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ORIGINAL ARTICLE

Adaptationism and the Logic of Research Questions: How to Think Clearly About Evolutionary Causes

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Abstract This article discusses various dangers that accompany the supposedly benign methods in behavioral evolutionary biology and evolutionary psychology that fall under the framework of "methodological adaptationism." A "Logic of Research Questions" is proposed that aids in clarifying the reasoning problems that arise due to the framework under critique. The live, and widely practiced, "evolutionary factors" framework is offered as the key comparison and alternative. The article goes beyond the traditional critique of Stephen Jay Gould and Richard C. Lewontin, to present problems such as the disappearance of evidence, the mishandling of the null hypothesis, and failures in scientific reasoning, exemplified by a case from human behavioral ecology. In conclusion the paper shows that "methodological adaptationism" does not deserve its benign reputation.

Keywords Adaptationism · Behavioral biology · Behavioral ecology · Evolutionary methods · Evolutionary psychology · Evolutionary theory · Female orgasm

Introduction

We do not usually think that the logic of our scientific methods leads to closed-mindedness, and the inability to see alternatives, or evaluate evidence, but that is exactly what sometimes happens in evolutionary biology of behavioral and morphological traits with one of its most popular methods, despite its benign reputation. In "The Spandrels of San Marco and the Panglossian Paradigm," Gould and Lewontin (1979) drew attention to several dangers in using this method. In this article, I present a framework for analysis that makes their worries clearer. I also warn of further risks of this methodological framework, expanding on the dangers it poses to scientific reasoning in evolutionary biology. At the same time, I emphasize that I am *not* attacking the notion of looking for adaptations in evolutionary studies: *I am not anti-adaptation*. The issues concern which framework is most appropriate and fruitful.

As evolutionary biology is usually taught and conceived, there are a variety of evolutionary forces or types of factors that can influence the form and distribution of a given trait in a population or species (Singh and Krimbas 2000; Futuyma 2013). While natural selection may be the most significant factor, we also have sexual selection, genetic linkage, phyletic history or "inertia," developmental factors, drift or chance, embryological constraints, and social, environmental, and niche coevolutionary factors (Wright 1931; Odling-Smee et al. 2001; Pigliucci and Müller 2010). Traits can also be byproducts, spandrels, or exaptations of any of these processes in a co-related or linked trait, among other causal and explanatory factors (Gould and Lewontin 1979; Gould and Vrba 1982; Futuyma 2013). Let us call this basic approach the "**evolutionary factors**" framework of evolutionary theory; its fundamental research question is: **"What evolutionary factors account for the form and distribution of this trait?"** Often, several of these factors are understood to operate simultaneously on a given trait, but only one or two are the major factors causing its form and distribution at a given time (e.g., Otsuka 2014; see Newman 1988; Amundson 1994, 1998, 2005; Griffiths 1996; Raff 1996;

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Carroll 2005; Newman and Bhat 2008). When we investigate the evolutionary origins of a given trait, we usually prioritize the functional factors, natural selection and sexual selection, as the most significant factors in evolutionary research, and we might start with the question: "**Does this trait have a function?**"[1] If the trait, after investigation, does not appear to have a correlation with fitness,[2] or does not appear to have evidence of design (hence, does not appear to have a current or past function), we pursue other possible evolutionary explanations, such as whether it might be due to genetic linkage with another trait, or be an exaptation, or a byproduct of selection (see Gould and Vrba 1982; Gould 2002; Lloyd and Gould ([2002]2014). Alternatively, it may be present due to developmental or embryological constraints, or due to phyletic inertia, and so on (Wake 1991, 2009; Newman and Bhat 2008, 2011; Linde-Medina 2011; Griesemer 2015). Pursuit of such explanations would consist of testing them against available evidence and searching for new evidence specific to those factors, against which they could then be compared.

There is another approach, dominant among leading animal behaviorists, behavioral ecologists, and many human evolutionists and evolutionary psychologists, called "**methodological adaptationism.**" Under this approach, the leading research question is: "**What is the function of this trait?**" or **"What adaptive explanation can account for this trait?"** And the research consists of an exploration and search for supportive evidence for adaptive hypotheses that can explain the trait's presence in the population.

The Logic of Research Questions: Alternatives

Issues about method in behavioral ecology and biology revolve around evolutionary adaptations, one of evolution's biggest successes. Evolutionary adaptations are traits that exist today because they were products of natural selection acting on a variety of developed phenotypes in the past history of the species (Burian 1992; West-Eberhard 1992; Griffiths 1996). In the ancestral population of anteaters, for instance, which resembled armadillos, tongue length was likely highly variable, with high fitness values accruing to those anteater-ancestors that

might be able to reach into ant nests with their long tongues and eat the most ants, and were thus most able to pursue their food resources. These longer-tongued anteater-ancestors—eventually with their 25-inch-long tongues—would represent the best fit—or closest-to-best fit—to their environment. The anteater example thus presents a good instance of a natural selection explanation that reinforces or produces an adaptation. I take it as given that our living world is filled with examples of such adaptations.

Consider a breed of scientist called a "methodological" (or "heuristic") adaptationist, an evolutionary biologist who *assumes*, at the beginning of investigation, that a trait is, indeed, an adaptation.[3] Assuming adaptation is standard operating procedure among most behavioral ecologists, evolutionary psychologists, and human evolutionists. Many of them cite Ernst Mayr's (1983) defense of an "adaptationist research program," written in reaction to Gould and Lewontin's critical 1979 "Spandrels of San Marco." Mayr sets up the problem so that selection is the only answer to the evolutionary question:

> Consequently, when one attempts to explain the features of something that is the product of evolution, one must attempt to reconstruct the evolutionary history of this feature…. The most helpful procedure in an analysis of historical narratives is to ask "why" questions; that is, questions (to translate this into modern evolutionary language) which ask what is or might have been the selective advantage that is responsible for the presence of a particular feature. (Mayr 1983, p. 325)

Mayr continues on to advocate an adaptationist methodology for pursuing evolutionary explanations:

> When one attempts to determine for a given trait whether it is the result of natural selection or of chance (the incidental byproduct of stochastic processes), one is faced by an epistemological dilemma. Almost any change in the course of evolution might have resulted by chance. Can one ever prove this? Probably never. By contrast, can one deduce the probability of causation by selection? Yes, by showing that possession of the respective feature would be favored by selection. It is this consideration which determines the approach of the evolutionist. He must first attempt to explain biological phenomena and processes as the product of natural selection.

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[1] See Rose and Lauder (1996) for some examples of the application of this evolutionary factors approach. Or Martins (2000), for some methodological details.

[2] Symons gives a variety of reasons against using correlation with fitness for detecting adaptations, and prefers evidence of design (1990). Thornhill (1990) provides another perspective of behavioral adaptationists.

[3] See Lewens (2009) for an extensive categorization of types of adaptationism. Amundson (2001) and Sansom (2003) have also emphasized the multiple nature of adaptationist questions and answers, but not in the way I do here.

Only after all attempts to do so have failed, is he justified in designating the unexplained residue tentatively as a product of chance. (Mayr 1983, p. 326)[4]

Thus, he promotes the key question: "The adaptationist question, '*What is the function of a given structure or organ?*' has been for centuries the basis for every advance in physiology. If it had not been for the adaptationist program, we probably would still not yet know the functions of thymus, spleen, pituitary, and pineal" (1983, p. 328; emphasis added). Moreover, and most significantly, Mayr defends the adaptationist program as *harmless* when applied correctly:

> The question whether or not the adaptationist program ought to be abandoned because of presumptive faults can now be answered. It would seem obvious that little is wrong with the adaptationist program as such, contrary to what is claimed by Gould and Lewontin, but that it should not be applied in an exclusively atomistic manner. There is no better evidence for this conclusion than that which Gould and Lewontin themselves have presented. (Mayr 1983, p. 332)

Mayr's approach to the methods of adaptationism is widely adopted among evolutionary psychologists, behavioral biologists, and evolutionary ecologists (e.g., Symons 1990; Thornhill 1990; Cosmides and Tooby 1994; Pinker 1999; Geary and Flinn 2001; Schmitt and Pilcher 2004). In a widely cited target article in *Behavioral and Brain Sciences*, "Adaptationism—How to Carry out the Exaptationist Research Program," Paul Andrews et al. wrote:

> To classify a trait as an adaptation is to identify its function (Thornhill 1997; Williams 1966). To identify a trait's function is to determine the specific selection pressures (if any) that were at least partially responsible for the evolution of the trait. (2002, p. 493)

Thus, *identifying the function* of the trait is the primary aim of the adaptationist program, which also aims to identify the formative selective pressures.[5] Note that a trait having utility now is not the same as having a

"function" in the selective sense. For example, a trait could contribute to fitness in the current population, without having been formed by selection to have done so. Gould and Vrba (1982) dubbed such traits "exaptations"; these have current utility but not functions in the selective sense. Evolutionary psychologists and behavioral biologists underuse this category of evolutionary outcome, rarely assigning traits to it, even when appropriate.[6] Alternately, a trait could have had a function in the past, and a correlation with fitness then, and be a "past adaptation," with no evolutionary function now, or even be an evolutionary "mismatch" now (Lloyd et al. 2014). Again, human and behavioral evolutionists rarely assign traits to this category, and usually claim current fitness benefits.

While the adaptationist approach may look biased on its face, since it starts with the assumption that the trait is an adaptation rather than one of the other possible features, this assumption is supposed to be only temporary. If it turns out that the trait does not appear to have a function, then the biologist is supposed to move on to other possibilities (e.g., Pigliucci and Kaplan 2000). This more benign program has been advocated by many biologists since Mayr, and here is a philosopher's characterization of it:

> …when the hypothesis of optimality [or adaptation] is investigated first, deviation from the optimum provides evidence that other factors are at work, and perhaps the nature of the deviation will give clues about where to look next. (Godfrey-Smith 2001, p. 342)

Thus, the methodological adaptationist approach is seen as the "most helpful way to proceed": look for selective explanation in every case, which upon failure of the selective explanations might lead you to nonselective explanations, which could then be pursued if that is where evidence led (Godfrey-Smith 2001, p. 342).[7] Adaptations

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[4] Martin Kreitman introduced a technique using DNA sequence data that same year that can create the statistical tests to discriminate between selection and drift (1983). Thank you to Michael Dietrich for highlighting this sequence.

[5] Note that it is not always true that to identify a trait's function is to identify its selection pressure: commonly, for example, we have multilevel selection, such as family and kin selection, and there are multiple processes responsible for the trait's form and function. The trait itself does not tell us how to describe its selection pressure, although the investigating biologist may play favorites about which process to privilege in his or her explanations (for examples, see Wade 2016).

