HOW TO STUDY ADAPTATION AND WHY TO DO IT THAT WAY: ADAPTATION, JUST SO STORIES, AND CIRCULARITY

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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 induction. 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.

KEY WORDS

abduction, induction, comparative methods, deduction, optimality models, population biology

INTRODUCTION

Some inferences of adaptation are accepted as solid, almost without question. Many are dismissed as just-so stories, while others are accused of being riddled with circularity. Here we outline the difference between a just-so story and a solid, widely accepted adaptationist explanation. We also 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 in popular statistical methods such as 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 strategies, before turning how to structure maximally supported explanations of the striking fit between form and funtion across the living world.

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 (as Gould and Lewontin 1981); Hull 2001; Hall 2002; Travis 2003 (as Gould and Lewontin 1970); Sosis 2009; Frost-Arnold 2010 (as Gould and Lewontin 1978)), even by Gould himself (1997, 2002). However, the *Spandrels* paper makes no mention of Kipling and does not use the "just-so story" term, though other essays by Gould (1977, 1978, 1997, and 2002) do. Just-so stories are of interest here because they help explore how an adaptationist explanation that is little trusted is constructed, and thus show the way to one that is 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 do 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, and so all giraffes have long necks. Based only on the trait "long neck" and that the necks are 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 an environment 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 (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 (McVaugh and Rzedowski 1965). MacColl (2010) 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 disciplinary 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 illustrate how to construct more robust adaptive 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, icthyosaurs, eurypterids, or squids. Convergence thinking finds a quantitative expression in methods that seek statistical relationships 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 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 all have the "circular" structure shown there. Similar things happen with the other adaptationist approaches.

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 heritable, 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 are detailed studies of very geographically and temporally 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 like plant or animal breeding, in which humans wish to produce a given selective response in a given time. 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. For example, fluid mechanics can be applied to study the morphology of fish. Because as they swim fish ram their heads through the water, pressure is positive there, but it becomes negative along their flanks. In between the sites of positive and negative pressure there is an area of relatively neutral pressure. Because a fish's vision could be affected if its eye is distorted by negative or positive pressure, selection would be predicted to favor individuals with eyes positioned at this neutral point. This it seems to do (Dubois et al. 1973; Vogel 2003). Predicting the optimal position for eyes can take into account not only the distribution of pressures about the body but also features such as the minimization of distance to the brain or the maintenance of a given visual field. 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). In the fish eye case, the performance criterion corresponds to undistorted vision. Coincidence between optimality predictions and nature by chance and not via the action of selection seems very unlikely.

However unlikely that model-nature coincidence not be the result of selection, 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 non-adaptive process is regarded as so unlikely that the trait must be due to selection (Orzack and Sober 1994). Based only on coincidence between nature and model, an adaptationist explanation takes the form that the there is 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.

Whether comparative, populational, or optimality, all 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. As we will show, though, even the best-supported explanation still involves "circularity."

While "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). Selection on this variation is assumed to have led to the pattern observed today (Figure 3B). All adaptationist explanations at some point invoke and accept 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 population 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 fins in aquatic ones seem 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 example from astronomy is an excellent example of loopy reasoning: "The 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 p. 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 exactly analogous to that in Figure 3B, loops and all.

Loopiness is well documented by philosophers of biology. Griffiths's (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 explanations. 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. ifferent authors have proposed epistemic and quantitative criteria for evaluating abductive statements (for a review see Douven 2011; also Scriven 1959), 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 embrace "loopiness" is motivated not so much by the need to tag adaptationist reasoning as "abductive," "Bayesian," or any other term, but because this recognition 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 in the philosophy of science. It is news, though, 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 saying that their science is deductive, non-loopy, and even Popperian. The next section gives a little more detail for these readers.

