



## HOW TO STUDY ADAPTATION (AND WHY TO DO IT THAT WAY)

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## ABSTRACT

*Some adaptationist explanations are regarded as maximally solid and others fanciful just-so stories. Just-so stories are explanations based on very little evidence. Lack of evidence leads to circular-sounding reasoning: "this trait was shaped by selection in unseen ancestral populations and this selection must have occurred because the trait is present." Well-supported adaptationist explanations include evidence that is not only abundant but selected from comparative, populational, and optimality perspectives, the three adaptationist subdisciplines. Each subdiscipline obtains its broad relevance in evolutionary biology via assumptions that can only be tested with the methods of the other subdisciplines. However, even in the best-supported explanations, assumptions regarding variation, heritability, and fitness in unseen ancestral populations are always present. These assumptions are accepted given how well they would explain the data if they were true. This means that some degree of "circularity" is present in all evolutionary explanations. Evolutionary explanation corresponds not to a deductive structure, as biologists usually assert, but instead to ones such as abduction or Bayesianism. With these structures in mind, we show the way to a healthier view of "circularity" in evolutionary biology and why integration across the comparative, populational, and optimality approaches is necessary.*

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## INTRODUCTION

THE study of adaptation aims to understand the fit between organismal form and function across the living world. Some inferences of adaptation are accepted as solid, almost without question. Many are dismissed as just-so stories, while others are accused of being circular arguments. Here we outline the difference between a just-so story and a solid, widely accepted adaptationist explanation. We examine the “circularity” that is so often criticized in evolutionary biology, why it is there, and the important part it plays in all evolutionary explanations. We show that the difference between a just-so story and a well-accepted adaptationist explanation is the amount of direct evidence available. Like all attempts to infer things about the deep past, adaptationist explanations are most trusted when they have a lot of evidence from a diversity of sources. That more evidence is better is obvious. Not so obvious is that some strategies for getting this information are better than others. Even less obvious is that some degree of “circularity” is necessarily present in all adaptationist explanations, no matter how well supported. This circularity can be thought of in terms of inference types such as induction, abduction, or Bayesianism. Whatever the name of inference type applied, the need for a diversity of evidence leads us to conclude by calling for integration across the adaptationist subdisciplines. We start by exploring “just-so stories” and the three main adaptationist subdisciplines before seeing how to structure maximally supported explanations of the fit between form and function across living things.

## JUST-SO STORIES

Adaptationist scenarios are often criticized as “just-so stories.” The term comes from the title of Rudyard Kipling’s (1902) children’s book of origin stories. In the context of adaptation, it is a derogatory term, implying that a given adaptationist explanation is unfalsifiable, fanciful, and is accepted not because of evidence, but based on plausibility alone (Lennox 1991; Durrant and Haig 2001). Reference to Kipling and just-so stories

is often attributed to Gould and Lewontin’s 1979 spandrels paper (Alcock 1998; Hull 2001; Hall 2002; Travis 2003; Sosis 2009; Frost-Arnold 2010), even by Gould himself (1997, 2002). However, the spandrels paper makes no mention of Kipling and does not use the “just-so story” term, although other essays by Gould (1977, 1978, 1997, 2002) do. Just-so stories are of interest here because they reveal the structure of little-trusted adaptationist explanations and thus the way to ones regarded as solid.

Adaptationist just-so stories are criticized for two reasons, one being “circularity” and the other their freedom to proliferate. Just-so stories are criticized for “circularity” because the presence of a given trait in current organisms is used as the sole evidence to infer heritable variation in the trait in an ancestral population and a selective regime that favored some variants over others. This unobserved selective scenario explains the presence of the observed trait, and the only evidence for the selective scenario is trait presence (e.g., Griffiths 1996; Frost-Arnold 2010). Gould (1996) called the giraffe’s neck the “canonical just-so story” because the story is so often repeated. The story consists of the notion that selection favored variants with relatively long necks in short-necked ancestral giraffe populations as a result of their greater ability to obtain food. Giraffe necks are long as a result of this unobservable selection on heritable ancestral variation in neck length, and this selection must have occurred because giraffe necks are long and because giraffes today can eat leaves from tall trees (Figure 1). The relative lack of information that leads to this “circular” structure also allows different potential explanations to proliferate.

Multiple accounts of selection in the distant past can be devised to explain the presence of any trait. In the absence of information beyond simple trait presence, it is hard to choose the best from among these alternative accounts. For example, the long neck of the giraffe might have been favored in reaching high leaves. Alternatively, perhaps males with longer necks prevailed in battles for females; perhaps long necks in males developmentally imply long ones in females,

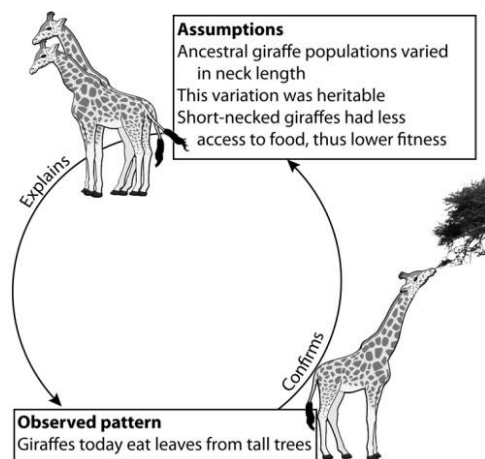


FIGURE 1. CIRCULARITY AND THE GIRAFFE NECK JUST-SO STORY

Giraffes in present-day populations use their long necks to reach leaves from tall trees. The presence of long necks is explained as the result of unobserved and unobservable selection in ancestral populations in the distant past. It is assumed that there was once heritable variation in short-necked ancestral giraffe populations, and that this variation had fitness consequences. Specifically, longer-necked individuals were favored because of greater access to food. This entire selective scenario, variation, heritability, fitness, and all is accepted as true because giraffes today at least sometimes use their necks to reach food from tall trees. The selective scenario in turn explains why giraffes have long necks. An adaptationist scenario with little direct evidence beyond the pattern to be explained is known as a just-so story.

and so all giraffes have long necks. Based only on the trait “long neck” and that the necks are at least occasionally involved in reaching high leaves as well as in male-male battles, it is hard to pick one or the other of these explanations as the best one (Gould 1996; Simmons and Scheepers 1996). When the available data are unable to distinguish convincingly between two or more hypotheses, the hypotheses are said to be underdetermined by the data (Ladyman 2002; Dietrich and Skipper 2007). The literature on adaptation is full of examples of underdetermination (Forber 2009). For example, carrion flowers might have been favored in drylands with a dearth of bees and an abundance of flies. But herbivores are apparently driven away by the scent of rotting flesh, so maybe stinky flowers

are instead an herbivore deterrent in plant-scarce drylands (Lev-Yadun et al. 2009). The colorful peeling bark of tropical trees in many plant families has been seen as an adaptation permitting photosynthesis of the living bark (Franco-Vizcaíno et al. 1990), a mechanism to shed epiphytes and thereby reduce mechanical loads (Stevens 1987), or even as a attractant of fruit dispersers (Rzedowski and Kruse 1979). MacColl (2011) details no less than six underdetermined adaptive explanations for the armor plates of sticklebacks. Evidence beyond simple trait presence is needed to choose between hypotheses and to minimize the “circularity” of just-so explanations. But some strategies for gathering evidence are better than others. To see why, it is necessary first to examine the three main adaptationist approaches.

#### “CIRCULARITY” AND THE THREE ADAPTATIONIST SUBDISCIPLINES

Approaches for studying adaptation fall into three subdisciplinary categories: comparative, populational, and optimality. Just-so stories, understood as “circular” arguments with little direct evidence, can be found in all of these approaches. The intent of this section is to describe the generalities of each of the three approaches briefly, to be able to examine how each is associated with “circularity” when little direct evidence is available. After, we will show that some “circularity” is in fact natural and necessary in all explanations involving adaptation, hence our scare quotes. Importantly, we show that the assumptions being accepted using “circular” reasoning are those that give each approach its broad relevance in evolutionary biology. We then argue that recognition of these assumptions points the way to more robust adaptationist explanations by simultaneous use of the three approaches.

