

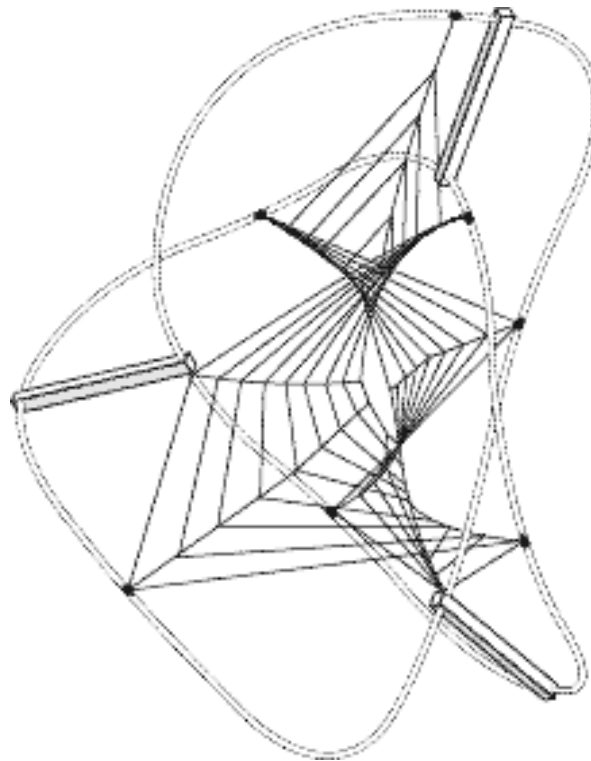
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*Common Ancestry and Natural Selection*

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# Common Ancestry and Natural Selection\*

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## **Abstract**

We explore the evidential relationships that connect two standard claims of modern evolutionary biology. The hypothesis of common ancestry (which says that all organisms now on earth trace back to a single progenitor) and the hypothesis of natural selection (which says that natural selection has been an important influence on the traits exhibited by organisms) are logically independent; however, this leaves open whether testing one requires assumptions about the status of the other. Darwin noted that an extreme version of adaptationism would undercut the possibility of making inferences about common ancestry. Here we develop a converse claim—hypotheses that assert that natural selection has been an important influence on trait values are untestable unless supplemented by suitable background assumptions. The fact of common ancestry and a claim about quantitative genetics together suffice to render such hypotheses testable. Furthermore, we see no plausible alternative to these assumptions; we hypothesize that they are necessary as well as sufficient for adaptive hypotheses to be tested. This point has important implications for biological practice, since biologists standardly assume that adaptive hypotheses predict trait associations among tip species. Another consequence is that adaptive hypotheses cannot be confirmed or disconfirmed by a trait value that is universal within a single species, if that trait value deviates even slightly from the optimum.

# 1 Two Darwinian Hypotheses

Modern Darwinian theory<sup>1</sup> contains the following two tenets:

- *The Tree of Life Hypothesis*: All organisms now on earth have a common ancestor.
- *The Hypothesis of Natural Selection*: Natural selection was an important cause of the similarities and differences exhibited by the organisms now on earth.

We believe that this theory is best understood as an historical hypothesis about life on earth; it does not fingo hypotheses about the laws of life that must apply everywhere and at all times. The theory does not say that *every* planet is such that the life forms found there trace back to a common ancestor nor does it say that the organisms on *all* planets must have been strongly influenced by natural selection. Darwinian theory and 'universal Darwinism' (Dawkins [1983]) are different. We'll return to this point shortly.

The tree of life hypothesis is located at one end of a continuum. It asserts that there is a *single* ancestor shared by all present day organisms on earth.<sup>2</sup> At the other end of the continuum is the hypothesis that every species now alive is the result of a separate origination event. Special creationists endorse this claim, but it needn't be given a formulation in terms of intelligent design. Other phylogenetic hypotheses can be located in between these two extremes; one might claim, for example, that all animals are related and that all plants are too, but that plants and animals are not. Although Darwin did present an argument for a single origin, he usually maintained a careful agnosticism on whether current life traces back to a few forms or to one.<sup>3</sup>

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<sup>1</sup>By 'modern Darwinian theory,' we mean the standard Modern Synthesis conception; whether this is exactly the theory that Darwin himself endorsed is open to question as we will explain.