[6] Buss et al. (1998) argued that this category is really "adaptations" in their destructive analysis of exaptation, while Reeve and Sherman argued that the past selective history of a trait should not be included in the notion of adaptation, which is based instead on current utility, exactly backwards from the Gould and Vrba's, and many others' definitions: "ask why certain traits predominate over conceivable others in nature, irrespective of the precise historical pathways leading to their predominance, and then infer evolutionary causation based on current utility" (1993, p. 1; in contrast, see Burian 1992 and West-Eberhard 1992; Lloyd and Gould ([2002]2014)).

[7] Godfrey-Smith offers three general categories of "adaptationism," including, besides "methodological adaptationism," "empirical adaptationism" and "explanatory adaptationism." We will not be dealing with these others, except to note that the evolutionary factors framework is independent of any commitment regarding empirical (or "metaphysical") adaptationism. That is, it does not matter how many adaptations actually exist in the world, with regard to the relative superiority of the framework in researching those adaptations and related traits. See also Lewens (2009).

are most often indicated by their "specificity, proficiency, precision, efficiency, economy, complexity of design, reliable production, costliness, etc." (Andrews et al. 2002a, p. 503 (from Williams 1966)). Optimality models can be used to investigate these features.

But failure of optimality is sometimes hard to see, e.g., when the optimum or most adaptive state is in the middle, like Goldilocks. And it is still an open question whether the method outlined here *in practice* allows nonadaptive explanations ever to win the day. This issue of "lip service" was a key concern in Gould and Lewontin's (1979) "Spandrels" paper. Do researchers *in fact* find themselves willing to embrace nonadaptive explanations when the evidence points away from adaptation? It is a basic fact of evolution that not every biological character is an adaptation, that there exist alternative evolutionary explanations available and sometimes appropriate, such as other "evolutionary factors," reviewed above.

Asking different questions makes contrasting classes of answers legitimate. I call this the "logic of research questions," which I shall use to help unpack and highlight the differences between theoretical approaches at stake. The logic of the research questions we ask constrains what classes of answers we can give. My analysis relies on distinguishing distinct classes of answers that will be appropriate for logically distinct research questions, ultimately based on a pragmatics of questions that follows Bas van Fraassen's proposals in his chapter, "The Pragmatics of Explanation" (1980). The most important feature of these questions is that each question carries with it an appropriate class of possible answers unique to it, and distinct from other contrasting classes of answers. My fundamental claim is that we need to think very hard about the research questions we ask and the answers they allow, because the questions can lead us to miss what's really going on, therefore to scientific failure. While I apply this logic to the adaptationist methodology, my fundamental claim is not about adaptationism exclusively, but rather about how scientific investigation is done, in general, and the "logic of research questions" is thus applicable to any scientific field that experiences controversy about methods and inference.

The *methodological adaptationist* asks, echoing Mayr's rebuttal to critics, "**What is the function of this trait?**" There are any number of possible answers to such a question, all of which take the common form:

Possible Answers:
A: The function of this trait is F.
A: The function of this trait is G.
Etc.

Someone following the *evolutionary factors* framework asks, quite generally:

"**What evolutionary factors account for the form and distribution of this trait,**" or, for example, "**Does this trait have a function?**"

This question has a series of possible distinct answers (that might be considered in any order, except that the adaptive answers usually go first in practice):

Possible Answers:
A: This trait occurs in the population because it has the function F, i.e., the trait is an adaptation.
A: This trait occurs in the population because it has the function G, i.e., the trait is an adaptation.
A: This trait occurs widely in this population because it is genetically linked to a trait that is highly adaptive in this species (genetic linkage or correlation).
A: This trait has its current form largely because of an ancestral pattern (phyletic inertia).
A: This trait has its current form and distribution because of pleiotropy with a trait that was under natural selection (pleiotropy or byproduct).
A: This trait has its current form and distribution because it is a byproduct or bonus of a trait that is strongly selected in the opposite sex in this species (byproduct or bonus of an adaptation).
A: This trait has its current form and distribution because of some combination of the above factors.
Etc.

We can now see a clear logical contrast between two distinct frameworks and their corresponding sets of questions and answers. Note that the first answer listed following the general question, "What evolutionary factors account for the form and distribution of this trait?" specifically, "Does this trait have a function?" is an adaptation answer, which was done to suggest that, pragmatically, adaptation is also explored, as a priority, in the evolutionary factors framework. But under this approach, the key question about adaptation is: "**Does this trait have a function?**" which is *logically different* from the key one asked by the methodological adaptationist. Here, there is no assumption that the trait is an adaptation, in sharp contrast to leading with: "**What is the function of this trait?**"

Since Mayr and other methodological adaptationists admit the possibility of nonadaptive alternatives, it would seem that they admit, at least in lip service, that there should be nonadaptive answers on the list of possible answers to their question. Should nonadaptive answers belong on the methodological adaptationist list? Should the methodological adaptationist list perhaps look like the evolutionary factors list, but with a few more entries like: "The function of this trait is P"? The answer to both of these questions is "no." Justification of these answers will come in the course of discussing problems with methodological adaptationism,

especially in the section below on the "null hypothesis" problem.[8]

Note that under either the methodological adaptationist or the evolutionary factors approach, there are standards of evidence for when a claim for that factor is supported; i.e., when a claim is made that a feature is an adaptation, then certain standards of evidence must be met, and the same goes for evolutionary byproducts/bonuses, etc. Some of the arguments over adaptationism concern these standards of evidence (see Symons 1990; Andrews et al. 2002a, p. 493),[9] and nearly all of the focus has been there, but I want to claim that some of the root issues concern the initial questions. Which question shall we start with? Is the methodological adaptationist question really harmless? Or is there much imported into the analysis with that question? Alternately, what if we were to start with the evolutionary factors question, as many evolutionists have implicitly done? Is there any harm done to the resulting scientific inquiry? Why not use this question?

Dangers of Methodological Adaptationism

The "Onerous Burden of Proof" and its Disappearance

The methodological adaptationists routinely assume, at the beginning of inquiry, that some trait under consideration is an adaptation. This is supposed to be using the assumption of adaptation as a research heuristic, in order to enact a good research method. Indeed, the research methods of adaptationism have proven very fruitful, and one understands why Mayr would appeal to their results in order to defend methodological adaptationism (1983, p. 328, quoted above).

The burden of proof has always been on the adaptationists to demonstrate that a trait has a function and is an adaptation of one sort or another, although this burden is frequently forgotten, because they are trying to replace an *assumption* of the existence of an adaptation with a claim about the actual *existence* of that adaptation. George C. Williams is usually quoted by adaptationists as testifying to the strong burden of proof required for an adaptive explanation:

Demonstrating adaptation, Williams argued, carries an onerous burden of proof. Moreover, "This

biological principle [adaptation] should be used only as a last resort. It should not be used when less onerous principles… are sufficient for a complete explanation" (1966, p. 11). Williams did suggest qualities of trait design that could help build a case for adaptation (e.g., precision, efficiency, economy) and claimed that formulation of "sets of objective criteria [of special design]" is a matter of "great importance (1966, p. 9). (Andrews et al. 2002a, p. 496)[10]

As we see in Andrews et al., there is also routine special pleading that goes along with the Williams quotes. They note that Williams himself applied only an informal probability standard for establishing that a trait was an adaptation: "whether a presumed function is served with sufficient precision, economy, efficiency, etc., to rule out pure chance… as an adequate explanation (p. 10)" (Andrews et al. 2002a, p. 496). So Williams himself allowed the "onerous burden" of proving adaptation to be satisfied, in practice, by something weaker than the "objective criteria" he claimed were importantly needed.

Leading behavioral ecologists Reeve and Sherman (1993) also assume adaptation under a wide variety of circumstances, rejecting a widespread definition of adaptation, articulated by philosopher Elliott Sober, as being too weak. The requirements for adaptation are described by Sober as follows. "A is an adaptation for task T in population P if and only if A became prevalent in P because there was selection for A, where the selective advantage of A was due to the fact that A helped perform task T" (Sober as quoted in Reeve and Sherman 1993, p. 7). Against this, Reeve and Sherman complain that, "While clear evidence of selective modification or functional design may be *sufficient* to implicate a trait as an adaptation, such criteria are not *necessary* to recognize adaptations" (1993, p. 7; italics in original).

Reeve and Sherman argue that the big problem with history-laden definitions of adaptation like Sober's is that they refer to both the product of the selective process and the process itself:

Using this definition, a trait can be recognized as an adaptation only if we know that the trait spread through natural selection. Endler's (1986) survey reveals that this knowledge is available for very few phenotypic attributes. This might mean that the majority of traits should be considered nonadaptations. *Alternatively, it might suggest the need for a*

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[8] I would like to thank the first reviewer from *Biological Theory* for discussion on this issue, and for posing these questions.

[9] Andrews et al. claim that, "The point of disagreement [concerning adaptationism] centers around the probative value of the evidentiary standards that adaptationists use to classify a trait as an adaptation" (2002a, p. 493).

[10] Note that Williams, here, is just as strict, or stricter, than Gould and Lewontin in his requirements for assigning the status of "adaptation" to a trait. There is an open question regarding how to read Williams on this topic (Lloyd 2013).

new kind of definition. (Reeve and Sherman 1993, p. 8; emphasis added)

Reeve and Sherman seem to think that we must be able to count traits as adaptations or nonadaptations in every instance, even though sometimes we do not yet have enough evidence to decide the case.[11] As animal behaviorists Patrick Bateson and Kevin Laland noted, in a useful recent article regarding the legacy of Tinbergen in the evolution of animal behavior: "In principle, confusion over 'function', 'design', and 'adaptation' can be obviated if a clear distinction is drawn between current utility and the historical processes by which its current state was reached…" (2013, p. 2).

What Reeve and Sherman then take to be the problem with Sober's definition appears to be that it does not allow us to count enough traits as adaptations. This motivates their presentation of a new definition that will allow us to count more things as adaptations at the current time, using current utility: "An adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment" (1993, p. 1). Reeve and Sherman use current fitness to infer evolutionary history, i.e., promoting inferences from "evolutionary causation based on current utility" (1993, p. 2). The advantage of their approach, they claim, is that it "decouples adaptations from the evolutionary mechanisms that generate them" (1993, p. 1). This approach to adaptation is akin to what philosopher Bertrand Russell called the "method of 'postulating,'" which he said "had all the advantages of theft over honest toil" (Russell 1919, p. 71). An initial problem with methodological adaptationism in practice is thus that it is prone to shirking its own "onerous burden of proof."