#### THE COMPARATIVE METHOD

The comparative method detects adaptation through convergence (Losos 2011). A basic version of comparative studies, perhaps the one underpinning most statements about adaptation, is the qualitative observation of similar organismal features in similar selective contexts. An example is the

observation that aquatic animals often have streamlined shapes and fins, regardless of whether they are fish, whales, ichthyosaurs, eurypterids, or squids. Convergence thinking finds a quantitative expression in methods that seek statistical associations in cross-species data (Bell 1989; Martins 2000; Blomberg et al. 2003). These include both studies of how organismal attributes change predictably across environmental gradients, such as the global negative relationship between the toothiness of plant leaves and temperature (Peppe et al. 2011), as well as between organismal attributes, such as bone length-diameter scaling (Christiansen 1999; Swartz and Middleton 2008; Kilbourne and Mackovicky 2012). Other examples of comparative approaches include those that aim to detect deviations from neutral substitution patterns in multiple molecular alignments (Nielsen 2009). Across this methodological diversity, the use of cross-species variation unites all comparative methods.

It is easy to construct “circular” just-so stories based on comparative data. These “circular” stories anchor comparative methods as a fundamental source of information for constructing evolutionary explanations. If the pattern in Figure 2 is regarded as reflecting adaptation, then it is implied that the occupied part of the plot corresponds to combinations of X and Y that are of higher fitness than the surrounding space (Arnold 2005). This view effectively asserts that “this space is filled in nature; because selection favors variants with high fitness, this space must be of high fitness. I know that this is the space corresponding to high fitness, because it is filled” (Figure 2).

Without assumptions regarding evolutionary process, comparative data would be no more than blank descriptions of how trait values are distributed. Assumptions about population-level phenomena such as developmentally possible variation, heritability, and fitness are the vital glue that connect comparative patterns to notions of evolutionary process and thereby give comparative patterns relevance beyond simple description (Table 1). However, based on the pattern in Figure 2 alone, any adaptive explanation is

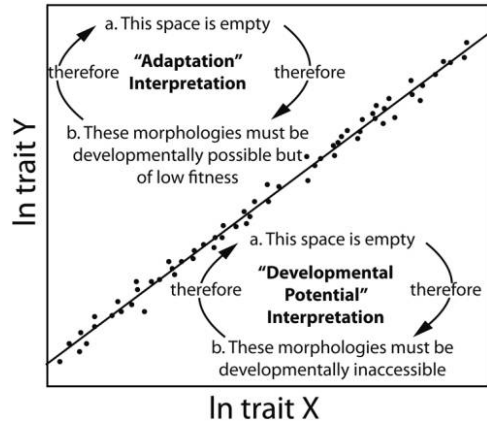


FIGURE 2. ADAPTATIONIST EXPLANATIONS AND CIRCULARITY: GENERAL CASE

Points on the graph refer to mean species trait values, and the line an allometric regression fit. The “adaptation” view sees the entire space defined by the mean values as potentially accessible in ontogeny, but that the configurations corresponding to the empty spaces are eliminated by selection. The “limited developmental potential” view sees allometry as the manifestation of a lack of developmental alternatives. Both perspectives make untested assumptions: adaptationist reasoning regarding empty spaces is shown above the scaling line, and thinking in terms of developmental potential below. Both loops can be read starting at a. or b., i.e., “a. This space is empty. Therefore, b. These morphologies must be developmentally possible but of low fitness,” or “b. These morphologies must be developmentally inaccessible, therefore a. This space is empty.” In both cases a. is used to infer b., which in turn is inferred based on a. The means to strengthen these “circular” inferences is via additional layers of evidence (see Figure 3).

rightly considered a just-so story in that it is hard to choose the adaptationist scenario over other potential explanations. For example, the pattern might be observed because the empty spaces are developmental impossibilities, even though they would be of much higher fitness than the observed morphologies (Olson 2012). The pattern might be due to drift or other chance alignments (Brandon and Fleming 2014). Based on the pattern in Figure 2 alone, all of these explanations will have the “circular” structure shown there. Similar things happen with the other adaptationist approaches.

TABLE 1

*The three principal approaches for studying adaptation, some typically cited advantages and disadvantages, and the key assumptions that give each method its relevance to evolutionary biology in general*

	<b>Definition</b>	<b>Advantages</b>	<b>Disadvantages</b>	<b>Key assumption</b>
Comparative/ convergence	The convergence on similar morphologies in similar selective contexts from ancestors with different states suggests adaptation	Studies species in nature that are the descendants of natural evolutionary processes; examines patterns applicable across evolutionarily relevant timespans and many species	Does not examine fitness or heritability directly; often relies on ancestral character state reconstructions or assumptions of tempo and mode that are impossible to test	Comparative patterns are produced by population-level processes, involving developmental variation, heritability, and differential fitness
Populational	Studies the raw material of selection directly, i.e., fitness/performance differences associated with heritable within-species trait variation	The focal approach for directly examining intraspecific variation, heritability, and the fitness impact of this variation	Examines relatively minor characters that have not gone to fixation; extrapolation of results to multiple species and large timescales debated	The population-level processes being studied are those shaping the entire diversity of life
Optimality	Predicts the configuration(s) maximizing a performance/fitness criterion given general biophysical principles and a set of competing considerations; concordance between model and nature suggests adaptation	Based on models that explicitly incorporate competing demands on an organism; even a lack of model-nature correspondence is useful because it highlights elements that need to be considered; explicitly includes fitness/performance indices	The process of selection of variables is often criticized; in addition, there is no directive emerging from nature to indicate where the cutoff in fit between nature and the model should be taken as congruent with model predictions or not	Adaptation is the only plausible explanation for trait optimality

#### POPULATIONAL APPROACHES

Another approach for studying adaptation focuses on the population level. Populational approaches include a wide range of tools for testing hypotheses of adaptation, from detailed studies of reproductive biology or intrapopulational variation to quantitative genetics (e.g., Lande and Arnold 1983; Bell 2008; Olson 2012). These studies reason that because natural selection acts on interindividual variation, the population level is the domain appropriate for studying adaptation. These studies focus directly on variation, heritability, and fitness between potentially competing individuals. In a particularly complete study, Travers et al. (2003) documented variation in the curvature of floral nectar spurs

in populations of the jewelweed *Impatiens capensis*. They found that the spurs, tubular projections from the backs of the flowers that attract pollinators with sugary nectar, varied in projecting almost straight back to almost completely recurved, with the tip facing the front of the flower. For a trait to be subject to selection, variation must be heritable, and many techniques are available for estimating the degree to which offspring tend to resemble their parents in a given trait. Travers et al. (2003) estimated heritability using a selfing protocol followed by a regression of progeny spur curvature on parental curvature. They found a marked tendency for parental curvature to predict progeny curvature. In addition to being her-



itable, a trait subject to selection must be associated with differences in fitness. Travers et al. (2003) studied the way that different spur curvatures resulted in different hummingbird visitation times. They found that flowers with more recurved spurs were associated with longer visitation times and more grains of pollen carried away. That spur curvature is heritable and associated with differential reproductive success is compatible with the hypothesis that curvature can be subject to selection and that some predictable patterns of variation in curvature could be adaptive.

As compared to comparative approaches, populational methods invoke a different but equally important set of “circular” assumptions. Like comparative methods, these assumptions also have to do with the fundamental justification that gives populational methods their general relevance in evolutionary biology. Populational methods involve detailed studies of very geographically and restricted sets of organisms under often unusual situations, e.g., purebred lines, over short times. This approach is of direct importance mostly to applied activities such as plant or animal breeding, in which humans wish to produce a given selective response in a given time (Pigliucci and Schlichting 1997). The relevance of populational studies to evolutionary biology at large is only via the assumption that population-level processes identical to those being studied in fact play important roles in generating the patterns of trait distribution observed over geological time and across clades (Table 1). This assumption is exactly the one invoked in forging the link between the fossil record and population genetics of the Modern Synthesis (e.g., Simpson 1953). In this way, the great just-so story of population biology is that very local population-level phenomena are in some way isomorphic with the factors shaping life on Earth at large. In populational studies, “circularity” takes the form that heritable variation with fitness consequences shaping local situations is taken as an explanation of the organismal form-function fit globally, and the form-function fit is taken as confirming population-level selection as the shaping factor. Based only on population-

level data, this assumption is as much a just-so story as the unobserved variation and fitness in the comparative example above (Figure 2). Missing from both the comparative and populational approaches are explicit notions of the biophysical reasons behind a given variant being favored, information provided by the optimality perspective.