<sup>2</sup>This does not mean that life originated just once; it may have had multiple start-ups, if all but one went extinct. Also, we do not construe the Tree of Life Hypothesis to mean that there is a single phylogenetic *tree* in the strict sense of that term. A tree is a structure that splits but never joins as one moves from root to tips. Species that arise by hybridization or experience a great deal of horizontal transfer do not form phylogenetic trees, but they still can trace back to a single common ancestor.

<sup>3</sup>For Darwin's argument for a single progenitor, see Darwin([1859], p. 484). However, the famous closing paragraph of the *Origin* describes the 'grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one'

Many current biologists are less hesitant; the hypothesis of a single common ancestor is often regarded as strongly supported by the near-universality of the genetic code (an argument we will consider shortly) and by other universals of biochemistry (e.g., the fact that all amino acids found in proteins are left-handed).

The second component of Darwinian theory - the hypothesis of natural selection - also occupies a position on a continuum, one that concerns the importance that natural selection has had in the evolutionary process. Here are three important benchmarks on that continuum (Orzack and Sober [1994a], [1994b]; Sober [1993]):

- (U) Natural selection has been an influence on the evolution of most traits in most populations.
- (I) Natural selection has been an important influence on the evolution of most traits in most populations.
- (O) Natural selection has been the only important influence on the evolution of most traits in most populations.

These propositions are listed in order of increasing logical strength; later entries entail earlier ones, but not conversely. For example, the claim that natural selection was *an* important influence on the vertebrate eye (I) does not entail that selection was *the only* important influence (O). We understand this latter claim to mean that selection was so powerful that it was able to sift through a rich range of variation and cause the fittest of the available traits to evolve. According to (O), the correct explanation for why we now observe a given trait is that it was present ancestrally, along with others that were less fit, and natural selection eliminated the alternatives; proposition (O) predicts that organisms should exhibit *optimal* trait values.<sup>4</sup>

In our view, the continuing debate about adaptationism concerns whether (O) is true, or only something weaker.<sup>5</sup> Proposition (O) embodies a relatively

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(Darwin[1859], p. 490); a few pages earlier, Darwin describes ‘all beings... as the lineal descendants of some few beings which lived long before the first bed of the Silurian system was deposited... (Darwin 1859, pp. 488-489).’

<sup>4</sup>Here “optimal” means the fittest of the *available* phenotypes, not the fittest phenotype that is *conceivable*; there is no prediction that zebras will evolve machine guns with which to repel lion attacks.

<sup>5</sup>This is the substance of adaptationism and anti-adaptationism as claims about nature. In addition, the debate has included a variety of purely methodological disputes. It is

monistic view of evolution, whereas (I) is more pluralistic. Furthermore, whether (O) is true can be decided only on a trait-by-trait basis. The question is whether nonselective processes, such as genetic drift, have been so negligible in their influence that they can be omitted from explanatory and predictive models. The problem concerns the legitimacy of certain *idealizations* (Orzack and Sober [1994a], [1994b]; Sober [1993]).

Given these clarifications of what the tree of life hypothesis and the hypothesis of natural selection mean, we return to our initial claim that Darwinian theory is an historical hypothesis about life on Earth, rather than a universal generalization. We do not rule out the possibility that arguments might be developed that show that the Darwinian theory must be true on any planet of a certain type. However, if one argues for the universal validity of the hypothesis of natural selection, one must do more than show that natural selection will be common. Demonstrating (U) - the ubiquity of natural selection—is not sufficient to show that (I) is true. Similarly, perhaps one can show that even if more than one start up occurs initially, the process of lineage extinction will have the result that at some sufficiently remote future time, all the organisms alive then will trace back to a single common ancestor. However, such 'theoretical' arguments do not exist in anything but a sketchy form at present (Sober [1999]); evolutionary biologists defend their claims about monophyly<sup>6</sup> and natural selection by 'data-driven' arguments that advert to the observed features of organisms on earth.<sup>7</sup>

## 2 Logical Independence

The two components of Darwinian theory are logically independent; the truth or falsity of the one does not entail the truth or falsity of the other (Mayr [1982], pp. 505-510). An easy way to see this is to note that all four of the cells in the accompanying table represent logically consistent positions.