FIVE MYTHS OF HYPOTHETICO- DEDUCTIVE EVOLUTIONARY BIOLOGY

The arguments above contradict more than 50 years of biological tradition. Evolutionary biology has a longstanding custom of regarding all forms of "circularity" with suspicion, 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 the 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 the philosophy of science. Because these traditional positions of biologists might cause resistance in 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 Vienna circle was formed by a group of philosophers also called logical positivists (Uebel 2007). Despite some diversity in their ranks regarding their view of what science ought to be, logical positivists have come to be regarded as defenders of a deductive vision of science. This vision had its crowning moment with the deductive-nomological model (DN model) developed by Carl Hempel and Paul 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, called the *explanadum*, is the logical consequence of a set of premises, called 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". The DN model was criticized from the outset. Not all philosophers of the time believed that all of science could really be fit into a deductive mold. 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. 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 got over the notion that science has to be entirely deductive quite quickly (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" (Salmon et al., Sober 2008), not deductive.

To show that studying adaptation cannot be a deductive enterprise, we can compare "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 2009). 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 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 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). Moreover, in adaptationist studies, faith in assumptions is a function of how well they explain the data (see Lipton 2008). For example, 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 p. 471 6th edition of the Origin). Explanations involving adaptation are thus not deductive, but instead "loopy" ones (Figure 3).

Even though biology cannot be deductive, in the late 1960s biologists began a firm tradition of describing their procedures as "deductive" and stuck with it to the present day. Some prominent examples include Ghiselin (1966) and Medawar (1967), both of whom persuasively stated again and again that biology is built on deduction (Medawar 1967). Their approach was mirrored exactly by Mayr in his influential 1982 *Growth of Biological Thought.* Gould (1980) even entitled a paper stating the aspiration of paleobiology to become a "nomothetic, evolutionary discipline." In the 1984 preface to his 1969 book, Ghiselin said, echoing Hempel and Oppenheim, that "Biology…is a hypothetico-deductive, predictive, deterministic, and nomothetic science" (p. xiii). These exact arguments are repeated by biologists to the present day, 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.

The position in biology regarding deduction has thus 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, cannot be built entirely on deduction. What, then, of the "hypothetico-deductive method"?

Myth 2: The hypothetico-deductive method is deductive. Even though biologists very often use the term "hypothetico-deductive method," their use does not really denote a wholly deductive method. As used by biologists, this method consists of three steps. The first the generation of a hypothesis. In a second, which potentially involves a deductive operation, predictions are generated from the hypothesis. Most often, these are of a non-deductive, 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. While the hypothetico-deductive method does describe scientific practice well, it never results in a deductively structured explanation, but instead a loopy one. In addition to being not deductive, it 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 3; Panchen 1992, Holcomb 1996, Sterelny and Griffiths 1999, Sober 2000, 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, Platinick and Gaffney 1975, Jaksić 1981, de Queiroz and Poe 2003, Ayala 2009, etc.). It is not clear why Popper has been made what Ruse 1979 calls a "patron saint of science" (p. 287), but Ruse (1979, 2005) suggests that it is the simplicity of Popper's scheme, that it makes scientists look daring and clever, and that it fulfills the 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.

Myth 4: Biologists are Popperian falsificationists. Popper's falsificationist scheme is 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"). *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. A well-known example of modus ponens is: If it rains then the floor will get wet. It rains, thefererore, the floor wil get wet (see TABLE 2). Contrary to *modus ponens, modus tollens* is the idea that if the condition If P then Q is true but Q is not the case, then P cannot be the case. Under *modus tollens* the previous example would be: If it rains then the floor will get wet but given that the floor is not wet, then it must be the case that it has not rained. Popper famously said that science proceeds through instances of *modus tollens,* a process he called falsificationism. His idea was that, given that it is very difficult to amass enough evidence to make valid inferences via *modus ponens*, 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 via experimentation is not. Either way, Popper envisioned the use of deduction, never statistics.

However, 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 one seems to be the best one (e.g. Templeton 2009). These 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 hypothesys. 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. These arbitrary thresholds are one reason why philosopher Elliot Sober notes that there is "no probabilistic *modus tollens*" (Sober 2008). This means that the procedures that biologists use and call falsification (see e.g. Forber 2011), while an important and accepted part of scientific practice, are definitely not deductive and definitely not Popperian.