#### OPTIMALITY MODELING

Optimality methods examine the ways that performance or fitness differences emerge as the result of predictable biophysical principles. Given a series of competing considerations, optimality models predict the combination or combinations that maximize fitness or some other performance criterion (Parker and Maynard-Smith 1990; Vincent and Brown 2005; Potochnik 2009). For example, the most influential optimality model of the past 20 years is that of West, Brown, and Enquist (West et al. 1997; WBE). WBE asks what organismal geometry simultaneously maximizes metabolite exchange surface area and minimizes transport distances and therefore transport energy investment. For a given amount of tissue, metabolite exchange area is maximal in a plane and transport distances are minimized in a sphere, so these functions cannot be globally maximal simultaneously. The intermediate “least bad” configuration is a fractal branching one, as found in trees, lungs, kidneys, and most other transport systems that innervate living things. Optimality models make no necessary reference to a given level of biological organization. That any given model does so is a contingent fact of that model, not a property of optimality models in general. For example, the exact same interpretation of WBE as applied to plant vasculature (West et al. 1999; Petit and Anfodillo 2009) has been tested with reference to individual plants (Bettiati et al. 2012), within populations of the same species (Petit et al. 2010), and across the flowering plants (Olson et al. 2014; see also West et al. 2002). In all of these cases, the empirical results, down to the allometric scaling exponents, are identical with those predicted by the model. Coincidence between optimality predictions and nature

by chance and not via the action of selection seems very unlikely.

However unlikely chance model-nature coincidence might seem, explanations built only on optimality models also involve “circular” acceptance of assumptions (Griffiths 1996). Coincidence between optimality predictions and nature that are due to chance or any other nonadaptive process is regarded as so unlikely that the trait must be due to selection (Orzack and Sober 1994). An optimality just-so explanation takes the form that coincidence between model and nature implies selection; this unobserved selection in turn explains why there is coincidence between the model and nature. As we will show, this sort of “circularity” can be minimized but never eliminated.

#### ADAPTATIONISM: A VIRTUOUS CIRCULARITY

Whether comparative, populational, or optimality, all of the approaches for studying adaptation have built-in “circular” assumptions, and these assumptions are the ones that justify each method as being of evolutionary relevance (Table 1). Without these assumptions, each of these methods produces only descriptive accounts of very limited local interest. When combined, an adaptationist explanation that includes comparative, populational, and optimality data is always considered well supported and much more than a just-so story (cf. Forber 2010). As we will show, however, even the best-supported explanation still involves “circularity.”

Although “loops” of reasoning are easy to detect in the just-so examples in Figures 2 and 3A, they are still present even in the best-supported studies of adaptation (Figure 3B). If a given pattern has an adaptive cause, then by definition at some time in the past, not just the observable present or moments captured in fossil traces, heritable variation with fitness consequences was present (Leroi et al. 1994; Forber and Griffith 2011; including assimilable plastic variation, see West-Eberhard 2003). Selection on this variation is assumed to have led to the pattern observed today (Figure 3B). All adaptationist explanations at some point invoke these assumptions

about unseen and unexaminable sets of organisms. That almost all swimming organisms have streamlined bodies and fins certainly suggests that these features are adaptive. Their being adaptive means that in some ancestral populations there was variation leading to differential survivorship and reproduction (Scriven 1959). These populations will never be seen, but that they must have existed is accepted because their having existed would explain the data so well if it were true (Figure 3). As more direct evidence is gathered (from Figures 3A to 3B), the relative importance of “circular” loops diminishes. But no matter how much direct evidence is accumulated or what method is used, the existence of unseen populations is assumed. That traits today are distributed the way that they are suggests that these populations must have existed, and the assumed existence of these populations helps explain why traits are distributed the way that they are. This apparent “circularity” is what we mean by “loopy” (cf. Rieppel 2003). “Loopiness” does not undermine the solidity of reasoning regarding adaptation. Because so much information is available from so many different sources, the notion that the presence of fins in aquatic animals involves adaptation seems as solid an assertion as can be hoped for in science (Figure 4).

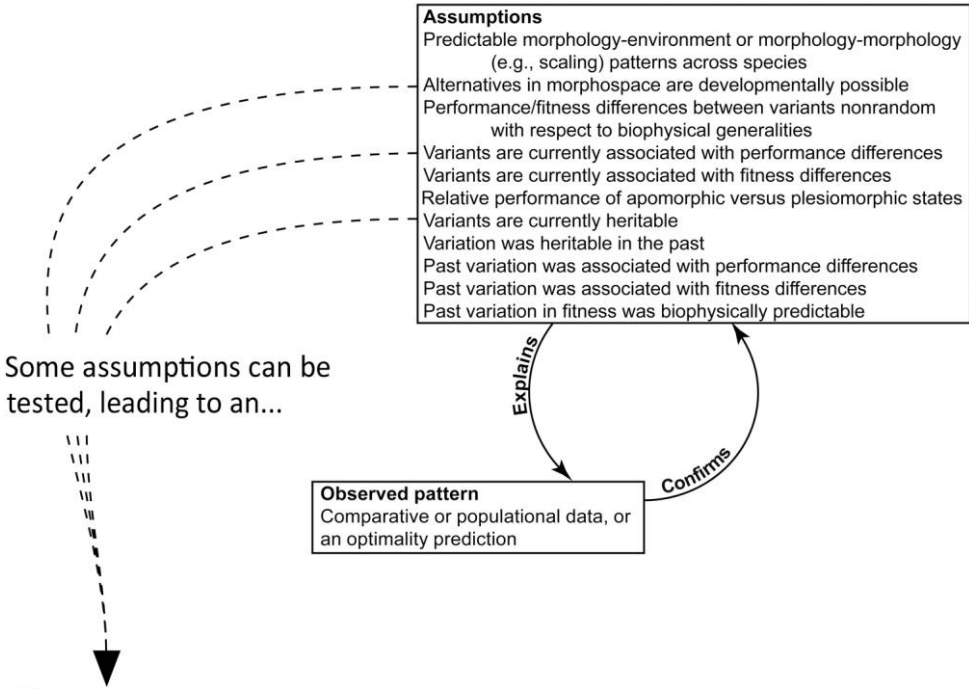
In fact, scientific explanations in general, not just evolutionary ones, have a loopy structure. This statement from astronomy is an excellent example of loopy reasoning: “[T]he transmission spectrum of [the super-Earth exoplanet] GJ 1214b [is observed to be featureless] at near-infrared wavelengths . . . [and its] atmosphere must contain clouds to be consistent with the data” (Kreidberg et al. 2014:69). The assumption that the planet has clouds is accepted because it would explain the data best if it were true. The featureless near-infrared transmission spectrum is observed because there are clouds; there must be clouds because of the featureless spectrum. The authors marshal other layers of direct evidence in favor of their interpretation of a cloudy planet, building an explanatory structure ex-

actly analogous to that in Figure 3B, loops and all.