Kimura ([1993]) accepts the tree of life hypothesis, but his neutral theory of molecular evolution asserts that the evolutionary dynamics of molecular

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important to see that these are conceptually separate (Sober [1993], Godfrey-Smith [2001]).

<sup>6</sup>The tree of life hypothesis asserts that all *current* life on earth is part of a single monophyletic group; it does not claim that all *past and present* living things form a monophyletic group. The latter claim would be incompatible with multiple start-ups.

<sup>7</sup>An example of a data-driven argument concerning common ancestry is Crick's argument about the (near) universality of the genetic code, which we will discuss.

	natural selection is important	natural selection is not important
one tree	contemporary Darwinism	Kimura(1993)
major groups of contemporary organisms originated independently	Haeckel (1876)	Lamarck(1809) Special Creationists Senapathy(1994)

Table 1: *The Tree of Life Hypothesis and the Hypothesis of Natural Selection are logically independent—all four of the positions depicted here are logically consistent.*

variation (e.g., DNA sequence polymorphism) are almost always governed by genetic drift, not natural selection. Of course, Kimura’s theory is consistent with the Darwinian theory, if the former is restricted to molecular traits and the latter is restricted to morphological, physiological, and behavioural traits; when not restricted in this way, the two theories conflict. However, our point is just that the upper-right cell is logically consistent.<sup>8</sup>

Lamarck’s ([1809]) theory of evolution entails that natural selection is not important and that the tree of life hypothesis is false. Lamarck thought that lineages originate by spontaneous generation and then evolve through a pre-programmed sequence of steps. The major changes that a lineage undergoes are the result of an endogenous drive towards increasing complexity; they are not an adaptive and opportunistic response to environmental conditions, which can result in only modest changes. For Lamarck, present day human beings belong to a very old lineage, because we are very complex; present day worms belong to a lineage that arose more recently, because worms are relatively simple. According to this theory, present day human beings and present day worms do not have a common ancestor, even though present day human beings are descended from worm-like ancestors ([Bowler 1984]). The Lamarckian picture is logically consistent. The same is true of the position of special creationists, who defend the hypothesis of separate origination by claiming that natural selection could not generate the diversity we observe if all current life stemmed from a single ancestor. Senapathy ([1994]) takes this view as well, without invoking the idea of intelligent design.

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<sup>8</sup>Mayr([1982], p. 506) constructs a similar table, and lists Hugo de Vries and T.H. Morgan as endorsing common ancestry but denying the importance of natural selection.

Finally, Haeckel ([1876]) argued that bacteria arose many times from pre-cellular ‘albumen’ (protein) and that the kingdoms of nucleated cells—plants (which for Haeckel included fungi), animals, and protists - arose polyphyletically from bacterial lineages. Haeckel also emphasized the importance of natural selection. Again, our point is not to defend the plausibility of the lower-left cell in the table, but to point out its logical consistency.

### 3 How Adaptive Hypotheses Bear on the Tree of Life Hypothesis

Even though the phylogenetic and the adaptive hypotheses in Darwinism are logically independent, it does not follow that they are evidentially independent. Darwin ([1859], p. 427) noted one way in which they are evidentially connected:

... analogical or adaptive characters, although of the utmost importance to the welfare of the being, are almost valueless to the systematist. For animals, belonging to two most distinct lines of descent, may readily become adapted to similar conditions, and thus assume a close external resemblance; but such resemblances will not reveal—will rather tend to conceal their blood-relationship to their proper lines of descent.

Darwin’s point is that similarities involving highly adaptive traits are apt to provide misleading information about ancestry; instead, the best evidence of common ancestry comes from neutral or even deleterious features. For example, the torpedo-like shape of dolphins and sharks does not strongly support the hypothesis that they have a common ancestor, since one would expect big aquatic predators to have this shape, even if they originated separately. In contrast, the fact that many mammalian fetuses and many fish have gill slits is evidence of relatedness, since gill slits in mammals have little or no adaptive function.