Myth 5: Modern evolutionary biology's stand against "induction." In the writings of authors such as Ghiselin (1966, 1969), Medawar (1967), through Gould (1980) and Mayr (1982), to Ayala (2009), and others, "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, in fact, proceeds in this way (e.g. Ghiselin 1969 p. 4, Gould 1980 p. 97). In reality, an induction is simply an inference whose conclusions are associated with some level of error (remember that in deduction, if the premises are true, the conclusion is true; see Table 2 for a comparison of inference types; see for example Hull 1973, Ladyman 2002). Most of our daily work in biology deals with measuring the strength of inductive conclusions using, for example, probabilities. Aware of the fact 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 our evidence and its underlying hypotheses (see Popper 1959; Hacking 1976; Sober 1988; de Queiroz and Poe 2001). Loopy reasoning is usually regarded as a type of induction. This means that "induction" is not the ingenuous "idyll" (Gould 1980) that so many authors have made it out to be. Instead, non-deductive, loopy procedures are the heart and soul of science.

To summarize, these "myths" illustrate five important points that cause confusion regarding the role of deduction in evolutionary biology. 1. The idea that science is deductive has been contested 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 a purely deductive approach. 3. Popper's scheme was a deductive one; science in general and e-bio in particular, are loopy and so cannot be Popperian. 4. Falsification in biololgy is not Popperian 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 uncertainty, like practically all operations in real science.

　　　Even though biologists say that biology is deductive and Popperian, when they describe how scientists work they usually accurately describe actual biological practice, loops and all. It could be argued that there is no real problem if biologists simply apply the wrong name to loopy procedures. But biologists really do accuse each other of "circularity" in the context of legitimate "loopy" explanations (Table Circ). A lack of appreciation of loopiness is the only condition that could permit taking the "tautology" of the theory of natural selection seriously for so long in evolutionary biology (taut cites). The debate regarding adaptationism (e.g. Gould and Lewontin 1979) 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 parochial approaches as sufficient for studying adaptation. These are all aspects that are encouraged by the misapplied "deduction" label. It is time to 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 it is time to forge true cooperation across comparative, populational, and optimality perspectives.

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

Though there is no conceptual reason to do so, populational and comparative biologists tend to work in isolation and even deride each other (Oakley 2010). Quantitative geneticists can be heard accusing their comparative biologist colleagues of being guilty 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 ingenuous view of inexorable progress to the best of all possible solutions. The result of this mutual hostility is that for the most part, proponents of comparative, populational, and optimality approaches work separately (Hadfield and Nakagawa 2010; Oakley 2010; cf. Parker and Maynard-Smith 1990; Harvey and Pagel 1991; Falconer and Mackay 1996). Amid this general separation, biologists do occasionally call for integration (e.g. Fisher 1985; Endler 1986; Wake and Larson 1987; Leroi et al. 1994; 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 being in competition with one another, the methods in fact provide equally important aspects of the adaptation puzzle, aspects 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 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 process, 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, 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. Forber and Griffith 2011, Ghiselin 1969[p 21]). 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.

Recognizing that adaptationist explanations require evidence from comparative, populational, and optimality approaches to be maximally supported helps explain why some adaptive studies that biologists would like to make are particularly sticky. Studies of single species or unique structures are an important example. Such traits can't be studied using comparative approaches, because the putatively adaptive states are unique. 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). Adaptive studies of unique features are not impossible, as some have charged (see Durrant and Haig 2001). It is simply that many sources of direct evidence will remain unavailable. 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. 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 winnowing 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.

However, internalist just-so stories are just as easy to concoct (Figure 2). Likewise, internalist explanations can be constructed just as robustly as externalist ones. 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. 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). Such studies include detailed studies of embryology and artificial selection (Bell 2008; Frankino et al. 2010; 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 (Baum and Larson 1991; Larson and Losos 1996; Losos 2011). Finding that developmental possibilities are sufficiently wide as to permit many other possible trait relationships, and that the "empty space" morphologies are inferior in performance, are findings that help shore up the idea that the pattern is an adaptive one. Developmental potential is thus a central part of any adaptation based explanation.