Loopiness is well documented by philosophers of biology. Griffiths' (1996) "adaptationist abduction" (see also Ruse 1975; Sterelny and Griffiths 1999; Durrant and

Haig 2001) is an account of "loopy" reasoning in terms of an inferential strategy known as abduction or inference to the best explanation (Lipton 2008). Griffiths's account maps the "loops" of reasoning that optimality studies use to construct adaptationist ex-

**A.** Adaptationist explanation based on very little direct evidence



**B.** Adaptationist explanation based on abundant direct evidence

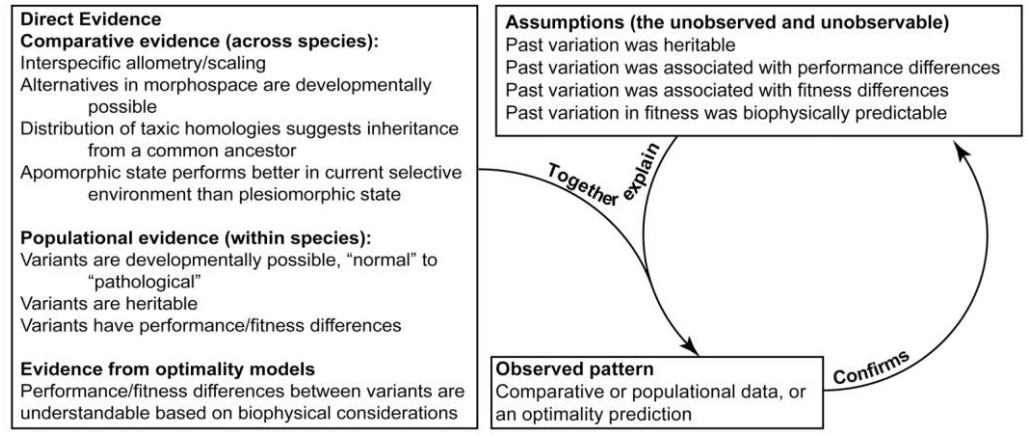


FIGURE 3.



planations. The notion of abduction was introduced by Charles Sanders Peirce in 1903 as a type of inference of the form

The fact C is observed;  
If A were true, C would be a matter of course,  
Hence, there is reason to suspect that A is true.

The assumption A is accepted because it would explain the data so well if it were true, exactly the way assumptions are accepted in Figure 3. Different authors have proposed epistemic and quantitative criteria for evaluating abductive statements (for a review see Douven 2011), but whatever way that abductive statements are judged, they involve “loopy” interplay between the phenomenon to be explained and the explanation itself. This interplay, in the form of assumptions that are accepted as a function of how well they would explain the data if they were true, is precisely how explanations in evolutionary biology are constructed (Haig and Durrant 2002; Ladyman 2002 offers a friendly introduction to inference types). Abduction is a form of reasoning that corresponds well to the way that studies of adaptation are genuinely carried out, but it is by no means the only one.

Loopiness can also be found in familiar statistical procedures. For example, the essence of Bayesian statistical methods is that confidence in a given hypothesis is strengthened in the light of new evidence. In Bayesianism, the probabilities involved are read as a measure of belief in a given hypothesis.

Evidence allows scientists to confirm or disconfirm the belief they have in the hypothesis (Table 2; Fisher 1985; Okasha 2000). With its back-and-forth relation between the posterior probability, the priors, and the hypotheses under consideration, Bayesian reasoning is an excellent example of loopy reasoning.

Our proposal to recognize “loopiness” is motivated not so much by the need to tag adaptationist reasoning as “abductive,” “Bayesian,” or any other term, but because recognition of loopiness shows how to make evolutionary explanations stronger. We have tried to show that the construction of scientific explanations is “loopy” by arguing first and foremost from common sense biological practice. The aim in the present section was to show briefly that this take is not just our personal view. Instead, loopiness is old news to philosophers who study the way that scientific explanations are constructed. It is, however, news to most biologists, and therefore has important consequences for everyday biological practice. At this point, based on the reasoning above and their own experience, many biologists will be convinced that evolutionary explanations are built with a loopy structure and will want to know what this means for the study of adaptation. They can safely skip the next section. Others will be left wondering why evolutionary biologists spend so much time insisting that their science is deductive, nonloopy, and even Popperian. The next section gives a little more detail for these readers.

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FIGURE 3. THE “LOOPY” STRUCTURE OF ADAPTATIONIST EXPLANATIONS: GENERAL CASE

A. It is easy to see that, when very little evidence is available, adaptive explanations of a given pattern have an element of “circularity” or loopy nature. This structure involves loops of reasoning in which, of the possible explanations (e.g., adaptation, limited developmental potential, drift/chance), adaptation is chosen as seeming the most likely. Declaring a given pattern as the result of adaptation immediately implies assuming many things about variation, heritability, performance, and fitness. These assumptions are accepted given how well they would explain the data if they were true. Biologists often call these adaptive explanations “just-so stories” and demand additional evidence. B. The “loopy” structure of adaptationist explanations persists even when abundant direct evidence is available. Explanations with diverse sources of direct evidence seem as solid as any in any branch of science. For example, the presence of fins in aquatic animals seems certain to involve adaptation (Figure 4). However, these explanations still require acceptance of assumptions based on how well they would explain the data if they were true. Adding more layers of direct evidence diminishes the relative importance of “loops” of reasoning, but they never disappear entirely.

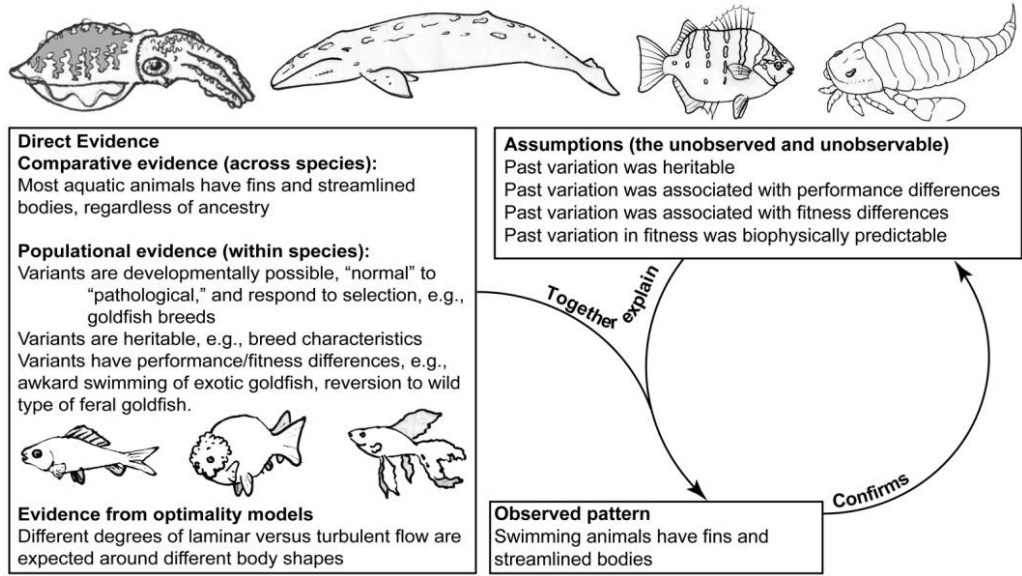


FIGURE 4. THE “LOOPY” STRUCTURE OF ADAPTATIONIST EXPLANATIONS: THE FINS AND FUSIFORM BODIES OF AQUATIC ANIMALS

That the possession of fins and a streamlined shape represent the effects of selection in an aquatic environment seems certain. This explanation is so solid because there is an abundance of evidence from across the three main adaptationist interdisciplinary approaches. There is the comparative observation that unrelated aquatic animals, such as squid, whales, fish, and eurypterids, have or had streamlined bodies and fins. From a populational point of view, it is clear that there is heritable variation in many body and fin traits, and that this variation is associated with performance differences, as in domestic goldfish breeds. That selection on these traits can be operative now strongly suggests that it also did in unobserved ancestral populations. Moreover, optimality models based on fluid mechanics illuminate the biomechanical basis for performance differences between variants. But no matter how much direct evidence accumulates, some reasoning “loops” remain. At some point in the distant past, there were presumably populations without these traits, and in which they arose, varied, and were favored. These ancestral populations are impossible to observe. The assumptions regarding their characteristics are accepted because they would explain the data so well if they were true.

FIVE MYTHS OF HYPOTHETICO-DEDUCTIVE EVOLUTIONARY BIOLOGY

The arguments above run counter to more than 50 years of biological tradition. Evolutionary biology has a long-standing custom of regarding all forms of “circularity” with suspicion (Table 3; Hull 1967), rejecting “induction,” and affirming biology’s deductive, Popperian, and falsificationist nature. In fact, like science in general, evolutionary biology is neither deductive nor Popperian. Induction and “circularity” in the loopy sense we use here are not the bad words biologists traditionally make them out to be. Terms like “hypothetico-deductive” and “falsificationism” imply very different things in biology than they do in their orig-

inal contexts in the philosophy of science from which biologists co-opted them. Because traditional biological positions might make many biologists resist accepting “loopiness,” in this section, we give some additional detail. Because these notions are pervasive in biology and confusing, we give some order by treating them as five “myths” of hypothetico-deductive evolutionary biology.