Darwin wrote that adaptive similarities are ‘almost’ valueless as guides to genealogy. Consistent with this hedge, modern evolutionary theory suggests that adaptive similarities can sometimes provide evidence of common ancestry. Suppose there are multiple adaptive peaks for a given trait; if so,



stabilizing selection will tend to keep a descendant on the peak that its ancestor occupied. Suppose we observe that present day organisms occupy just one of those peaks. Since there are many possible peaks, we can interpret this observation as evidence that these organisms trace back to a common ancestor. This is the logic underlying Crick's ([1968]) argument that the (near) universality of the genetic code provides evidence that all present day organisms are genealogically related. Crick says that the code is a 'frozen accident'—it is one of a large number of equally fit alternatives. However, once a code is in place, changing it would likely be difficult. Notice that the argument for the tree of life hypothesis that appeals to the code's near universality does not require that the alternatives be equally fit; this is important, since it is arguable that the code is optimal (e.g., see Freeland *et al.* [2000]).

Despite the fact that multiple peaks allow adaptive similarities to provide evidence of common ancestry, a general point remains: *The stronger the role that natural selection has played, the less evidence there will be for the hypothesis of common ancestry.* The more a trait's distribution can be explained solely on the basis of natural selection, the less evidence the trait will provide for shared ancestry. This point entails that the most extreme form of adaptationism leads to epistemological disaster. If every feature of every organism could be explained solely by appeal to the hypothesis of natural selection,<sup>9</sup> we would have no evidence of common ancestry.

## 4 How the Tree of Life Hypothesis Bears on Adaptive Hypotheses

Partly in response to the controversy over adaptationism sparked by Gould and Lewontin ([1979]), there has been a proliferation of methods for testing adaptive hypotheses that take account of phylogenetic relationships (see Harvey and Pagel [1991] for an introduction). These methods are motivated by the fact that common ancestry poses an epistemological problem. Standard statistical theory usually requires that the data one uses to test hypotheses be independent. However, if species have common ancestors, their traits may

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<sup>9</sup>Notice that with multiple adaptive peaks, a species' trait value cannot be explained *solely* by citing natural selection; the lineage's initial condition also is relevant. For a simple illustration of this idea, see the discussion of heterozygote inferiority in Sober ([1993, p. 129]).

fail to be independent.<sup>10</sup> One response to this problem is to transform the data so that the transformed data are independent (Felsenstein [1985]; see Orzack and Sober [2001] for further discussion).

In the previous section, we discussed the point that adaptationism poses a problem for testing hypotheses of common ancestry. The comparative methods that have recently been developed are responses to the converse problem—that common ancestry poses a problem for testing adaptive hypotheses. Yet, it has not been noticed that common ancestry *solves a problem* that arises in connection with testing adaptive hypotheses. Adaptive hypotheses that assert that natural selection has been an important influence on trait values are untestable unless they are supplemented by suitable background assumptions. We will argue that the hypothesis of common ancestry helps provide this needed supplementation.

## 5 What do Adaptive Hypotheses Predict?

As noted earlier, adaptive hypotheses can be given stronger or weaker formulations. The strongest formulation—proposition (O)—says that selection has been the only important influence on a trait’s evolution. For example, consider an instance of (O) that asserts that the length of a bear’s fur is an *optimal* adaptation to ambient temperature. Given facts about their biology and about the environments they occupy, a bear’s fur should have the length that maximizes fitness. One hypothesis about the optimal relationship of fur length to ambient temperature is represented by the line in Figure 1. The hypothesis that different bear species have optimal fur lengths in the sense specified by this optimality hypothesis can be tested without information about their common ancestry. The question is simply whether a species’ fur length matches that predicted by the optimality line. The fact that species are close to their optima is not enough to accept proposition (O), nor is the fact that the data show a downward trend.

We are interested in a reaction that many biologists have to the kind of data depicted in Figure 1. They would insist that the observed dependence of fur length and ambient temperature is evidence that fur length evolved

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<sup>10</sup>All claims about trait independence are conditional on the strength of selection, the topology of the phylogenetic tree, and the absolute amount of time involved. For example, tip species in a bifurcating tree can be independent, provided that the lineages are sufficiently old and selection is sufficiently powerful.