Mistake Alternatives as Mutually Exclusive Rather than Complementary or Cooperative Accounts

The logic of research questions under the evolutionary factors framework is a bit different from the one described by many animal behaviorists, evolutionary psychologists, and other behavioral biology adaptationists, when they practice their craft of explaining the evolution of interesting animal traits. Rather than seeing the alternative evolutionary factors and forces as *mutually exclusive* to a selective approach, the evolutionary factors researcher sees them as potentially supplementary and complementary. Thus, a given trait can be explained primarily through a selective force, but also through a genetic or developmental constraint on that selection, which narrows the range of

selective results (see Mayr 1983, p. 332; this solution bears some similarity to the complementarity of nature and nurture). This approach is very common among evolutionary biologists. (I would like to emphasize that I am not in any way against adaptive explanations themselves. But rather than simply assuming that a trait is an adaptation, we can start our examination of any trait by asking whether it has a correlation with fitness and/or has design features and is adaptive or has a function; thus, the question, "Does this trait have a function?"[12])

Contrast the evolutionary factors approach with this dualist methodological recommendation from Andrews et al.:

> Because hypotheses about constraint, exaptation, and spandrel, and hypotheses about adaptation are often **mutually exclusive** to each other, we have argued that *confidence* in these alternatives increases only when plausible adaptationist hypotheses have been considered, subjected to special design scrutiny, and *systematically rejected.* (Andrews et al. 2002b, p. 535; italics in original, boldface added)

Andrews et al. are here making a logical point about how to increase confidence in a hypothesis: if p and q are exhaustive disjuncts, then increasing your confidence in p commits you to decreasing your confidence in q, and vice versa. This claim about confidence is a logical one, not an empirical one, but we need *empirically* based confidence to decide between options in science. There is thus something misdirected about this dualist methodological recommendation, as it neglects empirical consideration of nonadaptive hypotheses. Mayr (1983) made the same erroneous setup: "Only after all attempts to [find an adaptive explanation] have failed, is he justified in designating the unexplained residue tentatively as a product of chance" (Mayr 1983, p. 326; note that Mayr's view is entirely binary, with "chance" referring to "the incidental byproduct of stochastic processes," where this is the only alternative to being an adaptation, p. 326; see Millstein 2008).

Elsewhere Andrews et al. emphasize:

> Moreover, building an empirical case that certain features of a trait are best explained by exaptation, spandrel, or constraint requires demonstrating that the

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[11] In contrast, Seger and Stubblefield (1996) find that the bias towards functions is what limits the number of traits that we can treat as adaptations, e.g., in clutch size in birds or in various life history traits. Thanks to Steve Downes for pointing this out.

[12] I do not mean to deny the common point about the division of scientific labor, by saying that it is a good idea for some to start by asking about the function of a trait. It would be more useful for a phylogeneticist to start by asking whether a trait is ancestral or derived, and more useful for a developmental biologist to ask how the trait is developed in the organism. (Thanks to James Griesemer.) See Beatty (1987). The question is: is it useful for *anyone* to be a methodological adaptationist rather than following an evolutionary factors approach?

trait's features *cannot be better accounted for by adaptationist hypotheses*. Thus, we argue that the testing of alternatives requires the consideration, testing, and *systematic rejection of adaptationist hypotheses*. (Andrews et al. 2002a, p. 489; italics added)

They claim, furthermore, that "*the testing of alternatives [to adaptive hypotheses] that Gould and Lewontin request implicitly requires the testing of adaptationist hypotheses*" (2002b, p. 541; italics in original). But there is a crucial conceptual difference here between their black-and-white testing and rejection of adaptive hypotheses and my recommendation in the evolutionary factors framework that adaptive hypotheses be tested first. Under their analysis of the structure of evolutionary theory, they see the rejection of adaptive hypotheses as logically necessitated for consideration or acceptance of any nonadaptive hypothesis, whereas I consider it only a pragmatic desideratum to start inquiry with investigations into fitness and adaptive hypotheses, all things being equal, possibly followed by independent investigation into alternative nonadaptive hypotheses.[13]

Another important issue concerns the combination of causes or forces of evolutionary importance. How does the methodological adaptationist address the combination of causes, once some aspect of adaptation has already been shown? By using a *binary and mutually exclusive setup of adaptive and alternative* evolutionary explanations of a trait or character, they are building in many confusions in terms of understanding how to test and confirm a variety of claims concerning this situation (exemplified in Reeve and Sherman 1993, p. 21; Andrews et al. 2002a, b).

Methodological adaptationists often want to set up a research situation so that they are eliminating other explanations in concluding that a trait *must* be an adaptation, i.e., to construct a crucial experiment to show that the trait must be an adaptation. The problem is that supporting a particular adaptive account does not, in itself, eliminate the plausibility or possibility of all the other causal processes and accounts; for example, drift is often required to

reach a particular optimum (e.g., Wright 1931; Wade 2016). In addition, such an elimination of constraints, byproducts, and other causal possibilities does not support a particular adaptive account. That is, an adaptationist model cannot eliminate all alternative models; that is not how the theory is set up, because at least some of the causes are potentially complementary. At least some of these nonadaptive causes therefore need independent testing and confirmation before they can be accepted or rejected. This testing is totally independent of the type of investigation offered under the adaptationist rubric.

Buss et al. also follow this same line of thought as Andrews et al.:

> As more and more functional features suggesting special design are documented for a hypothesized adaptation, each pointing to a successful solution to a specific adaptive problem, the alternative hypotheses of chance and incidental by-product become increasingly improbable. (Buss et al. 1998, pp. 536–537)

Buss et al. (1998) narrow the alternatives to adaptation down to chance and "incidental byproducts," omitting all the other sorts of evolutionary alternatives. This narrowing allows them to create the appearance of having two mutually exclusive disjuncts, but in fact, accumulating evidence for one is not disconfirming all other hypotheses.

According to Andrews et al. (2002a, b), in order for an alternative, nonadaptive evolutionary explanation to even claim any evidence in its favor, it has to first show that all of the adaptive explanations are wrong. This fits their logic because to them, in a sense, there really are only two mutually exclusive hypotheses to test: adaptation, and nonadaptation. So in order to show that nonadaptation has any support, you have to falsify adaptation. But this logic only makes sense if there really are only two alternatives: A and B. If there are only two mutually exclusive choices, A and B, and one of them is true, evidence against A will be support for B, and vice versa.

But this is faulty logic according to evolutionary science. Actually, as evolutionary biology is usually taught and conceived, there are a variety of evolutionary forces or types of factors that can influence the form and distribution of a given trait, only one of which is natural selection (Singh and Krimbas 2000; Futuyma 2013). Usually, many of these processes are understood to operate simultaneously on a given trait, but only one or two are the major factors causing its form and distribution at a given time (e.g., Wright 1931; Otsuka 2014; Wade 2016).

Only a proper and careful explication of the structure of evolutionary theory and explanations, along with coordinating standards of evidence, as outlined in ordinary evolutionary texts and papers, can serve as the foundation to sort out the questions raised by these authors. The

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[13] But note that there is a problem with our running definitions of "adaptation" and "function": the first generation feature, arising from exaptations, byproducts, spandrels, or any source—e.g., a change that provides additional protection, enables association with a new food source, or otherwise brings a new niche into existence — does not yet have a "function" under our chosen definition, because it has not yet had a chance to be selected. Thus, in the first generation, we cannot tell whether it is an exaptation or an adaptation, just that it is an aptation (Gould and Vrba 1982). See discussion of Reeve and Sherman's definition of "adaptation," based on current utility rather than historical function (1993) in footnote 6 and "The Onerous Burden of Proof" section, above. An approach from developmental byproducts and novelties might clarify the arena of problems. Thank you to Stuart Newman for this example.

argument is based on the structure and confirmation of evolutionary theory, as presented currently in the evolutionary factors framework of evolutionary theory: there is a cluster of models using distinct evolutionary causes; any of these may answer the question, "What evolutionary factors account for the form and distribution of this trait?" Under this analysis, the causes are not mutually exclusive; they can be combined and serve as complementary causes of evolutionary change, as in Wright's combination drift and selection models (1931), and in the hierarchical selection models of Wade (1978, 1985, 2016) or Odling-Smee et al. (2001).

We can also see from the above considerations why it is that a division of labor solution will not work to mitigate the damage of methodological adaptationism. It might be suggested, for example, that methodological adaptationism is relatively harmless if we divvy up the labor of evolutionary biologists into a variety of pursuits, with some pursuing avid (or "ardent," in John Alcock's term) methodological adaptationism, while others are pursuing an evolutionary factors approach that considers solutions to trait formation and distribution other than adaptation.[14] The division of labor solution imagines that methodological adaptationists are merely researchers who look for functional explanations for traits, and if they cannot find one for a trait, move on to look for another functional solution for another trait. If that were all they were doing, they would be quite harmless. But that is not an accurate description of methodological adaptationism in practice. As we will also see below, methodological adaptationism leads to bad logic, bad reasoning about evidence, and inferior biology. It is positively destructive of good science and good evolutionary biology; it is *not* just a matter of overemphasis on adaptation in the biological community.

The Lack of a Stopping Rule

Two of the best known problems with adaptationism—in this case, targeted towards what I'm calling "methodological adaptationism"—are articulated by Gould and Lewontin in the following:

> [1]We would not object so strenuously to the adaptationist programme if its invocation, in any particular case, could lead in principle to its rejection for want of evidence. We might still view it as restrictive and object to its status as an argument of first choice. But if it could be dismissed after failing some explicit test, then alternatives would get their chance. Unfortunately, a common procedure among

evolutionists does not allow such definable rejection.... [2] The criteria for acceptance of a story are so loose that many pass without proper confirmation. Often, evolutionists use consistency with natural selection as the sole criterion and consider their work done when they concoct a plausible story. But plausible stories can always be told. (Gould and Lewontin 1979, pp. 587–88)

Note here that in the first complaint, Gould and Lewontin are appealing for a "stopping rule" of some kind, some standard that would signal the abandonment of the search for adaptive stories, or the time to investigate alternative accounts from the evolutionary canon. The second complaint is about the just-so stories getting accepted as scientific without real evidence supporting them. No one should be happy with the standard of evidence in evolutionary science allowing for the acceptance of just-so stories on the sole criterion of consistency with natural selection.