Myth 1: Deduction is the standard of good science. The importance of deduction versus loopy thinking has had two different trajectories in the philosophy of science and in biology. The deductive vision of science has been controversial in the philosophy of science since the birth of the field in the early 20th century with the Vienna Circle. The

TABLE 2  
Major types of inference

Type of inference	A conclusion is correct because. . .	Formal representation*	Example	Kind of explanation
Deduction	If the premises are true, the conclusion is true	If A then B. <u>A.</u> Then B.	If it rains the floor is wet. <u>It rains.</u> The floor is wet.	Pattern
Induction	Numerous observations from numerous sources such as experimental results, statistical analyses, and previous information strengthen the cogency of a conclusion	If A then <i>probably</i> B. <u>A.</u> <u>Then <i>probably</i> B.</u>	80% of the time, when it rains, the floor gets wet. <u>It rains.</u> There is an 80% chance that the floor is wet.	Pattern/Loopy
Abduction	Theory and available evidence make it likely that a conclusion is correct	A. If B obtained then A would be a matter of course. <u>B.</u> Then A.	The floor is wet. If it rained, then the floor being wet would be a matter of course. <u>It rained.</u> Rain is likely the reason why the floor is wet.	Loopy
Bayesianism	Belief in a conclusion increases as more and more relevant evidence is gathered	$P(A B) = P(B A) * P(A)$ P(B)	I believe that it rained (A). The floor is wet (B). Then my belief that it rained has been increased given the available evidence $P(A B)P(A)$ .	Loopy

\*Following convention, deductive inferences are written with the premises and the conclusion being separated by a single line to indicate that they are “truth preserving,” i.e., that given the truth of the premises the conclusion will be true as well. By convention two lines indicate nontruth preserving arguments, such as those that are upheld by probability and loopy reasoning. Inductive arguments are often though not necessarily probabilistic, given that there are many different ways to compute the strength of a given conclusion. Bayesianism is included to exemplify a popular form of reasoning using probabilities, but the same example can be generalized to other statistical procedures, for example, to Neyman-Pearson hypothesis testing. In Bayesianism, beliefs are quantified in probabilistic terms. P(A|B) is read as “the probability of A given B.”

Vienna Circle was formed by a group of philosophers who are regarded largely as defenders of a deductive vision of science (Uebel 2007). This vision had its crowning moment with the deductive-nomological (DN) model developed by Hempel and Oppenheim in the late 1940s. The “deductive” part of the DN model specified that scientific explanations are deductive arguments in which the phenomenon to be explained, the *explanandum*, is the logical consequence of a set of premises, the *explanans*. The “nomological” aspect of the DN model said that the *explanans* must contain at least one law of nature, *nomos* being Greek for “law.” Accordingly, for any valid deduction, accepting the premises of an argument implies accepting the conclusion. The DN model was criticized from the outset. Not all philosophers

believed that all of science could really be fit into a deductive mold (Uebel 2007). In addition, it is not entirely clear what a “law of nature” actually is, or how to tell one from a generalization or a model (Salmon 1989). Another criticism was that perfectly valid deductions can result in perfectly invalid explanations, e.g., the conclusion that the height of a flagpole is caused by its shadow (see Bromberger 1966). As a result, philosophers quickly got over the notion that science has to be entirely deductive (see, for example, Scriven 1959; Salmon 1989; Ladyman 2002). In the ensuing decades, the DN model has been replaced by a consensus viewing scientific explanations as “loopy” (Sober 2008), not deductive.

To show that studying adaptation cannot be a deductive enterprise, we can compare

TABLE 3

*Examples of the ways that biologists discuss circularity in evolutionary biology and especially in the study of adaptation*

Authors	Year	Quotes
Waterman	1962	"[C]ircularity is inherent in the methodology of science since one must proceed from data to construct or model and thence back to new data or from model to data and back to model again. . . . In a well-developed science a multiplicity of such intersecting circular pathways form a coherent system of consistent relations" (p. 549).
van der Steen and Boontje	1973	A critique of the view that definitions of "homology" in terms of common ancestry represent circularity (homology is manifest as similarity due to common ancestry; common ancestry is inferred due to similarity).
Peters	1976	Because stressful habitats are identified by low species diversity, "the stability-time hypothesis" [which specifies that nonstressful habitats give rise to higher species diversity] cannot be accepted as a scientific theory as it now stands" (p. 10).
Raven	1976	It is circular to infer homology between chromosomes from pairing experiments, and explain pairing because of homology.
Tattersall and Eldredge	1977	"[M]uch of the reasoning that goes into . . . [phylogeny] construction is circular: the many elements involved feed back upon each other in an extremely intricate way" (p. 205).
Stevens	1980	It is circular to use distributions to inform the reconstruction of the phylogenetic relationships between species and then make inferences regarding the evolution of distributions on the basis of the resulting phylogeny (see also Schaefer and Lauder 1986).
Tyler	1986	"[A]ccording to Popper, the difficulty the historical sciences face, whether the biological sciences or the social sciences, is that the systems they study can only be identified through change. And yet it is the changes themselves, rather than the systems, which are the main object of interest. Hence there is an unavoidable circularity in the historical sciences" (p. 727).
Landres et al.	1988	"[C]ircularity arises when using indicators to predict habitat conditions, because the initial choice of the indicator depended on those habitat conditions" (p. 320).
Sage et al.	1993	"Another approach [to test the accuracy of methods of reconstructing the evolutionary relationships between species] has been to use computer simulations to generate evolutionary divergence in sets of genes. These simulated data can be used to evaluate the efficacy of various computer algorithms to reproduce the simulated genetic history. Unfortunately, the assumptions used to simulate the data can often be matched almost exactly by the assumptions of the algorithm used" (pp. 545–546).
Blackstone	1995	"Further, constructing a hypothetical ancestral form by assembling suites of shared primitive characters introduces an element of circularity and can have unintended results such as erecting paraphyletic taxa (e.g., see discussion of the 'hypothetical ancestral mollusk' in Brusca and Brusca 1990)" (p. 786).
Neal et al.	1998	"More sophisticated bees are said to be found on more complex flowers. The argument sometimes becomes circular because the bees are often classified by the flowers they visit, rather than by experimental tests of learning ability" (p. 362).
Pennington et al.	2006	"[S]tudies [of the ages of clades] that rely too heavily on single geological calibrations . . . have been criticized . . . for their circularity" (p. 607).
Waters and Craw	2006	New Zealand inherited its flora and fauna when the great southern landmass Gondwana broke up; this is inferred from New Zealand sharing lineages with other southern landmasses. The similarity is explained by the breakup, the breakup inferred from the sharing of lineages.

"loopy" explanations with what we will call "pattern" explanations. Pattern explanations are considered correct if they conform to a particular structure or pattern (Nagel 1961; Schaffner 1993; Strevens 2008). This is the case of deductive explanations, which must

conform to a pattern given by the rules of formal logic. If an argument conforms to such a pattern, then it is certain that its conclusion is correct (see, for example, Hempel 1965). In contrast to loopy ones, explanations built on deduction do not shore up