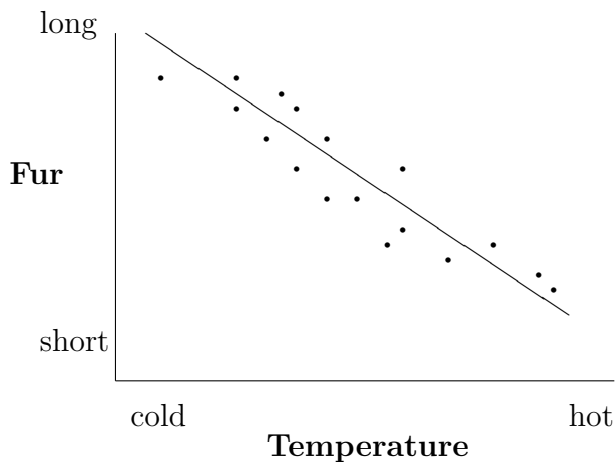


Figure 1: *The observed trait values of extant bear species show a downward trend; the values are close to, but not on, a hypothesized optimality line.*

via natural selection in response to changes in ambient temperature. The data provide evidence that natural selection has significantly influenced the trait’s evolution. An instance of proposition (I) is confirmed, even though proposition (O) is not.

This interpretation of the data poses a problem. After all, we have data only on extant species. But adaptive hypotheses describe the changes that natural selection supposedly effected in lineages; an instance of proposition (I) predicts that bear lineages evolved in the direction of the optimal trait values depicted in Figure 1.<sup>11</sup> How can observations of the present test hypotheses about the changes that allegedly took place in the *past*? As noted, instances of proposition (O) can be tested. But how are we to test instances of (I), if all we observe are the fur lengths that species now have and the temperatures of their environments *now*?

Consider Figure 2, which depicts two scenarios in which species evolve in the direction of an optimal relation between fur length and temperature. The arrows represent lineages that are ancestral to the species we observe, which are represented by data points. In Figure 2a, the result of this evolution is a set of species that show a downward trend; in Figure 2b, the result is a set of species that show the opposite trend. This illustrates the general point

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<sup>11</sup>More precisely, instances of proposition (I) predict that lineages will exhibit a probabilistic tendency to move in the direction of the optimality line; they need not do so invariably.

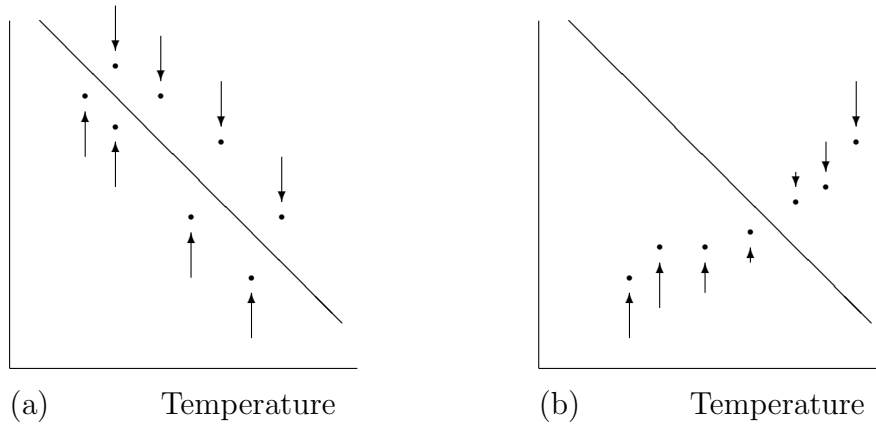


Figure 2: *Two scenarios in which bear lineages evolve in the direction of a hypothesized optimality line. Depending on what trait values those lineages have when they start evolving, the result can be a set of extant species (represented by dots) that (a) exhibit a downward trend, or (b) exhibit an upward trend.*

that the hypothesis in question - that lineages tend to evolve in the direction of their optima - does not by itself entail that there should be a downward trend in the data. What trend the adaptive hypothesis predicts depends on the traits of ancestors. But ancestral character states are rarely known when an adaptive hypothesis is being tested.<sup>12,13</sup>

Before explaining how instances of proposition (I) can be tested, we want to emphasize that the problem illustrated in Figure 2 arises even when a single species' trait value is 'very close' to that predicted by an optimality model - even one that is biologically well-motivated. Parker ([1978]), for

<sup>12</sup>An observed fossil can't be assumed to be an *ancestor* of an extant species, though its traits may licence the inference that it is a *relative*. Since fossils are older than extant organisms, they are temporally closer to some of the phylogenetic tree's interior nodes and therefore may provide stronger evidence about the character states of ancestors than an extant species does.