The methodological adaptationists agree that we should not accept just-so stories, and take themselves to have absorbed Gould and Lewontin's complaints quite thoroughly. For instance, here are Andrews et al. characterizing Gould and Lewontin as having complained that adaptationists

> … often use inappropriate evidentiary standards for identifying adaptations and their functions, and that they often fail to consider alternative hypotheses to adaptation….[they discuss] the standards of evidence that could be used to identify adaptations and when and how they may be appropriately used. (Andrews et al. 2002a, p. 489)

As Andrews et al. understand Gould and Lewontin's first complaint, it is best responded to by testing nonadaptive hypotheses through testing adaptationist hypotheses as discussed in the previous section. This is supposed to blunt the stopping rule problem, as it provides testing of the appropriate kind. However, it does not do so, because the two are not really mutually exclusive disjuncts, adaptation versus nonadaptation. This attempt to reply to Gould and Lewontin's first complaint actually opens them to Gould and Lewontin's second complaint, as can be seen in the following quotation from the same article:

> … a major thrust of our article was to argue that a consistency standard is inadequate. In effect, we argued that one should not accept a particular hypothesis *until all alternative hypotheses are shown to be very unlikely to account for a trait.* (Andrews et al. 2002b, p. 541; their emphasis)

In this passage, Andrews et al. attempt to spell out just what sorts of hypotheses need testing to reject hypotheses

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[14] Thanks to Archie Fields III and Carla Fehr for discussion of this issue.

in their binary pairings of adaptive and nonadaptive evolutionary causes (Millstein 2007). The problem is that in their "switching rule," as I call it, they do not distinguish between live options that offer plausible lines of inquiry supported by some evidence, and mere hypotheticals that have no plausibility or supporting evidence at all in the evolutionary context, which are the sort of thing that Gould and Lewontin called "just-so stories." This was supposed to be the methodological adaptationists' way of responding to Gould and Lewontin's complaint about the lack of a stopping rule, but in trying to dodge Scylla they have landed in Charybdis. Their conceptual confusions about the variety of evolutionary factors and their roles in evolutionary theory have led them to do just what Gould and Lewontin complained about, while trying to reply to them: adaptive just-so stories are getting unearned credit.

There is another type of stopping rule problem that may lead even methodological adaptationists to want to reconsider their own standards of when to stop looking for adaptive explanations. Take the example of the glass tree frogs. Both regular tree frogs and glass frogs are green, which is traditionally explained as an adaptation for camouflage against the green leaves of their environment. But the two types of frogs attain their green color differently: regular tree frogs are green through absorbing parts of the visible spectrum of light, in the usual way, while glass frogs are green through refracting light. Does this make any difference?

Adaptationists interested in exploring why the glass tree frogs used refractive color to be green investigated the two types of frog under infrared light, and found that regular tree frogs absorb infrared light, contrasting with the plant leaves on which they sit, which reflect infrared, while the glass frogs are invisible, as they also reflect infrared, and are thus totally camouflaged (Schwalm et al. 1977). It also turns out that the geographic range of the glass frogs exactly overlaps the range of pit vipers, snakes that hunt using infrared sensitivity. Thus, we end up with a totally new, updated adaptive explanation for the green color of the glass frog. But suppose that no one had been curious about the refraction method of coloration of the glass frog? We would have ended up stopping with the old story about why frogs are green, which we now believe is only half right in the case of the green glass frogs. This type of example provokes a puzzle: when do we stop looking for adaptive explanations? It seems that we should not stop looking just because we have one. Neither methodological adaptationists nor proponents of the evolutionary factors framework have a definite solution to this dilemma; the latter are in a better state only in that they tend to be more alive to the worry.[15]

Loss of Ability to Evaluate and Weigh *Evidence* for Alternative Causal Hypotheses

But there are even more serious problems that have arisen from methodological adaptationism. In practice, methodological adaptationists sometimes cannot compare the *weight of evidence* for various hypotheses, one against the other. This is a more serious problem than the stopping rule problem because even when consideration of evolutionary hypotheses involving the *other evolutionary factors* really does happen, what counts as *evidence* supporting those hypotheses fails to come into view.

I have spent over 30 years researching and analyzing the evolutionary explanations for female orgasm. In my 2005 book, I concluded that the byproduct/bonus account had the most evidential support, a position I still hold. The account was first proposed by anthropologist Donald Symons in 1979.[16] It is based on developmental symmetries in the sexes, much like the sharing of nipples in men and women. Female nipples clearly provide a reproductive advantage to *female* mammals, but there is no known contribution to fitness of male nipples for the males. The evolutionary explanation for the existence of male nipples is based on the development of the embryo, and the fact that nipples are adaptations in females. Males and females share the same embryological form at the beginnings of life—they start off with the same basic body plan, and only if the male embryos receive a jolt of hormones during the eighth week of pregnancy do any sexually distinguishing characteristics appear. Similarly, in males, orgasms are adaptations—we believe they are the active consequences of stabilizing selection—but the females get them for free. The tissues involved in orgasm for males and females are homologues, shared between males and females, including nerve tissues, erectile tissues, and muscle fibers. This whole embryological pattern, not just the clitoris (and potentially involving the five afferent pathways I mention in my 2005 book), is involved in producing orgasm in females, and is produced in them through their embryological connection to the same tissues in males. So females get the functioning orgasmic tissues, and are often capable of having orgasms under the right conditions of rhythmic stimulation.[17]

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[15] Thanks to Michael Wade for this example.

[16] Interestingly, Symons identifies himself as an "adaptationist," but an analysis of his research shows that he is not a methodological adaptationist in the Mayrian sense used in this paper, but rather an "adaptationist" following the path of the evolutionary factors framework's first questions (see Symons 1990).

[17] While apparently most often these tissues involve primarily the total clitoris and lower vaginal areas, Barry Komisaruk and his colleagues had noted that the cervix could serve as a center of orgasmic pleasure in some women under appropriate conditions of stimulation (2006; Kinsey et al. 1953). Komisaruk et al. have more recently shown that the human vagina, cervix, and clitoris are innervated by different afferent pathways, which project to different

Female orgasm is seen, technically, as a *byproduct* or *bonus* of selection on male orgasm.

In a discussion of my early work on the evolution of female orgasm, evolutionary writer Stephen Jay Gould presented a variety of empirical evidence in favor of Symons's byproduct/bonus view, under which female orgasm is understood to arise as a consequence of strong stabilizing selection on male orgasm (Gould 1987). Adaptationist Donald Dewsbury, a distinguished psychologist studying animal reproductive behavior, claimed in response to Gould's discussion,

> … But Gould (1987) goes too far in asserting that "female orgasm is not an adaptation at all" (p. 17). We need to study the consequences of [female] orgasm for differential reproductive success and then determine whether a plausible case can be made for drawing the loop from present consequences to the past history of natural selection. These need to be studied, *not asserted or denied* a priori. (Dewsbury 1992, p. 103; my emphasis)

But Gould is actually representing Symons' views in this quote; the full quote says: "In all the recent Darwinian literature, I believe that Donald Symons is the only scientist who presented what I consider the proper answer—that female orgasm is not an adaptation at all. (See his book, *The Evolution of Human Sexuality* (1979))" (Gould 1987, p. 17). The perception of Dewsbury's was, clearly, that no good evidence had entered into the debate, despite Symons's entire book chapter detailing empirical evidence supporting his theory, and Gould's appeals to the empirical support that I had amassed,[18] involving 14 studies, which now consist of 66 years of sexology evidence involving 141,229 women in 35 studies (see Lloyd 2005 for a collection of the evidence and analysis; Kinsey et al. 1953). But all of that evidence (discussed below, in the "'Null' Hypotheses" section) was invisible to these researchers. Apparently adaptive hypotheses could be favored or disfavored by the evidence (and they had not been favored in the female orgasm case so far), but a nonadaptive hypothesis like the byproduct/bonus account could only seem to be "asserted or denied a priori."

Note that the repeated failure of adaptationist accounts does not have any bearing on the positive evidence

available supporting the bonus/byproduct account, although many adaptationists incorrectly believe that this failure of the adaptationist accounts is the sole evidence supporting the bonus/byproduct explanation (e.g., Alcock 1998; Linquist 2006). Because the logic of the methodological adaptationists' function question demands a function answer, no bonus/byproduct answer can be considered a positive answer to their research question, and thus bear support in its favor (see Mayr 1983).

Andrews et al., in considering Gould's discussion of the case of the female orgasm, claimed that Gould gave no positive evidence for the trait not being an adaptation, under either the contemporary fitness view of adaptation or under a historical functional account, and simply "proclaimed that the female orgasm is *not* an adaption but a byproduct" (2002a, p. 499, footnote 6, p. 504). They ignored Gould's discussion of the reasons that the available adaptive accounts are not persuasive, and of the positive reasons for thinking it is not an adaptation, in the essay, which were drawn from both Symons' (1979) book, and an unpublished paper of mine that later became the 2005 book. Andrews et al. complain about Gould's methodology that:

> Gould's conclusion may be correct but his argument does not warrant it. As we point out later, demonstrating that the female clitoris and orgasm are byproducts requires the failure to find evidence for its special design and, hence, an adaptationist testing strategy. (Andrews et al. 2002a, p. 499)

Note Andrews et al.'s requirements for something to be shown to be a byproduct/bonus. They acknowledge that Gould may well be right about the fact of the female orgasm being a byproduct, but complain that Gould did not fulfill their requirements and make a case for the byproduct/bonus conclusion because his positive evidence did not count for the methodological adaptationists.

But what about the other evolutionary factors that are allowed in all evolutionary textbooks? Reeve and Sherman (1993) allow that there are "mechanisms of persistence other than natural selection," and they list them as follows: "a relatively non-adaptive trait may persist because of several processes including prolonged lack of genetic variation, unbreakable genetic correlations with other traits, recurrent immigration, and genetic drift" (Reeve and Sherman 1993, p. 19; cf. Futuyma 2013). But it turns out that in practice they take these alternative causes, such as developmental constraints or genetic correlation to either actually be serving the adaptive functions as well, or to not really be viable as *alternative causal explanations* to adaptive explanations. From this we can see why the list of answers to the methodological adaptationist research question does not actually include these other answers besides the function ones.

For example, they argue that we cannot use genetic correlation as a genuine alternative causal explanation to an adaptive one, on the basis of their denial that genetic correlations are an independent causal evolutionary factor when doing research into the presence of a genetic trait. They argue:

> We do not deny that genetic correlations can impede adaptation. Moreover, we acknowledge that in some (special) instances the breakdown of genetic correlations may be unlikely, as with correlations between male traits and female mating preferences that build up automatically due to female choice (Fisher 1958; Lande 1981). We merely suggest it is inappropriate to assume that genetic correlations *cannot* be broken. In particular, finding a genetic correlation between two traits is insufficient for invoking that correlation as the *explanation for the presence of either of them. The relative fitnesses of alternatives for each trait still must be examined to address the possibility that both traits are selectively maintained over their alternatives*. (Reeve and Sherman 1993, p. 20; emphasis added)

They discuss the case of Halliday and Arnold (1987), who proposed that male and female reproductive tendency may be genetically correlated in a variety of species, and that multiple mating by females was genetically correlated to a polygenic trait selected in males, but not selected in females.