TABLE 4  
*How biologists classify evolutionary inference*

Author	Year	Evolutionary biology (mostly the study of adaptation) is. . .	Cites
Ghiselin	1966	“obviously hypothetico-deductive” (p. 210)	Popper
Medawar	1967 (revision of a 1963 original)	hypothetico-deductive	
Ghiselin	1969	“Biology . . . is a hypothetico-deductive, predictive, deterministic, and nomothetic science” (p. xiii, preface to the 1984 edition)	Popper, Mill, Whewell
Williams	1970	deductive	
Platnick and Gaffney	1978	hypothetico-deductive	Popper
Gould	1980	abductive, defined as “the creative grabbing and amalgamation of disparate concepts into bold ideas that could be formulated for testing” (p. 102), but see definition in Table 2	mentions Peirce
Jaksić	1981	hypothetico-deductive	Popper (1959)
Mayr	1982	hypothetico-deductive	Ghiselin (1969) among others; mentions Hempel and Popper
Fisher	1985	hypothetico-deductive, also “strong inference” (p. 131)	Platt (1964)
Calow	1987	hypothetico-deductive	
Bock	1988, 1994	deductive-nomological and “historical-narrative” (p. 205)	
Murray	1992	hypothetico-deductive	Newton, Popper
Thornhill	1996	hypothetico-deductive	Hempel
Anelli	2006	hypothetico-deductive	
Eldredge	2006	hypothetico-deductive	
Ayala	2009	hypothetico-deductive	Popper (1959); Hempel (1965)
McKnight	2009	“hypothesis-driven” with “inductive inquiry” (p. 818)	Ayala (2009)
Sulloway	2009	hypothetico-deductive	Ghiselin (1969)

faith in the underlying assumptions. For example, in the addition of 1+1, the conclusion of “2” does not increase confidence in definitions of what “1” and “+” mean. In real science, conclusions do increase confidence in assumptions (see Lipton 2008), as in the cloudy exoplanet example above, and in Figures 3 and 4. In adaptationist studies, faith in assumptions is clearly a function of how well they explain the data. This quote from Darwin could be a textbook illustration of loopy acceptance of assumptions given their ability to explain the data: “It can hardly be supposed that a false theory would explain, in so satisfactory a manner as does the theory of natural selection, the several large classes of

facts above specified” (Darwin [1876] 2009: 471). Moreover, in real-life studies of adaptation, instead of deductive certainties and ineluctable laws there are at best statistical probabilities and likelihoods (e.g., Scriven 1959; Ruse 1975; Rieppel 2003; Sober 2008). Explanations involving adaptation are thus loopy, not deductive (Figures 3 and 4).

Even though biology cannot be deductive, in the late 1960s biologists consolidated a firm tradition of describing their procedures as “deductive,” ascribing this position to certain philosophers, and have stuck with the practice to the present day (Table 4). Some prominent examples include Ghiselin (1966) and Medawar (1967), both of



whom stated again and again that biology is built on deduction. Their approach was mirrored exactly by Mayr in his influential work *The Growth of Biological Thought* (1982). Gould (1980) even entitled a paper stating the aspiration of paleobiology to become a “nomothetic” discipline. Ghiselin said, echoing Hempel and Oppenheim, that “Biology . . . is a hypothetico-deductive, predictive, deterministic, and nomothetic science” (Ghiselin 1984:xiii). These exact arguments are repeated by biologists to the present, perhaps most prominently by Ayala (2009). Thus, in exactly the period in which philosophers were acutely seeing the limitations of deductive accounts of science and looking beyond them to “loopy” structures, the tradition of citing deduction was hardening in biology and to a large extent remains to this day. In this way, the position in biology regarding deduction has followed a very different trajectory from that in the philosophy of science. However, it is clear that explanations in evolutionary biology, like science in general, are loopy and cannot be built entirely on deduction. What, then, of the “hypothetico-deductive method”?

Myth 2: The hypothetico-deductive method in biology is deductive. Even though biologists very often use the term “hypothetico-deductive method” (Table 4), their use does not really denote a deductive, nonloopy method. As used by biologists, this method consists of three steps. The first is the generation of a hypothesis. In the second, which potentially involves a deductive operation, predictions are generated from the hypothesis. Most often, these are of a nondeductive, probabilistic nature (e.g., “if X is true, then Y should be common”). The third step involves empirically testing the predictions. This step is also not deductive (Table 2). Deciding whether observations conform or not to predictions is always a probabilistic effort. Generating and testing predictions in the context of a hypothesis is a firm part of everyday science, but it results in loopy explanations, never deductively structured ones. In addition to being not deductive, science is also not Popperian.

Myth 3: Science is Popperian. Following a similarly divergent trajectory as statements about deduction, there is a long tradition of

biologists saying that what they do is Popperian (Table 4; Panchen 1992; Holcomb 1996; Sterelny and Griffiths 1999; Haig and Durrant 2002; Ladyman 2002; Rieppel 2003; Morange 2009; Lancaster 2011). Biologists go to great lengths to show that Popper supports one or another position (e.g., Wiley 1975; Platnick and Gaffney 1978; Jaksić 1981; de Queiroz and Poe 2003; Ayala 2009). It is not clear why Popper has been made a “patron saint of science” (Ruse 1979:287), but Ruse (1979, 2005) suggests that it is the simplicity of Popper’s scheme, that the scheme makes scientists look daring and clever, and that it fulfills desires to see progress in science. These considerations notwithstanding, the essence of Popper’s vision was a deductive one, meaning that there is no way that science in general and evolutionary biology particular can be Popperian.

Instead of trying to justify their practices by appealing to the supposed authority of a given philosopher, biologists need to select adaptationist explanations that they consider satisfactory and then dissect the structure of these explanations. If a given structure produces an explanation that is considered satisfactory in the field, then this is the proper starting point for building stronger studies of adaptation regardless of whether they conform to a given philosopher’s stipulation of what science should be (cf. Rieppel 2003). These explanatory structures turn out to be loopy, not Popperian. Biologists also do not use falsification in the sense that Popper intended.

Myth 4: Biologists are Popperian falsificationists. Popper’s falsificationist scheme was a deductive one. Confirming or falsifying hypotheses correspond to two different rules of deductive inference known as *modus ponens* (Latin for “the way that affirms by affirming”) and *modus tollens* (“the way that denies by denying”; see Sober 2008). *Modus ponens* is the idea that if the condition “if P then Q” is true, and P is the case, then Q must be the case (see Table 2 for examples). Contrary to *modus ponens*, *modus tollens* is the idea that if the condition “if P then Q” is true, and Q is not the case, then P cannot be the case. Popper famously said that science proceeds through instances of *modus tollens*, a process

he called falsificationism. His idea was that it makes more sense to proceed via *modus tollens* given that positive predictions or confirmations of particular instances may be hard to come by but disconfirming hypotheses should be more achievable. Either way, Popper envisioned the use of deduction, never statistics.

But most biologists thinking in falsificationist terms use statistics. For example, biologists often identify a set of possible explanations and then use statistical tests to exclude them one by one to see which seems to be the best one (e.g., Templeton 2009). Statistical operations such as hypothesis testing are probabilistic and by definition non-deductive. For Popper, falsification meant constructing a deductive argument using *modus tollens*. Because statistical null hypothesis testing is not deductive, there is a margin for error. This margin for error is quantified via the statistical significance of the test in rejecting a given hypothesis. Statistical significance thresholds are arbitrary, with the choice of  $P < 0.05$  as a threshold for significance being one of convention but not salient from nature. The arbitrariness of these thresholds is one reason why philosopher Elliot Sober notes that there is “no such thing as probabilistic *modus tollens*” (Sober 2008:192). This means that the procedures that biologists use and call falsification (see, e.g., Forber 2011), although an important and accepted part of scientific practice, are definitely not deductive and definitely not Popperian. There is no reason to expect them to be, given the loopiness of real scientific explanation.

Myth 5: Modern evolutionary biology takes a stand against “induction.” In the writings of authors such as Ghiselin (1966, 1969), Medawar (1967), Gould (1980), Mayr (1982), Ayala (2009), and the many who follow them, “induction” is presented as the random collection of facts in the hope that a universal generality will spring unaided from the data. That this is a caricature is revealed by the fact that even these authors admit that no one really proceeds in this way (e.g., Ghiselin 1969:4; Gould 1980:97). In reality, an induction is simply an inference whose conclusions are associated with some level of error (Table 2; in deduction, if the premises

are true, the conclusion is true; Hull 1973; Ladyman 2002). Because all of their conclusions are associated with some degree of uncertainty, every adaptationist study, like science generally, involves some flavor of induction. Statements such as “the confidence interval of the metabolic rate-body mass scaling slope includes  $3/4$ ,” “feathers originally evolved in the context of thermoregulation,” or “the broad sense heritability of this trait is significantly different from zero,” no matter how well supported clearly all involve some degree of uncertainty. All are expressions of induction. Aware that most of science proceeds through induction, philosophers and mathematicians have long been interested in coming up with degrees of certainty or likelihood functions to quantify the relation between evidence and hypotheses (see Popper 1959; Hacking 1976; Sober 1988; de Queiroz and Poe 2003). Being associated with uncertainty, loopy abductive reasoning is usually regarded as a type of induction. “Induction” is not the ingenious “idyll” (Gould 1980:97) that so many authors have made it out to be. Instead, nondeductive, loopy procedures are the heart and soul of science.