<sup>13</sup>It is widely held (e.g. by Ridley [1983]) that cladistic parsimony provides a solution to this problem—if the observed species are tip species in a phylogenetic tree, then parsimony allows one to reconstruct the character states of the tree's interior nodes, this affording a test of adaptive hypotheses that make claims about the changes that occur in the tree's branches. Notice how this procedure uses the idea of common ancestry to test adaptive hypotheses. However, this solution is problematic; see Sober ([2002b]) for discussion.

example, constructed an optimality model for dung fly copulation time; the observed time, he reports, is 35 minutes and the optimal time, according to the model, is 41. Can one conclude from this that natural selection, as described in the optimality model, has been an important influence on the trait? We believe the answer is *no*; the observed value of 35 does not settle whether the lineage evolved towards or away from the hypothesized optimum, and so the observation, by itself, cannot confirm the hypothesis. Unfortunately, the trait values of dung fly *ancestors* are not something we observe. So how do the observed features of *descendants* bear on the adaptive hypothesis?

## 6 Common Ancestry and Quantitative Genetics to the Rescue

Fortunately, instances of proposition (I) *are* testable. *If species have common ancestors and if the response to selection is proportional to the intensity of selection, then we can test instances of proposition (I) by looking just at extant species; information about the traits of ancestors is not needed.* We'll explain this claim in terms of our bear example. Figure 3 shows a species A that is the ancestor of species  $D_1$  and  $D_2$ . After speciation occurs,  $D_1$ 's environment gets colder while  $D_2$ 's gets warmer. Fur length in both species then evolves towards the optimal value for the given temperature.<sup>14</sup>

How far should we expect the lineages leading to species  $D_1$  and  $D_2$  to evolve? According to the adaptive hypothesis, selection favours a reduction in fur length in each lineage, but how much reduction should we expect? Notice that the adaptive hypothesis says that  $D_1$  starts closer to its optimal fur length than  $D_2$  does. This means that  $D_2$  is subject to more intense selection than  $D_1$ . Quantitative genetic theory predicts that the response to selection is proportional to the product of the trait's heritability and the intensity of selection; this prediction is borne out in many experiments (Falconer and Mackay [1996]). As a consequence, if fur length is equally heritable in the two lineages,<sup>15</sup>  $D_2$  should evolve a greater distance than  $D_1$  (as shown in Figure 3), since the intensity of selection is greater in the former species. Since these

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<sup>14</sup>It is not essential to our argument that descendant lineages experience instantaneous changes in temperature.

<sup>15</sup>In fact, a weaker assumption suffices—that the heritability in  $D_1$  isn't greater than that in  $D_2$ .

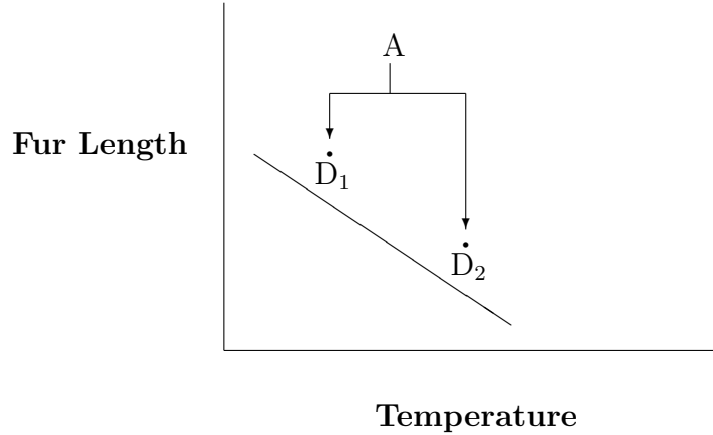


Figure 3: *The adaptive hypothesis under test asserts that lineages evolve in the direction of the optimality line, which has a negative slope. If lineages  $D_1$  and  $D_2$  stem from a common ancestor  $A$ , then the adaptive hypothesis predicts that a line through the endpoints of the two lineages will have a negative slope, provided that the heritabilities in the two lineages are approximately the same.*

lineages respond differently to selection,  $D_1$  will end up with longer fur than  $D_2$ . The result is that the relationship between  $D_1$ 's and  $D_2$ 's trait values “mirrors” the slope of the optimality line towards which the two lineages are evolving—that is, the optimality line has a negative slope and so does the line joining the endpoint of  $D_1$  and the endpoint of  $D_2$ . Notice that this line of argument would apply, no matter what trait values the ancestor  $A$  happened to have.