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 perhaps the most promising aspect 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, while selection might cull from the possible, resulting in a narrow range of commonly observed morphologies (say 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. Recognizing 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 inferences of adaptation 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, 1989). 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 involves many more layers than just "fit" and "survival" (Hull 1969). As in any evolutionary explanation, "circular" loops of reasoning are present, e.g. the form-function fit is explained by selection and that selection is identified as an important process because of the global form-function fit. A well-supported explanation gives abundant evidence to accept them (Figure 3). The situation in Figure 3B, even though it includes "loops," is hardly a tautology. In fact, across evolutionary biology at large, most of the accusation of "circularity" that biologists sling at each other almost always simply refer to "loops" of reasoning in abductive/IBE/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 offered here. Many of the other 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 the pollinators that visit the flowers. 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 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. Some examples might be more perniciously circular. Using the same assumptions to simulate data to validate 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.

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. Assurances that science produces deductive certainties has in many ways played into the hands of critics, such as advocates of intelligent design (Oakley 2010; Lancaster 2011 Barnes and Church 2013). Public demands for "proof" and criticism of "circularity" in debates over evolution (and others such as global climate change) almost always fail to take into account the loopy nature of the legitimate explanations in these fields.

CONCLUSION

Studies of adaptation would necessarily seem to 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 p. 2 with Haberlandt, 1914 p. 12). Instead, as providers of complementary sources of direct evidence, no single approach has a monopoly on tests of adaptation. 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, how scientists know the best explanation when they see it, or how best to weave disparate sources of evidence into a single explanation. By accepting that studies of adaptation require multiples types of direct evidence, evolutionary biologists can improve current research practice by designing a compelling and long-overdue integration of comparative, populational, and optimality approaches.

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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

	Definition	Advantages	Disadvantages	key assumption
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 time spans 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/ peformance 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 many species and large time scales unproven	Population-level processes are isomorphic with the factors 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 the model or not	Adaptation is the only plausible explanation for trait optimality

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. A. _____ Then B.	If it rains the floor is wet. It rains. _____ The floor is wet.	Pattern
Induction	Numerous observations from numerous sources such as experimental results, statistical analyses, previous information, etc. strengthen the cogency of a conclusion	If A then *probably* B. A. _____ _____ Then *probably* B.	80% of the time, when it rains, the floor gets wet. It rains. _____ _____ 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. B. _____ _____ Then A.	The floor is wet. If it rained, then the floor being wet would be a matter of course. It rained. _____ _____ 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	$P(A|B) = \dfrac{P(B|A)*P(A)}{P(B)}$	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 characterized by 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 non-truth preserving arguments, such as those that are upheld by probability and loopy reasoning. Inductive arguments are not necessarily probabilistic as there are many different ways to compute the strength of the 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's hypothesis testing. In Bayesianism, beliefs are quantified in probabilistic terms. $P(A|B)$ is read as "the probability of A given B".

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	"…circularity 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 non-stressful 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	"…much 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	"…according 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. 726
Landres et al.	1988	"…circularity 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." p. 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
Pennington et al.	2006	"…studies [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 NZ sharing lineages with other southern landmasses. The similarity is explained by the breakup, the breakup inferred from the sharing of lineages

