Preston on Exaptation: Herons, Apples, and Eggs

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COMMENTS AND CRITICISM

PRESTON ON EXAPTATION: HERONS, APPLES, AND EGGS

Beth Preston's[1] attempt to exploit the concept of exaptation in her proposed theory of function puts a salutary strain on it, thereby exposing its weaknesses better than its critics have done. Stephen Jay Gould and Elizabeth S. Vrba[2] once proposed a contrast between adaptations and what they called *exaptations*: "characters evolved for other usages (or for no function at all) and later 'coopted' for their current role" (*ibid.*, p. 6). The term never caught on among evolutionary biologists (I can find only one use of the term by Gould himself outside the original article[3]), and Ruth Millikan[4] and I have independently argued that exaptation is nothing but the early stage of any adaptation, rather than a distinguished phenomenon in its own right. As I put it:

> every adaptation is one sort of exaptation or the other—this is trivial, since no function is eternal; if you go back far enough, you will find that every adaptation has developed out of predecessor structures each of which either had some other use or no use at all.[5]

Preston claims that Millikan and I both make the same mistake: we "neglect to ask whether there are any ongoing exaptations that do not get transformed into adaptations [in the way just described]...and so enjoy an independent status" (242 fn. 31). Let us see, then, if there are exaptations that are not just the juvenile stages—as one might say—of adaptations.

Preston: "The case of the mantling heron shows that there are indeed ongoing exaptations" (241). African black herons use their out-

[1] "Why Is a Wing Like a Spoon? A Pluralist Theory of Function," this JOURNAL, XCV, 5 (May 1998): 215-54.

[2] "Exaptation: A Missing Term in the Science of Form," *Paleobiology*, VIII (1982): 4-15. The paper is often cited by philosophers, and is reprinted in David L. Hull and Michael Ruse, eds., *The Philosophy of Biology* (New York: Oxford, 1998).

[3] *Bully for Brontosaurus: Reflections on Natural History* (New York: Norton, 1991), p. 144n. "Gould and Vrba offer the term 'exaptation' for such traits, but even though their paper was published 16 years ago the term has found little use in biology"—R. McN. Alexander, "Finding Purpose in Life" (review of Colin Allen, Marc Bekoff, and George V. Lauder, eds., *Nature's Purposes: Analyses of Function and Design in Biology*), *Science*, CCLXXXI, 14 (August 14, 1998): 927.

[4] *Language, Thought, and Other Biological Categories* (Cambridge: MIT, 1984); *White Queen Psychology and Other Essays for Alice* (Cambridge: MIT, 1993).

[5] *Darwin's Dangerous Idea: Evolution and the Meanings of Life* (New York: Simon and Schuster, 1995), p. 281.

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spread wings to shade the shallow water in which they wade, cutting the reflective glare and permitting them to see their prey. The example is drawn from Gould and Vrba's paper, but instead of providing the support she supposes, it actually undermines her reading of their concept. As Gould and Vrba point out, there is a genetic basis for the mantling behavior pattern. So, although the shape of the wings may not (yet) have been significantly adjusted to this new use, there is no doubt that the use has been shaped by selection pressure, and hence that mantling is an adaptation after all. Preston surmises that "the fact that only one species of heron does do it indicates that the selection pressures favoring it are not very strong. Since wings of birds that do not fly rapidly become vestigial, the pressure would have to be strong to maintain wings suitable for mantling in a flightless heron" (240-41). This hypothetical speculation is both dubious and beside the point. Compare the prospects of herons that can mantle but not fly with herons that cannot do either; the selection pressure for mantling would be very strong indeed in that imagined scenario, and the fact that the behavior is found in only one species of heron is no indication at all of weakness of selection pressure. But in any case, since multiple-selection pressures act simultaneously, and since the mantling behavior is clearly under selection, we need not attempt the thankless task of apportioning the relative contribution of flight and mantling (and other yet unnoticed functions) to the maintainance of the shape (and opacity, and weight, and so on) of the wings.