We have just tested the claim that fur length is an adaptive response to ambient temperature by looking only at the traits of extant species. Proposition (I), applied to an optimality line, predicts that species will evolve towards their optima, not that they will necessarily attain them. If the species in question have common ancestors, and if the heritability of fur length is about the same across lineages, then we can test the adaptive hypothesis by seeing if the sign of the regression of those species' trait values on temperature is the same as the sign of the slope of the optimality line.<sup>16</sup> This procedure can be adapted to optimality lines that are nonlinear—the question is whether the trend in the data ‘mirrors’ the shape of the optimality

<sup>16</sup>A similar proposal was endorsed, but without this rationale, by Burt ([1988]).

line. It also can be used in testing adaptive hypotheses in which lineages are not said to evolve towards an optimality *line*, but rather are hypothesized to evolve in the direction of a region - an optimality *band*, so to speak.<sup>17</sup>

To understand the role that common ancestry plays in this argument, compare Figure 3 with Figure 2. In Figure 3, the common ancestry of  $D_1$  and  $D_2$  insures that the two lineages start evolving with the same trait values. This, plus the assumption about differential response to selection, suffices for the adaptive hypothesis to predict a downward trend in the data. In contrast, the different species in Figure 2 do not have common ancestors and so the lineages may start evolving from different initial trait values; even if there is a differential response to selection, there is no guarantee that the species in Figure 2 will exhibit a downward trend.

The two assumptions we have identified, which together allow adaptive hypotheses to predict trait associations among tip species, will strike most biologists as having rather different standings. As noted earlier, the idea of common ancestry is standard in contemporary evolutionary biology, and will not strike practicing biologists as problematic.<sup>18</sup> However, the idea that heritabilities are roughly the same in different lineages is anything but obvious. Why should one believe this assumption? We will not address this question in detail here, except to note that the idea of common ancestry plays a justifying role in this instance as well. If the lineages in question had no common ancestors, there would be little reason to expect them to have similar heritabilities. The hypothesis of natural selection predicts that heritability will *decline* in each lineage, but it says nothing about the heritability that each lineage has when it *starts evolving*. In contrast, the problem becomes more tractable if tip species trace back to a common ancestor. The effect of common ancestry is that lineages begin evolving with the same *heritability*, just as they begin evolving with the same *trait value* (Figure 3).<sup>19</sup>

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<sup>17</sup>Suppose we wanted to test a *nonadaptive* hypothesis concerning the distribution of a trait. For example, consider the hypothesis that a trait's distribution was strongly influenced by genetic drift. If the species are not related, and we do not know the trait values that were present at the start of each lineage or the amount of time that the lineages have been evolving, the drift hypothesis makes no prediction about the trait's distribution across the descendant species we observe. However, if the species have a common ancestor, the drift hypothesis does make a prediction—more closely related species should be more similar. Once again, common ancestry comes to the rescue.

<sup>18</sup>However, see Sober and Steel ([forthcoming]) for discussion of this standard assumption.

<sup>19</sup>Once the lineages split, it is possible that they acquire different trait values and

We have argued that common ancestry and similar heritabilities *suffice* to render adaptive hypotheses testable. But are they *necessary*? *Prima facie*, there seem to be other possible conditions that would suffice. For example, an examination of Figure 2 reveals that if sufficient time elapses, then evolution towards the optimality line must result in the end points of lineages exhibiting a negative trait association; in this case, the positive association depicted in Figure 2b must be a transitory phenomenon. A second possible scenario is depicted in Figure 4. Here two unrelated lineages each begin with the ancestors  $A_1$  and  $A_2$  at their optimal trait values. If ambient temperature increases by the same amount in the two lineages, and the lineages then evolve in the direction of the optimality line, it is inevitable that the tips of those lineages ( $D_1$  and  $D_2$ ) will exhibit a negative trait association. Both of these scenarios involve separate ancestry, and each suffices to render the adaptive hypothesis testable. The trouble with these possibilities, however, is that we usually are in no position to *know* that they obtain. When biologists test an adaptive hypothesis, they usually don't already know that enough time has elapsed for near-optimal trait values to have evolved or that ancestors had optimal trait values. This is why we conjecture that the sufficient conditions we have identified are also, in practice, necessary.