TABLE 4

How biologists classify evolutionary inference

Author	year	Evolutionary biology (mostly the study of adaptation) is…	Cites
Ghiselin	1966	"obviously hypothetico-deductive"	Popper 1962
Medawar	1967	hypothetico-deductive	
Ghiselin	1969	Biology…is a hypothetico-deductive, predictive, deterministic, and nomothetic science (p. xiii 1984 edition)	Popper 1965, etc.
Williams	1970	deductive	
Platnick and Gaffney	1978	hypothetico-deductive	Popper 1972, 1976
Gould	1980	abductive, defined as "the creative grabbing and amalgamation of disparate concepts into bold ideas that could be formulated for testing"	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"	Platt 1964
Calow	1987	hypothetico-deductive	
Bock	1988, 1994	deductive-nomological and historical-narrative	
Bowler	1989	hypothetico-deductive	
Murray	1992	hypothetico-deductive	Newton 1729; Popper 1968, 1972
Thornhill	1995	hypothetico-deductive	Hempel 1966
Anelli, Eldredge	2006	hypothetico-deductive	
Ayala	2009	hypothetico-deductive	Popper 1959, 1963; Hempel 1965
McKnight	2009	"hypothesis-driven with inductive inquiry"	Ayala 2009
Sulloway	2009	hypothetico-deductive	Ghiselin 1969

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

	comparative studies	populational studies	optimality studies
variants present in ancestral populations	no direct evidence	no direct evidence	no direct evidence
variants were heritable in ancestral populations	no direct evidence	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, etc.	no direct evidence
intrapopulational variants are currently heritable	no direct evidence	quantitative genetic measurements of heritability, etc.	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 performace understandable based on functional generalizations, engineering principles, etc.	no direct evidence	no direct evidence	the optimality approach broadly construed is required to deploy thinking in terms of functional generalizations
variants fill morphospace evenly or there are constraints that may lead to patterns of trait association	studies of how species fill morphospace, incl. 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

Following the notion of adaptation of Gould and Vrba (1982) and Larson and Losos (1996); other definitions of adaptation will lead to different sets of criteria
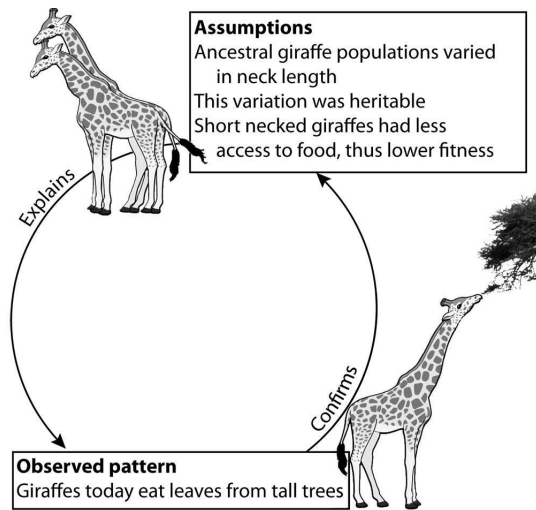
FIGURE 1. CIRCULARITY AND THE GIRAFFE NECK JUST-SO STORY
Giraffes in present day populations use their long necks to reach leaves from tall trees. The presence of long necks is explained as the result of unobserved and unobservable selection in ancestral populations in the distant past. It is assumed 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 use their necks to reach food from tall trees. The selective scenario in turn explains why girafffes have long necks. An adaptationist scenario with little direct evidence beyond the pattern to be explained is known as a just-so story.
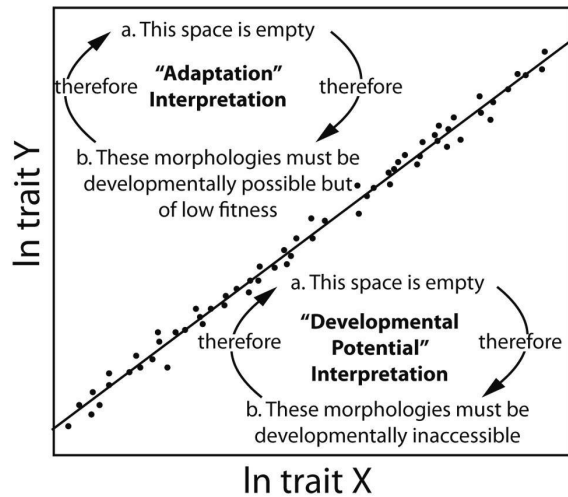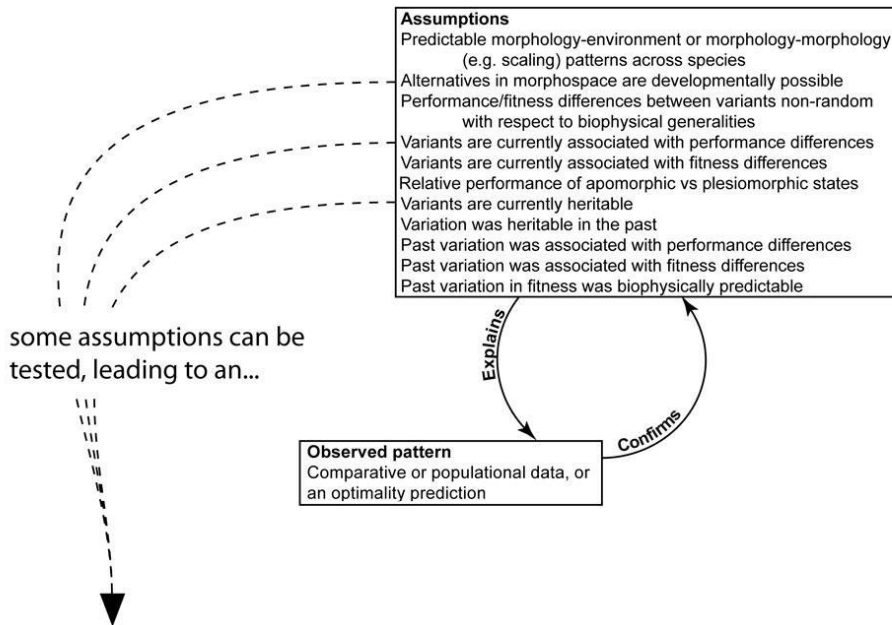
FIGURE 2. ADAPTATIONIST EXPLANATIONS AND CIRCULARITY, GENERAL CASE
Points on the graphs refer to mean species trait values, and the line an allometric regression fit.
The "scaling as adaptation" view sees the entire space defined by the mean values as potentially
accessible in ontogeny, but that the configurations corresponding to the empty spaces are
eliminated by selection. The view of scaling as reflecting limited developmental potential 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. This example is a comparative one, but similar "loops" of reasoning are found in
population and optimality methods as well. The means to strengthen these "circular" inferences
is via additional layers of evidence (see Figure 3).

