Thoughts about Adaptiveness

Stimulated by and Intended to Stimulate the Systematics Study Group

Natural selection is the principal guiding force of evolution.

-- almost everybody

. . . the practices of chapters 5 and 9 carry a curse. By equating phylogenetic consistencies of characters with phylogenetic constraints (p. 168), one banishes evolution by natural selection to a small set of characters that happen not to covary with the characters used in phylogenetic reconstruction.

--Brown 1994

I regard it as unfortunate that the theory of natural selection was first developed as an explanation for evolutionary change. It is much more important as an explanation for the maintenance of adaptation.

-- Williams 1966

Williams [1992] offers a characteristically simple, positivistic, and yet sufficient definition of constraint that avoids the usual implicit references to occult forces such as phylogenetic inertia: "any restriction on a population's responsiveness to selection."

-- Pagel 1993

Adaptive change is an intrapopulational phenomenon. The process of adaptation, or adaptive change, occurs when the members of a population possess heritable differences in traits and some of the variations outreproduce others. If one's cogitations about evolution, of whatever kind, lead to discussions of situations for which this particular intrapopulational phenomenon apparently cannot be relevant, then either the subject has been changed or it wasn't understood in the first place.

Because adaptive change is an intrapopulational phenomenon, answering the question whether a difference between two extant species is adaptive entails working out how selection is working, or has worked, within each of the involved species. The exception (see below) is when one species is rapidly extinguishing another (i.e., without either of them having time to change much), and then the answer is likely to be obvious.

Traits or trait changes on which selection acts must at every stage be reproductively either more or less effective for their bearer than their alternatives within the species. Because there is no question of "half-formed" changes (novelties, mutations), in the sense of usefulness, there also is no question of "fully formed, fully functional" changes being something special and evidence of some kind of "less important role" for natural selection. All changes saved by selection necessarily are "fully functional" at every stage at which selection saves them. Adaptive (as opposed to maladaptive) changes are special only in their rarity, adaptive mutations being increasingly unlikely during evolution because the causes of mutation and the causes of selection are independent.

Natural selection is thus not diminished by observers being able to infer correctly the adaptive nature of some changes and not others. Every trait spread by selection has to be reproductively more effective than its alternative at every stage of its evolution, no matter what it looks like.

Form-function fits cannot safely be inferred intuitively (it's called making up an adaptive story). In this phrase, function has but one meaning: reproductive effectiveness. In turn, that means adaptiveness as a result of natural selection. Knowing about a form-function fit therefore implies knowing how a particular trait or variant leads to better or worse reproduction. Obviously, function in this sense is not easy to assess. Adequate knowledge of the function of thermoregulation is a problem requiring knowledge of precisely what regulating body temperature did for the organisms, with respect to Darwin's hostile forces of nature, when the ability to thermoregulate originated and spread, and what it does now for reproduction that would not be done in its (imagined) absence (i.e., precisely why it is maintained). We almost never have such answers. "Keeping body temperature up" is insufficient. The function of wings is a problem requiring knowledge of how the ability to locomote by flight contributes to the reproduction of the flier. We don't know (see below). More study of the organisms in their natural environments, and of fossils, is the way to find out.

Any newly formed more (or less) reproductive heritable variant has to run the selection gauntlet unless it is lost or fixed by drift through such as a bottleneck or founder effect. Reductions in form-function fits will disappear by selection; improvements in form-function fits will spread by selection. Slow or gradual changes can escape selection only if they do not affect reproduction. These are reasons why genetic drift is relatively trivial compared to selection.

Natural selection does not produce the initial variants that lead to adaptive change. Their ultimate source is mutations -- any genetic changes leading to heritable phenotypic variations. Natural selection only saves some traits or variations and fails to save others.

Thus, natural selection is not diminished as an agent of evolutionary change from the realization that it does not create the heritable changes on which it works. It's pretty much stuck with last year's model and the mutations tacked on to it.

Selection probably is rarely responsible for fixation of a trait or variation. As a variant becomes less frequent it has some likelihood of disappearing from selection's view, owing either to an initial recessiveness of the gene effects responsible for the less reproductive variant or to the adaptive evolution of such recessiveness as a consequence of the trait being less reproductive than its alternatives. Selection almost certainly <u>more often</u> causes less reproductive traits to become less frequent, and as a result to be more susceptible to disappearance through drift, and <u>less often</u> leads to their actual disappearance (hence, fixation of an alternative).

Thus, natural selection is not diminished by the realization that it does not typically fix traits.

When one asks if a difference between two species is adaptive, there are three possible underlying meanings. It is necessary to be aware of this, and to know which of the three is relevant to the particular question being asked.

1. The two species have each been undergoing evolutionary change involving natural selection, in which neither species has any connection with the other, so that the divergence they are undergoing is an entirely incidental consequence of their genetic separation. In this case, both traits would be adaptive, owing to the different environments of selection, and to mutational or other changing events to which they were subjected. In this case it would be strange to ask if the <u>difference</u> between the species is adaptive, unless someone wished to predict an outcome if they should be placed together.

2. The two species are each a part of the selective environment of the other, with the consequence that their competition for the same resources is causing them to diverge. Biologists use the term character displacement for this kind of interaction. Again, both traits would be adaptive, and in this case so would the difference.

3. The two species are each a part of the selective environment of the other, with the consequence that one of them is eliminating the other; differential reproduction (selection) in this case is effective at the species level. An example is the interaction of a sexual species with its permanently parthenogenetic daughter population(s). In this case, the traits enabling one species to eliminate the other would be adaptive, the corresponding traits of the other species maladaptive. Of course, we have every reason to believe that even the maladaptive trait was adaptive in environments not including the other species, or in the environments in which it originally spread, which may have included lower frequencies of the other species.