To summarize, these “myths” illustrate five important points that might make biologists resist the idea that loopy explanations are the true structure of evolutionary reasoning. 1. The idea that science is deductive has been refuted in philosophy of science since early on but continues, incorrectly, to receive lip service in biology to this day. 2. Much of this lip service is in the form of references to the “hypothetico-deductive method.” In biology this simply means generating hypotheses, deriving predictions from these hypotheses, and testing them. It does not correspond to a purely deductive approach. 3. Popper’s scheme was a deductive one; science in general and evolutionary biology in particular are loopy and so cannot be Popperian. 4. Falsification in biology is not the Popperian version because what biologists call “falsification” is statistical and not the deductive procedure that Popper stipulated. 5. Induction is not random data collection, but instead a type of inference in which the conclusion is associated with some uncer-

tainty, like practically all operations in real science.

These misconceptions have had major consequences for evolutionary biology. Biologists can often be found accusing each other of “circularity” and disqualifying legitimate “loopy” explanations (Table 3; see Hull 1967). A lack of appreciation of loopiness is the only condition that could permit taking the “tautology” of natural selection seriously for so long in evolutionary biology (Peters 1976; Campbell and Robert 2005). The debate regarding adaptationism (e.g., Gould and Lewontin 1979; Orzack and Sober 1994) could only have continued so long because practitioners of comparative, populational, and optimality methods work in isolation. This isolation, in turn, can only exist if biologists regard their individual interdisciplinary approaches as autonomously sufficient for studying adaptation. The perception of autonomous sufficiency is encouraged by the misapplied “deduction” label: if a given method is regarded as being “deductive,” and deduction implies certainty of conclusions, then there is no reason to combine results across adaptationist subdisciplines. It is time for biologists to recognize and value the true “loopy” structure of scientific explanations. It is time to recognize the complementary nature of the data the three adaptationist approaches generate, and forge true cooperation across comparative, populational, and optimality perspectives.

#### HOW TO STUDY ADAPTATION: THE VITAL COMPLEMENTARITY OF COMPARATIVE, POPULATIONAL, AND OPTIMALITY APPROACHES

Although there is no conceptual reason to do so, populational and comparative biologists tend to work in isolation and even criticize each other (Oakley 2009). Quantitative geneticists can be heard accusing their comparative biologist colleagues of studying fitness by “intuition and clairvoyance.” Comparative biologists concede that quantitative genetic studies may be interesting for their detail but note that they can only focus on traits “so trivial” that they have not gone to fixation—surely the aim of evolutionary biology is to account for the great

patterns of trait variation across all of life, and not just inconsequential local variation. As for studies of adaptation from the optimality modeling perspective, they are caricatured as the naive view of inexorable progress to the best of all possible solutions. The result of this mutual aversion is that, for the most part, proponents of comparative, populational, and optimality approaches work separately (Oakley 2009; Hadfield and Nakagawa 2010; cf. Parker and Maynard-Smith 1990; Harvey and Pagel 1991; Falconer and Mackay 1996).

Amid this general separation, adaptationists do occasionally call for integration (e.g., Fisher 1985; Endler 1986; Wake and Larson 1987; Brandon 1990; Leroi et al. 1994; Sinerio and Basolo 1996; Baum and Donoghue 2001; Durrant and Haig 2001; Matos et al. 2004). For example, Larson and Losos (1996) proposed a procedure for testing adaptive hypotheses integrating various layers of direct evidence. Their methodology involves a series of steps sequentially examining trait heritability, trait individuality/quasi-independence, restricted versus ample developmental potential, and comparisons of ancestral versus contemporary selective regimes, as well as documenting the relative performance of variants. Recognizing the “loopy” nature of adaptive explanations makes clear why schemes that integrate multiple lines of evidence generate satisfying results (Figure 3).

Integration provides satisfying results because, rather than one method being superior to another, they in fact provide equally important pieces of the adaptation puzzle, pieces that are moreover complementary (Table 5). They are complementary because important evidence not provided by one method is provided by the others (Table 1, Figure 3). Comparative methods are the only ones that address the true products of real evolutionary diversification in the wild, on evolutionarily relevant time scales beyond the ecological moment. However, the comparative method leaves unexamined the details of heritability, variation, and fitness, details that only populational methods can address. In addition, which variant has higher fitness should be predictable given

TABLE 5

*Comparative, populational, and optimality approaches provide complementary sources of direct evidence regarding hypotheses of adaptation, with none having a more privileged perspective than any other*

	<b>Comparative studies</b>	<b>Populational studies</b>	<b>Optimality studies</b>
Variants present/producible in ancestral populations	no direct evidence	no direct evidence	no direct evidence
Variants were heritable/assimilable in ancestral populations	no direct evidence (but note the loopy assumptions regarding heritability in the case of synapomorphy)	no direct evidence	no direct evidence
Variants differed in fitness in ancestral populations	no direct evidence	no direct evidence	no direct evidence
Variants differed in performance in ancestral populations	no direct evidence	no direct evidence	no direct evidence
Intrapopulational variants currently produced/producible	no direct evidence	study variation across populations within a species, additive genetic variance	no direct evidence
Intrapopulational variants are currently heritable	no direct evidence	quantitative genetic measurements of heritability	no direct evidence
Intrapopulational variants vary in fitness	no direct evidence	studies of survivorship, mating success, fecundity, response to selection	no direct evidence
Population-level processes plausibly produce interspecific patterns	cross species organism-environment or trait-trait (allometry) relationships	no direct evidence	no direct evidence
Difference in performance understandable based on functional generalizations, engineering principles	no direct evidence	no direct evidence	the optimality approach broadly construed is required for thinking in terms of functional generalizations
Variants fill morphospace evenly or there are constraints that may, even in the absence of selection, lead to patterns of trait association	studies of how species fill morphospace, including comparative embryology	studies of how variants natural and induced, including teratologies, fill morphospace; artificial selection	predict the range of morphologies that should be observed; may predict "holes" in morphospace
Trait (quasi-) independence (i.e., the trait is a "part" that can be subject to selection)	study how traits vary independently across species	study how traits vary independently in ontogeny, G matrix	explicit focus on functionally coupled and competing traits
Current utility/function	compare performance of different character states	compare fitness of variants in a population	generate explicit expectations regarding performance differences between variants
Arose for its current function in its current selective context	compare performance of apomorphic state in current selective context with plesiomorphic state	no direct evidence	no direct evidence

considerations of biomechanical performance or energetic efficiency. The only method that examines this aspect directly is the optimality approach. All of these aspects, including the patterns of trait distribution across clades and continents, population-level processes, and optimality considerations, are essential for a maximally supported adaptationist explanation (summarized in Table 5). Intensive studies from just one of these points of view cannot provide all of the layers of direct evidence needed to diminish the relative importance of loops of “circular” reasoning caused by acceptance of assumptions about the unobservable past (Figures 3 and 4; Griffiths 1996; see also Figure 3 of Ruse 1975). The shortcomings of each method are almost perfectly filled by the strengths of the others (cf. Ghiselin 1969:21; Forber and Griffith 2011). As a result, the best-supported adaptationist explanations have not just an abundance of information, but information carefully drawn from across the three adaptationist approaches.

Maximally supported adaptationist explanations require evidence from comparative, populational, and optimality approaches. This requirement highlights from the outset which adaptationist studies are likely to have fewer layers of direct evidence available. Studies of single species or unique structures are important examples. Such traits cannot be studied using comparative approaches, because the putatively adaptive states are unique (cf. Maddison and FitzJohn 2015). When the traits are fixed within populations, the typical tools of populational studies are unavailable. In humans, experimental methods such as surgical intervention or selective breeding are unethical (Ruse 1979). As a result, many aspects of humans continue to be debated, such as the female orgasm, human language, or rape (Travis 2003; Lloyd 2005; Nielsen 2009; MacColl 2011). To the extent that less information is available, in many cases it will continue to be hard to distinguish between different alternative explanations to decide which is the likeliest (Forber 2009). By asking what information is ideally needed to generate a given explanation, a maximally robust explanation can be constructed. Because its history is so vexed

and it is of such broad interest, we have focused on adaptation here. However, a similar search for the optimal combination of layers of direct evidence can be used to guide the effort to turn any evolutionary just-so story into a well-supported explanation.