Reeve and Sherman say:

> Halliday and Arnold's (1987) explanation suffers from an incomplete phenotype-set specification, since the possibility clearly exists that male and female mating frequencies were in the past free to evolve separately, with a positive correlation between the two becoming established later when it was favored. Thus regardless of male polygyny, the reproductive consequences of multiple mating for females would still merit investigation (e.g., Westneat et al. 1990; Birkhead and Miller 1992). (1993, p. 20)

But there is no evidence concerning a past in which the traits were independent, as they seem to have been correlated throughout, according to the evidence presented by Halliday and Arnold. Reeve and Sherman intend, in setting up the optimality models for the studies, that the evolutionists should assume full independence of the states. This testifies to the usual methodological adaptationist assumption: if the genetic correlations are good, selection will create them; if they are bad, selection will remove them (see Marrow and Johnstone 1996). But Halliday and Arnold think the correlation "merits investigation," as suggested here, and are proposing something much more

useful than further speculation about what selection has done, which is that geneticists expertly studying various species actually perform genetic studies to empirically discover whether or not (instead of speculating about whether or not) the females of the various species *do have* the genetic correlations that they are hypothesized to have—not to create yet more adaptive stories or assumptions about it!

This suggestion about how to set up optimality models reflects an atomization project on the part of Reeve and Sherman. They propose to methodologically assume that they have separable traits in the face of biological evidence that the separability of these traits is false (e.g., Halliday and Arnold's experimental research). About these atomized traits they then ask the methodological adaptationist question: "What is the function of this trait?" and give separate answers for each trait.

"Null" Hypotheses

"Does this trait have a function?" The evolutionary factors researcher asks this precise question. Note that it has a very different logic from the methodological adaptationists' question. The evolutionary factors approach assumes that we can identify the trait under investigation even though it may *not have* a function, or a correlation with fitness; many adaptationists in practice act as if one cannot identify traits unless they have functions, that they are not within the purview of evolutionary explanations if they lack functions. But this is indefensible, given that there are a number of nonadaptive evolutionary explanations potentially available for traits, as Gould and Lewontin emphasized in their "Spandrels" paper (1979). The logic of the evolutionary factors framework, under which a leading question asked is whether or not the trait has a function, is more holistic, less atomistic, more open, less presumptive, and less reductionistic.

To ask "Does this trait have a function?" we need to have a method of identification of the trait, independent from the breakdown and atomization of traits we get from adaptationists. This can get tricky. For example, consider Michael Wade's "larval count" of willow beetles in his field studies (Wade and Breden 1986; Breden and Wade 1987; McCauley et al. 1988; Wade 1994). When in the field, Wade sought to find a count of all the group-living larvae clustered together in the groups of beetles on each leaf. Is this trait of "larval count" a biologically significant one in nature, or a mere figment of the researcher's imagination? Consider one of the predators who eat the larvae, the warblers. They bite off the whole chunk of leaf that the entire group lives on together, all at once, thus confirming that "larval count" is a useful trait for both biology and nature. However, there is also a bug (a species

of plant bugs, *Miridae*), that eats the larvae, but does so one by one, seemingly never encountering the whole larval group embodied in Wade's "larval count." In between, we have the ladybird beetles, that sometimes eat whole groups of larvae, and sometimes eat only one or two at a time, depending on how desperate they are for food. Thus, we have an entire array of biologically meaningful ways to carve up the willow beetle larval groupings, depending on which predator we are focused on, only one of which is captured by Wade's "larval count" (Wade and Breden 1986; Breden and Wade 1987; McCauley et al. 1988; Wade 1994). We can put Wade's emphasis on interdependent and non-atomistic traits within the evolutionary factors methodology, as a relevant sharp contrast with the methodological adaptationists. The atomization of traits that Gould and Lewontin were concerned with was a fundamental element in their concerns about adaptationism.

Ritual recitation of Gould and Lewontin's "Spandrels" paper in the adaptationist literature usually includes only the lesson that not *everything* is an adaptation. But this misses one of the primary points of their paper, which includes the problem of the neglect of developmental constraints, phyletic inertia, and Baupläne as evolutionary causes (or the breakdown of these into atomic *bits* via their optimization methodology). Attention to the logic of research questions illuminates this problem. How can these other factors ever appear on the methodological adaptationist's list of real answers?

I argue that methodological adaptationists are committed to this neglect by the logic of their initial orienting question. Once this first move is carried out, which seems so innocent, methodological adaptationism is rationally going to lead to error in some cases. This is because starting our biological inquiry by asking the methodological adaptationists' function-question involves treating nonadaptive hypotheses as something like statistical nulls. For example, David Barash says explicitly in a discussion regarding a byproduct/bonus theory of female orgasm, that the possibilities include "the 'null hypothesis' that it might not be a direct product of evolution after all" (2009, p. 133).[19] In general usage in science or biology, a null hypothesis is usually a negative alternative to a positive correlational hypothesis, often used in Neyman-Pearson statistical analyses; the use of the "null" hypothesis by behavioral biologists tends to be much more informal, and not to signify necessarily the application of any formal statistical test at all. The positive hypothesis in this case would be one in which a trait was positively correlated with fitness or some component of fitness, while the null hypothesis would be simply a non-correlation with fitness,

often indicating non-selection. An example will bring this out.

Stefan Linquist, writing about my analysis of a byproduct/bonus explanation for the evolution of human female orgasm, asserted that "[t]he burden of Lloyd's argument [in her 2005 book] is to show that none of the available adaptationist hypotheses are defensible" (Linquist 2006, p. 413). If this were right, then defending the byproduct/bonus view would in effect be to show that we must settle for the null hypothesis, since we fail to reject it. This is why researchers like Alcock and Sherman equate the bonus/byproduct account with scientific surrender; it would amount to giving up on having a causal account (e.g., see the language in Alcock 1987, 1998; Sherman 1989). This, however, is the wrong standard. It presents the scientific situation as all-or-nothing, the adaptation account or no scientific account at all. The byproduct/bonus theory *is* a causal evolutionary account, and has its own kind of evidence in its favor (see Beatty (1987) for a parallel point about drift). Analysis of the logic of research questions helps make the source and nature of this confusion quite clear. But Alcock's case also verifies that the methodological adaptationists' list of questions is all adaptation answers, and no other kinds of answers.

Let's review the questions asked by the methodological adaptationists and the holders of the evolutionary factors framework, and their samples of relevant well-formed answers here:

Analysis according to the Logic of Research Questions:

Methodological Adaptationists: What is the function of this trait?"

Possible Answers:
A: The function of this trait is F.
A: The function of this trait is G.
A: The function of this trait is H, or I, J…Z, AA, BB,…ZZ, AAA, BBB…????
(Faulty A: This trait has no known function or correlation with fitness, and may not be a direct product of selection at all (i.e., adaptationists' "null" hypothesis, which, e.g., Linquist treats as equivalent to the bonus/byproduct hypothesis))

Evolutionary Factors Approach: What evolutionary factors account for the form and distribution of this trait? Does this trait have a function?

Possible Answers:
A: This trait occurs in the population because it has the function F, which is an adaptation.
A: This trait has its current form and distribution among one sex largely because it is a byproduct of selection on the opposite sex's trait.

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[19] By "evolution," Barash means "selection," in context. This mistake is discussed in the next section.

A: This trait occurs widely in this population because it is genetically linked to a trait that is highly adaptive in this species.

A: This trait has its current form largely because of an ancestral developmental pattern that provides a contemporary developmental constraint.

A: This trait has its current form and distribution largely because of a phyletic pattern from an ancestor that is continued in this trait.

Etc.

As can be seen by analysis of the logic of these research questions, then, those using the methodological adaptationist approach cannot appreciate the accumulated evidence for the byproduct/bonus approach. This evidence is in some sense *only visible on the evolutionary factors framework*, where the weight of evidence is the right approach to use in evaluating the byproduct/bonus hypothesis and its alternatives. Methodological adaptationism is much more restrictive or limited than it at first appears. The evolutionary factors framework works very differently from the methodological adaptationist one in terms of how to treat evidence: an adaptive hypothesis can be compared directly to a nonadaptive one, for example a byproduct/bonus hypothesis, *by comparing evidence in favor of each view*. Under the function question asked by the methodological adaptationists, the byproduct/bonus account gets incorrectly classified as a null hypothesis, and a null hypothesis cannot have independent evidence in its favor (thus they were following something like a Fisher-type approach to nulls in statistics, informally).[20]

Two points emerge from the discussion above. First, characterizing the byproduct/bonus alternative as a "null" hypothesis leads to the impossibility of positive evidence for what is, in truth, a causal hypothesis, which needs empirical support or refutation. Thus, the attribution of a "null" is completely mistaken and illegitimate. Secondly, if, in attempting to pursue the evolutionary factors methodology, the research community gets stuck on the first, adaptationist step of pursuing only functional answers to the question of whether the trait has a function, then the other characterizations of the trait will not be pursued, and a balanced view of the weight of evidence will not appear. Logically, they would be behaving as methodological adaptationists. Both of these errors must be avoided if the reasoning processes about evidence are to go smoothly, and the evidence weighed appropriately, e.g., in the byproduct/bonus case we are considering.

To see this, it is important to analyze questions by looking at what counts as valid answers to them. A "verbal

twin"[21] of the evolutionary factors methodologists' "does this have a function" question could, in practice, only allow answers that affirm that it does. This would be to *logically* ask the methodological adaptationist question *in the guise of* asking the evolutionary factors question. So what question is logically being asked cannot be detected by looking at the surface syntax of the sentences the scientist uses to express questions. Two syntactically indistinguishable questions may be expressing logically distinguishable questions. One can also express the same question by using syntactically different sentences; the details of the wording are in some sense logically arbitrary. The logic of the research question is revealed by the answers attached to it. Thus, both the methodological adaptationist and the evolutionary factors approach theorist can ask about adaptive traits or functions, but the full meaning of the question will not be revealed until we can see what list of answers are *live options* and under full consideration. As we have shown, the methodological adaptationists may claim to have the same items on their lists as the evolutionary factors theorists, but when push comes to shove, they deny treating them as live options, on their own accounts.

This is a subtle but crucial point. You need to look at the logic of the research questions themselves, not just the verbal formulations of them, in order to really understand what is being compared and investigated. They could investigate very different things, depending on what answers are actually being allowed—either a range of function answers, or a full range of evolutionary factors. Only investigating the logic of these research questions can bring out this difference.

As an answer to the more inclusive evolutionary factors question, a byproduct/bonus account is an alternate causal hypothesis to an adaptive account, with a set of specific evolutionary mechanisms involving byproducts of selection, which can *accumulate evidence* in its favor: it is not merely a null result, *pace* Barash. The identity of the embryological origins of the tissues, biochemistry, nerves, and muscles involved in orgasm has been established in human beings (Komisaruk et al. 2006). The existence and use of these identical tissues and nerves has been established also in nonhuman primates, a nice piece of comparative evolutionary evidence (Lloyd 2005). The lack of the performance of the trait in females during the most common and ordinary sexual encounters, i.e., vaginal intercourse, has been abundantly documented, thus undermining theories that treat female orgasm as an obvious adaptation (Lloyd 2005). More importantly, the search for genetic correlations between numbers of offspring and

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[20] Thanks to Eduoard Machery for discussion. See Meehl (1954) for corrections to similar confusions in the comparison between statistical and causal hypotheses.