A. Adaptationist explanation based on very little direct evidence

Assumptions
Predictable morphology-environment or morphology-morphology (e.g. scaling) patterns across species
Alternatives in morphospace are developmentally possible
Performance/fitness differences between variants non-random with respect to biophysical generalities
Variants are currently associated with performance differences
Variants are currently associated with fitness differences
Relative performance of apomorphic vs plesiomorphic states
Variants are currently heritable
Variation was heritable in the past
Past variation was associated with performance differences
Past variation was associated with fitness differences
Past variation in fitness was biophysically predictable

some assumptions can be tested, leading to an...

Explains

Confirms

Observed pattern
Comparative or populational data, or an optimality prediction

B. Adaptationist explanation based on abundant direct evidence

Direct Evidence
Comparative evidence (across species):
Interspecific allometry/scaling
Alternatives in morphospace are developmentally possible
Distribution of taxic homologies suggests inheritance from a common ancestor
Apomorphic state performs better in current selective environment than plesiomorphic state

Populational evidence (within species):
Variants are developmentally possible, "normal" to "pathological"
Variants are heritable
Variants have performance/fitness differences

Evidence from optimality models
Performance/fitness differences between variants are understandable based on biophysical considerations

Assumptions (the unobserved and unobservable)
Past variation was heritable
Past variation was associated with performance differences
Past variation was associated with fitness differences
Past variation in fitness was biophysically predictable