#### EXTERNALIST VERSUS INTERNALIST JUST-SO STORIES

The traditional perspective of the Modern Synthesis is that variation is ample and observed morphologies represent the winning effects of selection (Amundson 1994; Jablonka and Lamb 2005). Because environmental factors “external” to the organism are viewed as determining which variants prosper, this adaptation-driven view is often referred to as externalism. In contrast, internalism is the notion that interactions between parts of developmental systems are such that developmental possibilities are severely limited and therefore the domain of action possible for natural selection is quite restricted (Alberch 1989). Up to now, we have focused on externalist just-so stories.

Internalist just-so stories are, however, just as easy to tell (Figure 2). Likewise, internalist explanations can be constructed just as robustly as externalist ones (Sober 1996). In fact, because examining developmental potential is essential for testing adaptationist hypotheses (Table 5), and because ruling out an externalist explanation is essential for shoring up an internalist one, the externalist and internalist approaches are both necessarily built in to a maximally robust loopy explanation and really not separate perspectives at all (cf. West-Eberhard 2003; Schwenk and Wagner 2004).

Whether starting from an internalist or an externalist perspective, biologists test the developmental accessibility of apparently empty patches of morphospace (e.g., above and below the line in Figure 2) via a number of approaches (Olson 2012). These include detailed studies of embryology and artificial selection or other types of manipulation (Sinervo and Basolo 1996; Bell 2008; Frankino et al. 2009; Vedel et al. 2010). Comparative studies can pit the performance or fitness of species with different character states against each other in different selective



contexts (Larson and Losos 1996; Losos 2011). Finding that developmental possibilities are sufficiently wide as to permit many other possible trait combinations, and that the “empty space” morphologies are inferior in performance, are findings that help shore up the idea that a pattern is an adaptive one. Developmental potential is thus a central part of any adaptation based explanation (cf. Forber 2010).

These detailed depictions of possible developmental variation, and study of the relative performance of variation natural and constructed, helps overcome the constraint-adaptation dichotomy. A move away from a simple constraint-adaptation dichotomy is one of the most promising aspects of loopy explanations built on a correct selection of sources of evidence. Moving away from the dichotomy is in part desirable because the vagueness of the term “constraint” makes it of little use in evolutionary thinking (see the catalog of meanings in Olson 2012). More importantly, the dichotomy is unacceptable as an explanatory formula because both selection and constraints, whatever the definition used, are involved in the generation of any given pattern in nature (Fusco 2001; West-Eberhard 2003; Schwenk and Wagner 2004; Minelli 2009; Badyaev 2011). For example, although selection might cull from the possible, resulting in a narrow range of commonly observed morphologies, as in Figure 2, factors such as minimum developmentally possible cell dimensions can limit the domain of the possible (see, for example, Amundson 1994). As a result, it is meaningless to ask whether the pattern in Figure 2 is “caused by adaptation or constraint” because every pattern in the living world is the result of both, however “constraint” is defined. By showing the way explicitly away from this unsatisfactory dichotomy with clear questions and a battery of empirical tools, studies that draw on multiple layers of direct evidence provide ever more satisfactory explanations of organismal form. One reason that these explanations are so satisfactory is that, when detailed information regarding the causes of a given pattern are available, dichotomous classing of “adaptation versus constraint” is unnecessary and uninformative

(e.g., Malagón et al. 2014). Correctly representing the way that robust explanations are constructed also should improve public understanding of science.

#### EMBRACING LOOPINESS: IMPROVING SCIENTIFIC PRACTICE AND THE COMMUNICATION OF EVOLUTION

That adaptationist explanations are necessarily loopy helps reorient discussions of “circularity” in evolutionary biology. It sheds light on the long tradition of accusing the entire study of adaptation as resting on tautology, i.e., circular reasoning. A popular version of this criticism goes that natural selection is the survival of the fittest, and the fittest are those that survive. The phenomenon to be explained is part of the premises, thereby rendering the formulation circular (Peters 1976; Bowler 1984). When the loopy structure of evolutionary explanation is recognized, the debate over adaptationism as a tautology appears to be predicated on the incorrect interpretation of “loops” as fatal flaws rather than natural and necessary. An explanation involving adaptation includes many more layers than just “fit” and “survival” (Hull 1969). As in any evolutionary explanation, loops of reasoning are present, e.g., the form-function fit is explained by selection and selection is identified as an important process because of the global form-function fit. The situation in Figure 3B, even though it includes “loops,” is hardly a tautology. In fact, across evolutionary biology at large, most of the accusations of “circularity” that biologists sling at each other almost always simply refer to loops of reasoning in abductive/Bayesian reasoning (Table 3).

Rather than accusing one another of circularity whenever “loops” are detected, biologists can more profitably discuss how rickety a reasoning loop is versus how well supported it might be, and what additional data would be desirable. In Table 3, the statements of Waterman (1962) and Tattersall and Eldredge (1977) are very close to the account we offer here. Most of the accusations of circularity in Table 3 bear reevaluating, to ask whether they might be reasonable “loopy” explanations that await testing via the accumulation of more layers of direct

evidence, moving them from the situation in Figure 3A to that in Figure 3B. For example, Neal et al. (1998; Table 3) discussed ways that floral morphology, scent, and rewards fit with pollinators. They noted that “sophisticated” bees, understood as those with greater manipulation skills, learning ability, or sensory perception, are often said to pollinate more complex and difficult-to-negotiate flowers. The problem is that some bees are identified as “sophisticated” precisely because they pollinate complex flowers. This reasoning certainly sounds circular. However, additional layers of direct evidence can be generated to see how well the explanations, assumptions and all, fit the observed patterns (see also Nielsen 2009; O’Malley and Koonin 2011). Neal et al. (1998) suggest that independent tests of learning ability of bees should be compared with floral complexity to see if there is a correspondence. Such studies could be conducted across species, within populations with floral variation, or even with artificially manipulated flowers. Any of these could potentially strengthen the sophisticated bee-complex flower hypothesis. This means that there is nothing flawed about the structure of the hypothesis, just that it is in a preliminary stage. Some examples might be more perniciously circular. Using assumptions to simulate data for validating a method built with those same assumptions might be such a case (Sage et al. 1993 in Table 3). By recognizing the loopy structure of evolutionary explanation, biologists can more effectively guide efforts to distinguish flawed reasoning from legitimately loopy explanations.

The lack of clarity regarding the loopy structure of adaptationist explanations not only affects science but also the way biologists present evolutionary biology to the public at large. That scientists lack clarity regarding the structure of the explanations that they themselves strive to construct has exacerbated public misunderstanding of how science works. Prominent authors have been implying for decades that evolutionary biology proceeds via deduction (e.g., Ghiselin 1966; Ayala 2009), and therefore produces deductive certainties. This entrenched tradition has in many ways played into the hands

of critics, such as advocates of intelligent design (Oakley 2009; Lancaster 2011). Public demands for certain “proof” and criticism of “circularity” in debates over evolution (and others such as global climate change) are fueled by the notion that science produces deductive certainty, almost always failing to take into account the loopy nature of the legitimate explanations in these fields.

#### CONCLUSION

Studies of adaptation necessarily require the sort of loopy reasoning depicted in Figure 3B (Holcomb 1996). Recognizing how adaptationist explanations are structured in actual practice helps give clarity to problems that have plagued biology, such as debates over tautology/circularity, and resolve false conflicts, such as the mutual scorn that often characterizes the adherents of the comparative, population/quantitative genetics, and optimality approaches (e.g., Calow 1987; Leroi et al. 1994; cf. Zimmermann 1983:2 with Haberlandt 1914:12). Instead, as providers of complementary sources of direct evidence, no single approach has a monopoly on tests of adaptation (Table 5). An understanding of the real, loopy structure of evolutionary explanation encourages biologists to discuss truly substantial issues awaiting attention, such as how to identify the population of hypotheses from which to select the “best” explanation (Forber 2010), how scientists know the best explanation when they see it, what observations most need explaining, or how best to weave disparate sources of evidence into a single explanation. By accepting that studies of adaptation require multiple types of direct evidence, evolutionary biologists can improve current research practice by implementing a long-overdue integration of comparative, populational, and optimality approaches.

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