## 7 Conclusion

Biologists often assume that adaptive hypotheses predict trait associations, but the justification of this assumption has not, to our knowledge, been explained before. For example, if ambient temperature causes bear lineages to evolve longer or shorter fur, what does this predict about the ambient temperatures and fur lengths that we should find among extant species? What does a claim about the causal processes at work *within* lineages predict about the features found at the *tips* of lineages? The answer is *nothing*, unless further assumptions are put on the table. We have described two assumptions that together render the adaptive hypothesis testable.

One of these is an assumption about common ancestry. If the adaptive hypothesis concerns fur thickness in *bears*, then the relevant phylogenetic assumption is that bears have a common ancestor; there is no need to invoke the stronger Tree of Life hypothesis, which says that *all organisms now on*

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different heritabilities. However, under many plausible models of speciation the two lines have the same *expected* trait values and heritabilities.



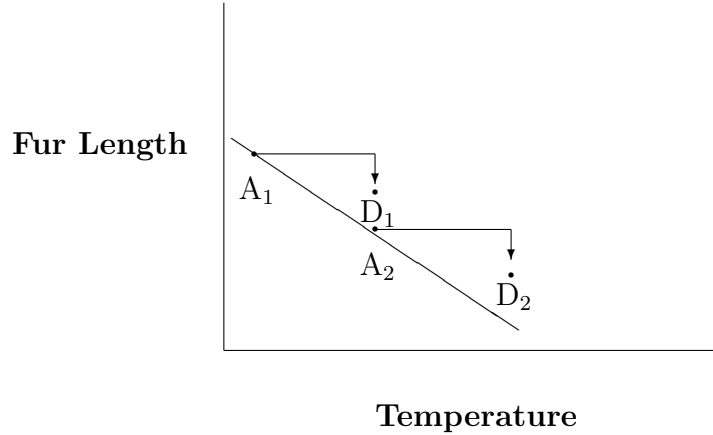


Figure 4: As before, the adaptive hypothesis under test asserts that lineages evolve in the direction of the optimality line, which has a negative slope. If lineages  $D_1$  and  $D_2$  stem from separate ancestors  $A_1$  and  $A_2$ , then the adaptive hypothesis predicts that a line through the endpoints of the two lineages will have a negative slope, provided that  $A_1$  and  $A_2$  have optimal trait values, the two lineages have their temperatures increased by equal amounts, and the heritabilities in the two lineages are approximately the same.

*Earth* trace back to a common ancestor. A parallel point applies to Darwin's observation that adaptation poses a problem if one wishes to draw inferences concerning common ancestry; if the goal is to infer how bears are related to each other phylogenetically, the relevant problem is not that the Hypothesis of Natural Selection, which makes a claim about most traits and most lineages, might be true; rather, the problem is more *local*—one has to worry about the adaptive character of the traits of bears that one proposes to use in drawing inferences about their phylogenetic relationships.<sup>20</sup>

We have argued that the tree of life hypothesis and the hypothesis of natural selection are logically independent, but that they are evidentially dependent, in an asymmetric way. If any or all of the adaptive hypotheses described by (O), (I), and (U) were false, that would not prevent us from testing and confirming hypotheses of common ancestry; quite the contrary—the

<sup>20</sup>In this paper we have discussed the problem of testing adaptive hypotheses and the problem of testing about common ancestry. We have not addressed the question of whether it might be possible to test *conjunctions* of adaptive and phylogenetic hypotheses *simultaneously*. On this, see Sober ([2002a]).

fewer adaptations the better, as far as the task of reconstructing phylogenetic relationships is concerned. On the other hand, if extant species were not genealogically related, it would be puzzling how instances of proposition (U) or (I) could be tested. The fact of adaptation *hinders* one's ability to test hypotheses of common ancestry, but the fact of common ancestry *helps* one test adaptive hypotheses.

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