[21] This language comes from Thompson Clarke, "The Legacy of Skepticism," (Clarke 1972).

occurrence of orgasm failed spectacularly, in a study of over 8000 women, thus undermining the claim that orgasm is associated with fitness in an evolutionarily influential way (Zietsch and Santtila 2013). It cannot be, if there is no genetic fitness advantage with women who have orgasm with intercourse, compared to those who do not.[22] Yet none of this evidence is recognized or weighed when considering this trait from the adaptationist methodology. Thus, even though the methodological adaptationists present their adherence to their research program and its attendant question as perfectly harmless and in fact very good and productive science, we can see here an example of where it goes astray.

In essence, the byproduct/bonus hypothesis *cannot* be an answer to the function question asked by the methodological adaptationist, while it is a perfectly acceptable answer to the evolutionary factors question. We can see in these various researchers' responses to the orgasm case how confused they become by focusing only on their primary research question, "What is the function of this trait?" As discussed in the previous section, when several adaptationists were launching arguments against Gould's presentation of Symons's byproduct/bonus hypothesis that was based on my analysis, they—very strangely—behaved as if no empirical evidence had been considered at all. The null hypothesis explanation of the methodological adaptationists' reasoning explains why this occurred. The byproduct/bonus hypothesis, as a nonadaptive hypothesis, is being treated as just a null hypothesis. Because they treat the positive, causal byproduct/bonus hypothesis as merely a null hypothesis, and because they implicitly assume that no null hypothesis may have evidence in support, they cannot see the evidence supporting the byproduct/bonus account. Demonstrating the truth of the bonus/byproduct hypothesis became for Andrews et al. just the failure to support any hypotheses of special design (Andrews et al. 2002a, b). For a methodological adaptationist, the nonselective hypothesis is often treated as the failure to find an explanation, which they view as scientific surrender and failure (Alcock 1987, 1998; Sherman 1989; see Lloyd 2005 for discussion). Mayr offers an especially clear example of this outlook:

> As a consequence of the adaptationist dilemma, when one selectionist explanation of a feature has been discredited, the evolutionist must test other possible adaptationist solutions before he can resign and say: This phenomenon must be a product of chance. (Mayr 1983, p. 326)

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[22] It may be that modern circumstances somehow block the historically relevant correlations from appearing in the data; however, the authors argue against such an interpretation (Zietsch and Santtila 2013).

Before we end the discussion of the dangers of methodological adaptationism, I must acknowledge that many (or almost all?) will object to my criticisms of adaptationism: But methodological adaptationism is so useful! Surely you are not advocating sacrificing our most fruitful research tool?! And no, I am not doing so, since the evolutionary factors framework includes the use of adaptation, and the search for connections to fitness or function, as a first "go-to" algorithm. The evolutionary factors framework advocates starting research by trying out the adaptive answer to "Does this trait have a function?" and learning and keeping at the top of the mind as real causal alternatives the other evolutionary factors. (Sometimes this different set of answers may require a different laboratory setup or tools, e.g., David Wake's work on salamanders, 1991, 2009; Griesemer 2013, 2015.) That is the difference between methodological adaptationism and the evolutionary factors framework: the non-adaptive explanations are real, causal, live alternatives that can be supported with evidence, and need to have their own support found for them. Moreover, this evidential support for the variety of non-adaptive evolutionary factors must be recognized when it is presented, and not treated within a mutually exclusive framework of evidence, in contrast to the recent past history I have touched on in this paper.

How to Apply Evolutionary Factors Methodology: A Case Study

"To show that female orgasm is most likely not an adaptation would require good evidence contradicting the upsuck hypothesis which is altogether absent" (Linquist 2006, p. 419). Linquist's suggested approach is significantly different from the evolutionary factors approach of weighing evidence discussed above in the "'Null' Hypotheses" section, where each explanation acquires evidence on its own account, independently, and not in relation to a privileged adaptive account. Developmental constraints are often discovered and understood during the investigation of adaptive traits, so in this case searching for a function of a trait may serve a useful research goal. However, when developmental constraints are uncovered, it becomes extremely important for the researcher to acknowledge that there is an independent, nonadaptive causal process involved in the evolution of this trait, and which is complementary to the selective process, and which provides limits and constraints upon it, and which also needs to be investigated independently. What is known about the genetics of this developmental trait–are there similar traits in related species? What can we find out about its evolutionary history? What about its social context and history in different regions? All of these questions are independent of the adaptationist research question involving

the function of the original trait. They are nonselective causes, and are customarily treated separately, and have their own set of confirmatory and evidential standards. As such, then, the original methodological adaptationist research question, "What is the function of this trait?" could be understood as quickly leading to information regarding another evolutionary cause, different and independent of selection, which then needs to be investigated under a distinct set of evidential standards as an answer to a different question.

For a concrete example, part (the male aspect) of the evolutionary explanation for the form and distribution of the original trait of female orgasm (as the evolutionary factors research question would pose it) is answered by the selection account, and part (the female aspect) by the nonselective, developmental constraint account. This is ordinary evolutionary theory, but there is little room for such an explanation in the approach outlined by Linquist, or Andrews et al. We could not narrow such a complex evolutionary explanation into a binary setup such as Andrews et al. proposed (2002a, p. 503).

In my 2005 book, I have shown the multiple and weighty lines of evidence favoring the bonus/byproduct hypothesis, in the form of conformance with the distribution of orgasmic performance, the nonhuman primate evidence for the separation of orgasm from reproductive acts, and the (admittedly inadequate) cross-cultural evidence confirming the lack of orgasm in reproductive contexts altogether. Since then a complete lack of genetic correlation between female orgasm and fitness has been documented, thus undermining attempts to pose the trait as an evolutionary adaptation (Zietsch and Santtila 2013). This is why the byproduct/bonus account cannot be treated as a "null" hypothesis; the byproduct/bonus theory has all this, and more, evidence weighing in its favor, which should not be allowed to disappear when compared with one or another adaptive hypothesis. For example, according to 37 studies of 148,346 women using 27 metrics, only about 20 % of the female population reliably has orgasm with intercourse, while about 90 % of the female population does have orgasm sometime during their lives. So while there is a wide variety of ease and frequency of orgasm among women, due possibly to differences in other developmental factors, social factors, and other environmental differences, orgasm is present in the vast majority of women, but it does not routinely appear in the evolutionarily relevant context, i.e., vaginal intercourse. The byproduct/bonus view gives an explanation for this.

Compare the status of the empirical evidence supporting the most favored current adaptive account (Puts et al. 2012; Wheatley and Puts 2015) with the bonus/byproduct account. The popular female choice account posits females mating multiple times over a short period of time with different males. It assumes that orgasm increases

fertilization through the mechanism of uterine upsuck, which makes it more likely that females will be impregnated by higher-quality males and produce more and better offspring. Alan Dixson, the world authority on comparative primate sexuality, denies that this sort of cryptic female choice selection occurs in human beings (2012, p. 630). As expected, then, the female choice set of claims is not supported, as can be seen by the following levels/quality of empirical evidence (see Lloyd 2005; Levin 2011, 2014a, b; Zietsch et al. 2011). (Each evolutionary model is supplied with traits, a hereditary basis, a connection of the trait to fitness, if there is one, and a selection pressure, if there is one.) Note that these authors do not evaluate the byproduct/bonus account on its own merits.

Female Choice/Good Males Hypothesis

Trait—[Mate with multiple males]: **Fair evidence**
Trait—[Female orgasm preferentially with high quality males]: **Fair evidence**
Trait—[Uterine upsuck]: **Evidence Against**
Hereditary basis—[Orgasm's heritability]: **Good evidence**
Connection to fitness—[More offspring with higher orgasm frequency]: **Evidence Against**
Selection pressure—[Strong pressure on women to have offspring of high-quality fathers; female choice, sperm transport]: **Poor evidence**

Contrast this evolutionary model with the one for the bonus/byproduct account, under which female orgasm occurs through a developmental homology between the penis and clitoris and orgasmic tissues shared between men and women, combined with stabilizing selection on the male orgasm. A few of the pieces of evidence supporting this account are listed below, including women's surprisingly low rate of orgasm with intercourse[23] (Lloyd 2005; Levin 2014b), the hereditary basis of orgasm (Dawood et al. 2005; Dunn et al. 2005), and the total lack of any genetic correlation with fitness (Zietsch and Santtila 2013).

Byproduct/Bonus Hypothesis

Trait—[Developmental homologies between orgasmic tissues]: **Excellent evidence**
Trait—[Effectiveness of female masturbation in producing orgasm]: **Excellent evidence**

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[23] This low rate is apparently explained by an anatomical correlation between the structure of the genitals and the rate of orgasm with intercourse. Those women with a longer distance between clitoris and urinary meatus have reliably many fewer orgasms with intercourse than those women with a shorter distance (Wallen and Lloyd 2011). Note again that the occurrence of orgasm is not correlated with fitness measures (Zietsch and Santtila 2011, 2013), so these different distances cannot be interpreted functionally, under the present information. Only Hrdy's, of the current theories, presents female orgasm as anything but a present adaptation.

Trait—[Low rates of female orgasm with intercourse]: **Excellent evidence**

Trait—[Female orgasm in nonhuman primates]: **Good evidence**

Hereditary basis—[Orgasm's heritability]: **Good evidence**

Connection to fitness—[NO correlation with fitness]: **Very good evidence**

Note that in both cases, there is evidence for *no function* of orgasm in females, which is *nonresponsive* to the research question of the methodological adaptationists, "What is the function of this trait?" Instead, the byproduct/bonus explanation is better seen in terms of the logic of the evolutionary factors research question, specifically, "What evolutionary factors account for the form and distribution of the trait of female orgasm?" What the byproduct/bonus explanation does is give a new possible alternative answer:

A: This trait has its current form and distribution largely because it is a byproduct/bonus of strong stabilizing selection on the male orgasm.

This is the correct reading of the bonus/byproduct theory of female orgasm, as a positive alternative causal hypothesis, not as a null hypothesis. It is an alternative to the previous, function answers to the methodological adaptationists' question, and it is an answer that is *not on their list of possible answers*, which only includes answers like: "The function of female orgasm is to preferentially mate with high-quality males," *or* "The function of female orgasm is to aid the pair bond," etc.