The last two cases are rarely observed, even though most people think that at least the second one is essentially universal. It seems likely, therefore, that both processes tend to occur rapidly.

To ask if a trait "is adaptive" implies: does it outreproduce its actual or some reasonable imagined alternatives in the current environment (e.g., Reeve and Sherman, 1993). Of course, this question involves only the thinnest skim on the top of biological history. There is no implication from a "no" answer that the trait did not come about (spread, accumulate changes) as a result of natural selection, and there is no implication from a "yes" answer that the trait had to come about as a result of the same selective processes that are going on currently. Insect wings certainly were not flying devices in their earliest stages. They may have been courtship devices then, or (larval or adult) locomotory devices (in water or on land), or something else that could function while it was still tiny -- thermoregulatory devices or aquatic respiratory devices or whatever. At some point they obviously became functional flying devices. No one has a clue why flying was "functional" (adaptive) at that point in the Devonian when insect wings became extensive enough to serve as aerial locomotor devices (Coincidentally, insects also began then to copulate directly for the first time -- and they did it with the female mounting the male's back, and all such female-above copulators today have special lures or claspers (mostly associated with the wings) that get and keep the female in the mating position. I believe no other organism copulates this way -- think about it). Thus, no one can say why wings are restricted to adult insects (except for those crazy subimagos of Ephemeroptera), or even why they are retained today -- a question quite separate from whether or not the details of form and function in modern insect wings influence one or another kind of flying as such; the functional question is: What good is flying?

After wings become flying organs we can consider the details of their structure that somehow enhance this ability (the respectable question), but that does not tell us why flying was an advantage in the first place or is maintained now (for some odd reason a not-so-respectable question). How you get better at something respectable like flying or thermoregulation is a perfectly legitimate question but precisely how it affects reproduction is not. Did the earliest "wings" interest or attract females, lengthen jumps (away from predators? toward females? as a means of dispersal? in exhibitionistic lekking behavior?), cause better landings from (the same different possible kinds of) jumps, assist glides (same different possible functions), all of these things at different stages of "wing" evolution, or something we haven't even thought of yet? We don't know. *But such questions, as with long-term maintenance of something identifiable throughout as "a particular trait" (used as evidence of "phylogenetic inertia") have little to do with the general question of whether or not something evolved through the influence of natural selection -- that is, whether or not it is a cumulative product of a process guided principally by natural selection.* The question has an unjustified implied answer if anyone asks if a particular trait is "adaptive" or "nonadaptive" simply in connection with whether it is primitive or derived, or has persisted a long time.

[Wings as initially courtship lures? It's certainly not respectable! WIlli Hennig (1981) called it one of several "fanciful hypotheses." But surely he either didn't comprehend the significance of the astonishing coincidence of wings and copulation (primitively wingless insects pass spermatophores indirectly and don't copulate) -- and a unique and uniquely appropriate form at that -- all the way back in the Devonian; or else he had a respectability hangup. Or maybe both. . . Incidentally, I recognize the possibility that wings could have led to copulation before or after they led to flight, and I haven't yet figured how to make the distinction].

One cannot acknowledge that natural selection is the principal guiding force of evolution (even Gould and Lewontin have each said it in print) and purport to reconstruct the history of life in a reasonably satisfactory fashion without it. If natural selection is capricious with respect to direction and rate, the solution is not to deny it, or to to be satisfied with models utilizing Brownian movement, neutral alleles, or molecular clocks to explain the rates and directions of evolution. If universal generalizations about evolutionary events such as adaptive change and speciation are trivial, and all the subgeneralizations at the next level have to be qualified with "usually" or "probably," then the evolutionary history of organisms is necessarily a little less amenable to global conclusions from blackboard biology. That's all. If particular traits do not change for long periods, the question of their adaptive significance is not thereby erased (!), even if alternative traits in related forms also persist for long periods, and even if the first trait is repeatedly replaced by the second. The appropriate methodology for answering the involved questions, regardless which of the above meanings is entailed, is not fancier statistics, but following the admonition of that old anti-evolutionist Louis Agassiz on the front of this building -- to study the two species further, in their natural habitat or the best possible facsimile thereof, as well as by investigating their history through every possible kind of comparison and reconstruction. Precisely what one-horned rhinoceruses do with their one horn, and the same for two-horned rhinoceruses, are important questions as soon as either species is discovered; and that is not to say that which came first has nothing to do with answering the question.

References

Alexander, R. D. 1964. The evolution of mating behaviour in arthropods. In: K. C. Highnam (ed). *Insect Reproduction.* Royal Entomological Society of London Symposium 2: 78-94.

Alexander, R. D. and W. L. Brown. 1963. Mating behavior and the origin of insect wings. *Occas. Pap. Mus. Zool. Univ. Mich.* 628:1-19.

Brown, Joel S. 1994. [Review of Brooks and McLennan. 1991. *Phylogeny, Ecology, and Behavior.* Univ. Chicago Press]. *Jour. Mamm.* 75:243-246.

Hennig, W. 1981. *Insect Phylogeny.* New York: Wiley and Sons.

Pagel, Mark. 1994. [Review of Williams, 1992. *Natural Selection: Domains, Levels, and Challenges.* Oxford University Press]

Reeve, H. K. and P. W. Sherman. 1993. Adaptation and the goals of evolutionary research. *Quart. Rev. Biol.* 68:1-32.

Williams, George C. 1966. *Adaptation and Natural Selection.* N.J.: Princeton University Press.