Together explain

Confirms

Observed pattern
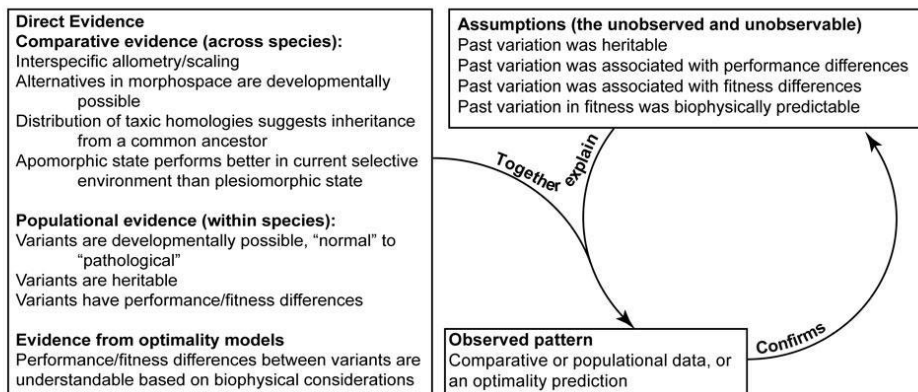Comparative or populational data, or an optimality prediction

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 etc., 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 inferences of adaptation persists even when abundant direct evidence is available. Inferences of adaptation 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 inferences 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.
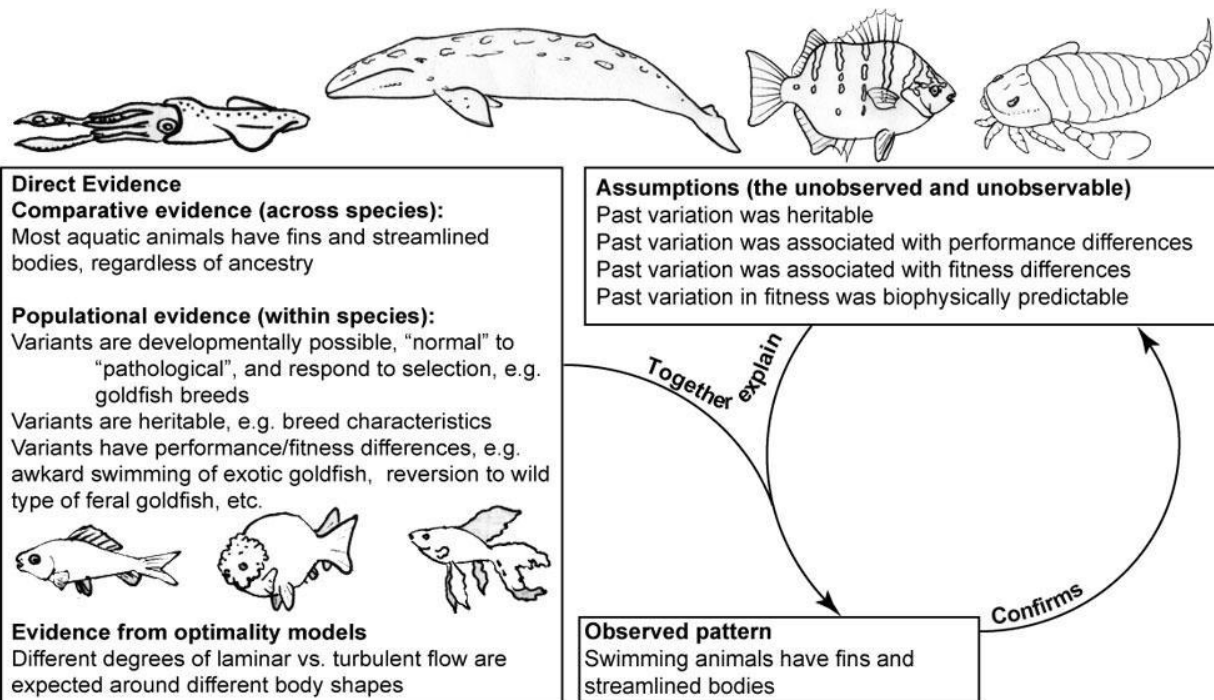
FIGURE 4. THE "LOOPY" STRUCTURE OF ADAPTATIONIST EXPLANATIONS: THE FINS AND FUSIFORM BODIES OF AQUATIC ANIMALS

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 disciplinary 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.