So, the problem is not simply that the methodological adaptationists are asking the wrong questions, but rather, they are ignoring a possible way to handle the question they are asking, namely, how to view the possible answer that, "This trait does not have a function." At that point, the adaptationist could move on to a different, more productive, question, such as, "What *other* evolutionary factors may play a role in the form and structure of this trait?" But they do not.

To illustrate the danger of methodological adaptationism in this particular case: several prominent adaptationists repeatedly complain that under the byproduct/bonus hypothesis, female orgasm would fade away and deteriorate over evolutionary time, and would tend to disappear from the population. This notion has been advanced not only by leading scientists such as John Alcock, Paul Sherman, and Barash, but also by outstanding primatologist and human evolutionist Sarah Blaffer Hrdy, and it is based on a misunderstanding of both how the byproduct/bonus account works, and about the evolutionary factors framework itself (Alcock 1998; Sherman 1989; Smith (Hrdy) 2005). These misunderstandings are likely a consequence of their adaptationist bias that a particular trait will only be

sustained in a population if it itself is under sustained selective pressure. But under the bonus/byproduct account, the basic muscle, nerve, and tissue pathways involved in female orgasm would be maintained in the female over the generations in virtue of the fact that they are under ongoing strong stabilizing selection in the male; male nipples are maintained in the same fashion. Thus, methodological adaptationist explanatory biases involving the necessity of selection have led to fundamental mischaracterizations of the byproduct/bonus hypothesis by these researchers.

Another example shows that, when discussing alternatives to adaptations, methodological adaptationists have been prone to make further scientific errors concerning what the byproduct/bonus account says and assumes. These biologists reason that if a trait is not *adaptive*, it cannot be part of an *evolutionary* account at all.

On leading animal behaviorist John Alcock's analysis, the byproduct/bonus hypothesis is a null result, and offers only a "proximate" explanation of how women come to have orgasms. This is quite implausible, so I will go into some detail here. Alcock emphasizes the difference between "proximate" explanations, i.e., the immediate developmental or physiological origins in an individual, and "ultimate" explanations, which concern the adaptive or reproductive value of the traits (1998, p. 328). Alcock accuses Gould, who defended the byproduct/bonus account of orgasm in 1987, of pursuing the following strategy: "Because the adaptationist is interested in evolutionary or ultimate explanations, he or she *would be out of business* if it could be shown that a proximate explanation of a trait makes it unnecessary to explain why *selection* resulted in the spread of the mechanisms underlying the trait" (Alcock 1998, p. 328; emphasis added). (Note that in this sentence, only selection is appealed to in giving evolutionary explanations, and not any other evolutionary forces.) Alcock then characterizes the byproduct/bonus account of female orgasm as a proximate explanation; in other words, it explains how female babies grow up to have orgasms as adult women, but does not offer an evolutionary account. Alcock accuses Gould of attempting "to obscure the complementarity of proximate and ultimate causation," in telling us "that this proximate explanation for female orgasm [the bonus/byproduct explanation] eliminates the need for adaptationist hypotheses" (1998, p. 329).

Alcock writes further:

Proximate explanations of a biological characteristic do not make it impossible to ask whether the trait of interest contributed to individual reproductive success in the past or does so currently. If we were to discover the female orgasm occurred with positive effects on female reproductive success, we would gain an *evolutionary* dimension to our understanding

of this trait that is not covered by *any* proximate explanation. (Alcock 1998, p. 330; emphasis mine, emphasis his)

Proximate explanations, as such, contrast with not only direct selection but also indirect selection explanations, because they are said to not be evolutionary. And this is clearly a result of the fact that the *only answer* to Alcock's adaptation question ("…orgasm occurred with positive effects…") had to do with describing a function for female orgasm.[24] With no reproductive function, the orgasm is seen as having no place in an *evolutionary* account at all. No room is allowed for an alternate, *nonadaptive evolutionary explanation* of female orgasm. This is a consequence of the logic of Alcock's methodological adaptationist research question.

Here we can also look to David Barash, the author of the most widely selling textbook on sociobiology for a couple of decades, and a grandfather of the field of human evolution, who writes, with his wife, in a sympathetic discussion regarding the impetus behind those favoring the byproduct/bonus theory, that it involves

> … a scientifically legitimate desire to explore all possible explanations for any biological enigma of this sort, including the "null hypothesis" that it might not be a direct product of *evolution* after all. (2009, p. 133; my emphasis)

Note the equivalence of evolution with selection in this statement; the bonus/byproduct explanation is mistakenly not considered *evolutionary*, just as we saw before with Alcock and Sherman. This is again the result of the logic of the research question, through methodological adaptationism. The total identification of evolution itself with natural selection [only] was also made by David Buss and coauthors in their 1998 piece defining "exaptation" for psychologists, a particularly unfortunate place for the error (Buss et al. 1998, pp. 534–535; Lloyd and Gould [2002]2014).

For these authors, unless we are allowed to assume there is an adaptation, then we cannot tell whether we can explain it in an evolutionary way. This happens partly because of the atomism that allows the inference that we must assume a trait is an adaptation in order to discuss it in evolutionary biology. Methodological adaptationists have a tendency to see the biological domain as the domain of adaptive explanations; otherwise, they assume we cannot talk about a trait in evolutionary biology (e.g., Alcock 1987, 1998). The rest of evolutionary biology that we have been discussing in the evolutionary factors methodology is

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[24] See Mitchell (2002) for an excellent critique of Sherman's similar "levels of analysis" approach to evolutionary explanations. Ian Jamieson rejected the "levels" approach (1989, p. 696).

invisible, under this account; *it is disappeared*. The methodological adaptationists' methodology was supposed to be benign, it was not supposed to be a risky endeavor with radical theoretical commitments, although that is where it seems to have ended up.

The Logic of Research Questions

Andrews et al. characterized Gould and Lewontin's complaints about adaptationism as the complaint that adaptationists "often use inappropriate evidentiary standards for identifying adaptations and their functions, and that they often fail to consider alternative hypotheses to adaptation" (2002a, p. 489). As quoted above, Andrews et al. also thought that others, such as Gould, may be guilty of giving nonadaptive explanations without sufficient evidentiary standards, accusing them of "Just-so Storytelling" a la Gould and Lewontin (1979).

In this article, I have been emphasizing the initial patterns of inference and explanation, of exploration and investigation, rather than the final "evidentiary standards," that are emphasized and discussed in the Andrews et al., Mayr (1983), Reeve and Sherman (1993), and Buss et al. (1998) papers, and in Gould and Lewontin's (1979) paper. My focus is much more on *the investigative standards*, and less on the evidential standards. My point is that if you use the methodological adaptationist research question, the evidentiary standards of the byproduct/bonus view, accurately portrayed, never come up, since they are buried under the assumptions regarding the null hypothesis and other myths. The just-so story objection is exactly about the standards of evidence, but I have identified the deeper danger earlier, which is in the logic of the research questions asked, particularly in the consequences of the methodological adaptationist framework. So the claim by Andrews et al. (2002a) that the center point of disagreement between the adaptationists and Gould and Lewontin concerns the standard of evidence makes sense, considering their focus on the just-so stories accusation, but it distracts us from the *more central issues concerning the research questions themselves*, and the research programs' reckoning with the full array of possible evolutionary answers.

I would like to close by again emphasizing that I am not in any way against adaptive explanations themselves. But I have highlighted some *risks* of a particular very popular approach to research into evolutionary causes. These dangers become obvious when we examine the logic of the research questions and their relevant answers, within the methodological adaptationist approach and the contrasting evolutionary factors framework. When a research method makes any particular types of hypotheses especially

difficult to entertain or accept, it deserves serious scrutiny. Keeping the logic of the research questions in mind when dealing with the scientific errors committed by adaptationists allows us to analyze and explain them straightforwardly. The presence of researchers like Symons who engaged in their research using the more inclusive evolutionary factors methodology exemplify a living available alternative method. Evolutionists say that they have learned their lessons about an inclusive approach to evolutionary explanation from Gould and Lewontin's 1979 "Spandrels" article, but methodological adaptationism seems to make it very difficult for them to act on those lessons.

References

Alcock J (1987) Ardent adaptationism. Nat Hist 96:4

Alcock J (1998) Unpunctuated equilibrium and the *Natural History* essays of Stephen Jay Gould. Evol Hum Behav 19:321–336

Amundson R (1994) Two concepts of constraint: adaptationism and the challenge from developmental biology. Philos Sci 61:556–578

Amundson R (1998) Typology reconsidered: two doctrines on the history of evolutionary biology. Biol Philos 13:153–177

Amundson R (2001) Adaptation, development, and the quest for common ground. In: Orzack SH, Sober E (eds) Adaptationist and optimality. Cambridge University Press, New York, pp 303–334

Amundson R (2005) The changing role of the embryo in evolutionary thought: roots of evo-devo. Cambridge University Press, Cambridge

Andrews PW, Gangestad SW, Matthews D (2002a) Adaptationism—how to carry out an exaptationist program. Behav Brain Sci 25(4):489–504

Andrews PW, Gangestad SW, Matthews D (2002b) Adaptationism, exaptationism, and evolutionary behavioral science. Behav Brain Sci 25(4):534–547

Barash DP, Lipton JE (2009) How women got their curves and other just-so stories: evolutionary enigmas. Columbia University Press, New York

Bateson P, Laland KN (2013) Tinbergen's four questions: an appreciation and an update. Trends Ecol Evol 28:712–718

Beatty J (1987) Natural selection and the null hypothesis. In: Dupre J (ed) The latest on the best. MIT Press, Cambridge, pp 53–75

Birkhead TR, Miller AP (1992) Sperm competition in birds. Academic Press, London

Breden FJ, Wade MJ (1987) An experimental study of the effect of group size on larval growth and survivorship in the imported

willow leaf beetle, *Plagiodera versicolora* (Coleoptera: Chrysomelidae). Environ Entomol 16:1082–1086

Burian RM (1992) Adaptation: historical perspectives. In: Keller EF, Lloyd EA (eds) Keywords in evolutionary biology. Harvard University Press, Cambridge, pp 7–12

Buss DM, Haselton MG, Shackelford TK et al (1998) Adaptations, exaptations, and spandrels. Am Psychol 54:533–548

Carroll SB (2005) Endless forms most beautiful: the new science of evo devo and the making of the animal kingdom. Norton, New York

Clarke T (1972) The legacy of skepticism. J Philos 69(20):754–769

Cosmides L, Tooby J (1994) Beyond intuition and instinct blindness: toward an evolutionarily rigorous cognitive science. Cognition 50(1):41–77

Dawood K, Kirk KM, Bailey JM et al (2005) Genetic and environmental influences on the frequency of orgasm in women. Twin Res Hum Genet 8:27–33

Dewsbury DA (1992) On the problems studied in ethology, comparative psychology, and animal behavior. Ethology 92:89–107

