s) governing parental care to produce caring behavior, rather than careless behavior, in the face of intentional representations of unrelated young.

I don't think it would be such a bad thing to allow for the existence of new categories of human behavior. Indeed, it seems eminently reasonable to do so. However such a move does not appear to be sustainable within the theoretical framework of current evolutionary psychology. What's more, the implications for evolutionary psychological experiments would be disastrous. For, if our evolved psychological mechanisms can produce evolutionarily novel categories of behavior, whatever basis evolutionary psychologists were supposed to have for predicting our behavior evaporates. The presumed ability to predict behavior is based on the evolutionary psychological tenant that our behavioral outputs are structurally the same now as the were during the Pleistocene, given structurally similar informational inputs. If now Daly and Wilson are saying that behavioral outputs need not be structurally the same, we no longer have a rationale for predicting behavior; we just don't know what to expect.

If the appeal to modern novelty and recent cultural invention is not available to Daly and Wilson, that leaves only the option that human adoption is *not* a recent phenomenon but is instead evolutionarily old. As I have outlined above, there aren't very good theoretical reasons to deny this possibility, and there certainly aren't any empirical reasons. We have examples of adoption of unrelated young in nonhuman animals which is clearly discriminatory and, at least in the cichlid case, is quite plausibly adaptive. What is more, we have a broad ranging theoretical paradigm—gregariousness as an anti-predator device—which can be applied as fruitfully to the case of Pleistocene human adoption as it can in the case of mixed species groups. Denying the possibility of EEA human adoption is only reasonable if one takes kin selection to be the only relevant causal force. But kin selection is probably not the only relevant causal force.

Acknowledging the possibility that human adoption is evolutionarily old, however, creates serious problems from Daly and Wilson's explanation of the Cinderella effect, and it is clear why they should want to avoid this possibility. For, if stepchildren are disproportionately abused because having a stepchild makes little adaptive sense outside of its effects on the stepparent's mating opportunities, then *adopting* a child makes even less adaptive sense. But if adoption can be shown to be well within the realm of adaptive possibility, and if there is a coherent theoretical story which we can tell which explains why adoption can be adaptive, then Daly and Wilson's explanation for why stepchildren are disproportionately maltreated disappears. If we apply the same explanation to stepparenting that we used for adaptive adoption, then stepchildren should not be expected to experience abuse any more than any other child. If it benefits parents to have more children (for example, by decreasing the likelihood of mortality of any one child) then the genetic relationship between caregiver and caregetter need not be the sole determining factor in the level of care provided. Unrelated young can still ultimately increase the adopter's reproductive success.

I have proposed the following dilemma for Daly and Wilson. On one horn of the dilemma, they hold that human adoption is a modern behavioral novelty but are forced to deny perhaps the most important theoretical tenant of evolutionary psychology—viz., that novel categories of behavioral outputs simply cannot emerge from our evolved cognitive architecture. Renouncing this article of faith is not an option for an evolutionary psychologist. This compels them to embrace the other horn of the dilemma—i.e., that adoption is evolutionarily old.

However, as I have argued above, accepting that adoption is not a modern novelty or a maladaptive aberration undermines their argument for why we should expect stepchildren should be disproportionately abused.

9. Conclusion

Readers will no doubt have noticed that I have bypassed what would appear to be a number of intuitive stops on the path to evolutionary psychology's gravesite. Nowhere have I take up the enormously important and complex issues of (e.g.,) genetic determinism, moral and political implications of natural and inescapable psychological differences between men and women, the supposed "biological basis for rape," or whether stepparents truly love their stepchildren. If I want to critique evolutionary psychology, why avoid the aspects of evolutionary psychology which are arguably what make it so controversial and which are most in need of critique?

This query misses the point of my project. In the introduction I suggested that what is important in evaluating evolutionary psychology is not the content of their conclusions but the methods by which those conclusions are reached. In this regard, it is utterly immaterial what evolutionary psychologists (or anyone else, for that matter) claim to be part of our genetically inherited human nature. What matters is whether those claims have been arrived at using reliable methods—e.g., the methods by which people working on evolutionary histories normally arrive at conclusions about any aspect of any phenotype. Thus, I do not believe that rape is an adaptation (as advocated by one line of argument in Thornhill and Palmer [2000]). But the reason that I do not believe is *not* because I find the very idea awful and incomprehensible. The reason I don't believe that rape is an adaptation is because Thornhill and Palmer (or anyone else) have not given me any remotely compelling reason to believe that rape is an adaptation. I admit that I find this idea loathsome. However, I would hope that I would be able to accept it given sufficient evidence.

This brings me to another obvious topic which I have until now failed to address. The quote with which our journey began continues:

> Critics of determinism seem, then, to be doomed to constant nay-saying, while readers, audiences, and students react with impatience to the perpetual negativity. "You keep telling us about the errors and misrepresentations of determinists," they say, "but you never have any positive program for understanding human life" (Lewontin *et al.*: 265-266).

When I first informed people that I was writing a critique of evolutionary psychology for my dissertation I was told that I must provide an alternative proposal, that part of a good critique is an outline of how the object of the critique might be transformed into something viable and worthwhile—a "positive program for understanding human life" in Lewontin's *et al.* words.

I, for the most part, agree with this exhortation. Complementing a negative critique with suggestions for improvement and redirection is not merely of methodological importance. In addition to structuring our search for knowledge in the wake of demolition, the positive program helps us gain a deeper understanding about what was wrong with the old, discarded program and which out of many possible new directions should be taken as a means of avoiding those old problems.

For better or for worse, however, I have ignored this obligation—but not without reason. I think there are two responses which, taken together, are sufficient to explain why providing a positive program is not within the purview of *any* critique of evolutionary psychology, least of all my own. First, and most importantly, this positive program already exists. It is the program to which practicing biologists have been committed for many years, since before the inception of evolutionary psychology (or the old human sociobiology). It is the program which has led on countless occasions to illuminating conclusions about the history of life and which, if employed with similar care and consideration, could in principle illuminate the evolutionary history of human psychology. By continuing to compare the work of evolutionary psychologists with that of evolutionary biologists, then, I *have* provided a positive program for understanding human life.

The "in principle" proviso in the penultimate sentence of the last paragraph signals my second reason for not providing suggestions for the transformation of evolutionary psychology. Because facts about humans are no different than facts about nonhumans, the former facts should yield to the same methods of investigation to which the latter facts have proved vulnerable, given the right conditions. The problem for facts about humans—specifically, the facts about their evolutionary history—is that as far as we know, the conditions are not conducive to retrieving the kinds of data we would need in order to know much about why some hominin forms followed others, eventually leading to the creation of *Homo sapiens.* This is especially true in the case of psychological capacities, which do not fossilize. Given the difficulties we have with obtaining this data from populations living in the wild today (information like genetic bases for particular traits, shifts in gene frequencies, and performance data for those traits), the likelihood of us obtaining it for roughly 2 million years of hominin evolution is fairly remote. I don't feel much compulsion to provide the details of how this might be done, because I don't believe that it can be done. Thus, I take a good deal of comfort in the belief that I most likely will never have to make good on my promise to accept that men have been selected to rape in certain circumstances. Of course, someone much smarter than me may figure out a way to obtain this data. In the meantime, it would seem that our best bet for understanding the descent of man is to continue to plod along the path beaten by researchers who have provided us with our understanding of the descent of other species.

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