Dixson A (2012) Primate sexuality, 2nd edn. Oxford University Press, Oxford

Dunn KM, Cherkas LF, Spector TD (2005) Genetic influences on variation in female orgasmic function: a twin study. Biol Lett 1:260–263

Fisher RA (1958) The genetical theory of natural selection, 2nd edn. Dover, New York

Futuyma D (2013) Evolution, 3rd edn. Sinauer, Sunderland

Geary DC, Flinn MV (2001) Evolution of human parental behavior and the human family. Parenting 1(1–2):5–61

Godfrey-Smith P (2001) Three kinds of adaptationism. In: Orzack SH, Sober E (eds) Adaptationism and optimality. Cambridge University Press, Cambridge, pp 344–362

Gould SJ (1987) Freudian slip. Nat Hist 96(2):14–21

Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge

Gould SJ, Lewontin RC (1979) The spandrels of San Marco and the Panglossian paradigm. Proc R Soc Lond B 205:581–598

Gould SJ, Vrba ES (1982) Exaptation: a missing term in the science of form. Paleobiology 8:4–15

Griesemer J (2013) Integration of approaches in David Wake's model-taxon research platform for evolutionary morphology. Stud Hist Philos Sci Part C 44(4):525–536

Griesemer JR (2015) What salamander biologists have taught us about evo-devo. In: Love AC (ed) Conceptual change in biology. Springer, Dordrecht, pp 271–301

Griffiths PE (1996) The historical turn in the study of adaptation. Br J Philos Sci 47:511–532

Halliday T, Arnold SJ (1987) Multiple mating by females: a perspective from quantitative genetics. Anim Behav 35:939–941

Jamieson IG (1989) Levels of analysis or analyses at the same level. Anim Behav 37(4):696–697

Kinsey A, Pomeroy WB, Martin CE, Gebhard PH (1953) Sexual behavior in the human female. Indiana University Press, Indianapolis

Komisaruk B, Beyer-Flores C, Whipple B (2006) The science of orgasm. Johns Hopkins University Press, Baltimore

Komisaruk BR, Wise N, Frangos E et al (2011) Women's clitoris, vagina, and cervix mapped on the sensory cortex: fMRI evidence. J Sex Med 8(10):2822–2830

Kreitman M (1983) Nucleotide polymorphism at the *alcohol dehydrogenase* locus of *Drosophila melanogaster*. Nature 304:412–417

Lande R (1981) Models of speciation by sexual selection on polygenic traits. Proc Natl Acad Sci USA 78:3721–3725

Levin R (2011) Can the controversy about the putative role of the human female orgasm in sperm transport be settled with our

current physiological knowledge of coitus? J Sex Med 8:1566–1578

Levin R (2014a) Recreation and procreation: a critical view of sex in the human female. Clin Anat. doi:10.1002/ca.22495

Levin R (2014b) Should the clitoris become a vestigial organ by personal 'psychological clitoridectomy'? A critical examination of the literature. J Women's Health Issues Care. doi:10.4172/2325-9795.1000159

Lewens T (2009) Seven types of adaptationism. Biol Philos 24(2):161–182

Linde-Medina M (2011) Adaptation or exaptation? The case of the human hand. J Biosci 36(4):575–585. doi:10.1007/s12038-011-9102-5

Linquist SJ (2006) When is an orgasm just an orgasm? Elisabeth Lloyd's The Case of the Female Orgasm: bias in the Science of Evolution. Metascience 15:411–419

Lloyd EA (2005) The case of the female orgasm: bias in the science of evolution. Harvard University Press, Cambridge. Italian edition: Lloyd EA (2006) Il caso dell'orgasmo femminile: Pregiudizio nella scienza dell'evoluzione (trans: Faravelli E). Codice, Torino

Lloyd EA (2013) Units and levels of selection. Stanford Encyclopedia of Philosophy. http://plato.stanford.edu/entries/selection-units/

Lloyd EA, Gould SJ ([2002]2014) Exaptation revisited (Unpublished manuscript)

Lloyd EA, Wilson DS, Sober E (2014) Evolutionary mismatch and what to do about it: a basic tutorial (Unpublished manuscript)

Marrow P, Johnstone RA (1996) Riding the evolutionary streetcar: where population genetics and game theory meet. Trends Ecol Evol 11:445–446

Martins EP (2000) Adaptation and the comparative method. Trends Ecol Evol 15:296–299

Mayr E (1983) How to carry out the adaptationist program? Am Nat 121:324–334

McCauley DE, Wade MJ, Breden FJ, Wohltman M (1988) Kin selection: geographic variation in relatedness in the imported willow leaf beetle, Plagiodera versicolora. Evolution 42:184–192

Meehl PE (1954) Clinical versus statistical prediction: a theoretical analysis and a review of the evidence. http://psycnet.apa.org/psycinfo/2006-21565-000

Millstein RL (2007) Hsp90-induced evolution: adaptationist, neutralist, and developmentalist scenarios. Biol Theory 2:376–386

Millstein RL (2008) Distinguishing drift and selection empirically: 'The Great Snail Debate' of the 1950s. J Hist Biol 41:339–367

Mitchell S (2002) Integrative pluralism. Biol Philos 17:55–70

Newman SA (1988) Lineage and pattern in the developing vertebrate limb. Trends Genet 4:329–332

Newman SA, Bhat R (2008) Dynamical patterning modules: physico-genetic determinants of morphological development and evolution. Phys Biol 5:1–14

Newman SA, Bhat R (2011) Lamarck's dangerous idea. In: Gissis SB, Jablonka E (eds) Transformations of Lamarckism: from subtle fluids to molecular biology. MIT Press, Cambridge, pp 157–170

Odling-Smee FJ, Laland KN, Feldman MW (2001) Niche construction: the neglected process in evolution. Princeton University Press, Princeton

Otsuka J (2014) Causal foundations of evolutionary genetics. Br J Philos Sci. doi:10.1093/bjps/axu039

Pigliucci M, Kaplan J (2000) The rise and fall of Dr. Pangloss: adaptationism and the Spandrels paper 20 years later. Trends Ecol Evol 15(2):66–70

Pigliucci M, Müller GB (2010) Evolution: the extended synthesis. MIT Press, Cambridge

Pinker S (1999) How the mind works. Ann N Y Acad Sci 882:119–127. doi:10.1111/j.1749-6632.1999.tb08538.x

Puts DA, Welling LLM, Burriss RP, Dawood K (2012) Men's masculinity and attractiveness predict their female partners' reported orgasm frequency and timing. Evol Hum Behav 33:1–9

Raff RA (1996) The shape of life: genes, development and the evolution of animal form. University of Chicago Press, Chicago

Reeve HK, Sherman PW (1993) Adaptation and the goals of evolutionary research. Q Rev Biol 68(1):1–32

Rose MR, Lauder GV (eds) (1996) Adaptation. Academic Press, San Diego

Russell B (1919) Introduction to mathematical philosophy. McMillan, New York

Sansom R (2003) Constraining the adaptationism debate. Biol Philos 18:493–512

Schmitt DP, Pilcher JJ (2004) Evaluating evidence of psychological adaptation: how do we know one when we see one? Psychol Sci 15(10):643–649

Schwalm PA, Starrett PH, McDiarmid RW (1977) Infrared reflectance in leaf-sitting neotropical frogs. Science 196:1225–1229

Seger J, Stubblefield JW (1996) Optimization and adaptation. In: Rose MR, Lauder GV (eds) Adaptation. Academic Press, San Diego, pp 93–102

Sherman P (1989) The clitoris debate and the levels of analysis. Anim Behav 37:697–698

Singh RS, Krimbas CB (2000) Evolutionary genetics: from molecules to morphology. Cambridge University Press, New York

Smith D (Hrdy) (2005) A critic takes on the logic of female orgasm. New York Times, May 17, pp 1–3

Symons D (1979) The evolution of human sexuality. Oxford University Press, New York

Symons D (1990) Adaptiveness and adaptation. Ethol Sociobiol 11(4):427–444

Thornhill R (1990) The study of adaptation. In: Bekoff M, Jamieson D (eds) Interpretation and explanation in the study of behavior. Westview Press, Boulder, pp 31–62

Thornhill R (1997) The concept of an evolved adaptation. In: Daly M (ed) Characterizing human psychological adaptations. Wiley, New York, pp 4–22

Van Fraassen BC (1980) The scientific image. Clarendon, Oxford

Wade MJ (1978) A critical review of the models of group selection. Q Rev Biol 53(2):101–114

Wade MJ (1985) Soft selection, hard selection, kin selection, and group selection. Am Nat 125(1):61–73

Wade MJ (1994) The biology of the willow leaf beetle, Plagiodera versicolora (Laicharting). In: Joliviet P, Cox M (eds) Novel aspects of the biology of chrysomelidae. Kluwer Academic Publishers Group, Dordrecht, pp 541–547

Wade MJ (2016) Adaptation in metapopulations: how interactions change evolution. University of Chicago Press, Chicago (in press)

Wade MJ, Breden FJ (1986) Life history of natural populations of the imported willow leaf beetle, Plagiodera versicolora (coleoptera: chrysomelidae). Ann Entomol Soc Am 79:73–79

Wake DB (1991) Homoplasy: the result of natural selection, or evidence of design limitations? Am Nat 138:543–567

Wake DB (2009) What salamanders have taught us about evolution. Annu Rev Ecol Evol Syst 40:333–352

Wallen K, Lloyd EA (2011) Female sexual arousal: genital anatomy and orgasm in intercourse. Horm Behav 59:780–792

West-Eberhard M-J (1992) Adaptation: current usages. In: Keller EF, Lloyd EA (eds) Keywords in evolutionary biology. Harvard University Press, Cambridge, pp 13–18

Westneat DF, Sherman PW, Morton ML (1990) The ecology and evolution of extra-pair copulations in birds. Curr Ornithol 7:331–369

Wheatley JR, Puts DA (2015) Evolutionary science of female orgasm. In: Shackelford TK, Hansen RD (eds) The evolution of sexuality. Springer, Berlin, pp 123–148. doi:10.1007/978-3-319-09384-0_7

Williams GC (1966) Adaptation and selection. Princeton University Press, Princeton

Wright S (1931) Evolution in Mendelian populations. Genetics 16(2):97–159

Zietsch BP, Santtila P (2011) Genetic analysis of orgasmic function in twins and siblings does not support the by-product theory of female orgasm. Anim Behav 82:1097–1101

Zietsch BP, Santtila P (2013) No direct relationship between human female orgasm rate and number of offspring. Anim Behav 86:253–255

Zietsch BP, Miller GF, Bailey JM, Martin NG (2011) Female orgasm rates are largely independent of other traits: implications for "female orgasmic disorder" and evolutionary theories of orgasm. J Sex Med 8:2305–2316