All adaptations start with some fortuitous aptness, a lot or a little, which then gets further refined (a little or a lot) to serve the new function better. If we want, we can honor the cases at one extreme with a term of their own—we can call *exaptations* those cases in which there is lots of initial aptness (by somebody's lights) and relatively little if any later adjustment (so far). Gould and Vrba observe that the *objets trouvés* that form the basis of adaptations are very often exaptations in this sense, and this is important, since it alerts us to the omnipresent possibility that features of adaptations may owe more to selection pressure under an earlier selectional regime than to any selectional shaping for current use. This salutary reminder may well serve to correct a variety of temporal myopia that sometimes afflicts adaptationists, but does not mark a major challenge or alternative to adaptationism, as Gould and Vrba suggest.

Preston tries to make good on their suggestion. She sees that, if exaptation is to be something that contrasts with adaptation, rather than just an early phase of adaptation, she needs to find cases which

are not evanescent and in which the aptness of a feature for a function is *clearly* independent of any "ongoing" selection pressure shaping or maintaining it. Gould and Vrba do not offer any such examples, nor do they harbor any such ambitions for their exaptations. One can see why. So long as the genetic variation for an exapted feature shares a genome with the genetic variation for whatever feature underlies the "exapting," the selection pressures determining their respective fates are inevitably intertwined, dissolving the imagined barrier between exaptation and adaptation. This becomes clear if we imagine varying the case of the mantling heron so that the chances for the sought-for independence are maximized. Suppose herons mantled by holding a large, broad leaf in their bills, flipping it aside at the last instant as they plunged their bills into the water. The shape of the leaf so used would be under selection pressure in the heron genome (shaping the leaf-choosing machinery, or even the leaf-shape-altering machinery, in the heron's brain), while the original shape of the leaf would be presumably beyond the reach of the heron's genome, under "independent" selection pressure to serve other ends in the plant's genome. I flag the presumption of independence, however, since even here, with two entirely distinct genomes, there is the omnipresent possibility of interaction effects: such herons would presumably favor fishing in locales with good shade leaves, and might even enter a symbiotic partnership with the favored plants, providing some benefit in exchange for leaves, thereby getting in position to have a selectional effect on the original leaf shape *for mantling*![6]

Exaptation-without-adaptation can thus be unstable even when the phenomenon is split between two different species. But other interspecific cases might provide the sort of independence Preston seeks. Consider a difference between apples and eggs. Both are mighty good eating. Apples are adaptations, naturally selected *for* being good to eat, in payment to frugivores for spreading seeds. (Cultivated apples enhance this adaptation, of course.) Eggs are not adaptations for being good to eat; there is no selection pressure for deliciousness in eggs. (Domesticated hen eggs are an interesting exception, of course, since they *have* been under artificial selection

[6] This sort of interaction is often overlooked, but its significance for evolutionary theory is the main message of Richard Dawkins's most important book, *The Extended Phenotype* (San Francisco: Freeman, 1982), which proposes and defends a new "central theorem": "*An animal's behaviour tends to maximize the survival of the genes 'for' that behaviour, whether or not those genes happen to be in the body of the particular animal performing it*" (p. 233).

pressure for excellence as food.) Even wild eggs are delicious and nutritious; they are apt for eating, as many ovivores attest. Haunch of antelope is also delicious and nutritious, I gather, and certainly lions often select it as food, but it was not designed to be food even though lions and other carnivores have been designed to use it as food. What if we were to consider eggs and antelope haunches as exaptations? This is clearly not what Gould and Vrba had in mind, however ubiquitous such aptnesses are in nature. They are better for Preston's purposes, though, since they are parallels, in biology, for the "standardized exaptations of artifacts" Preston proposes in her pluralistic theory. All living things are food for some other living things, and *food* is certainly a functional category (like *medicine, lubricant,* and the like). Yet living things and their parts are not in general designed by natural selection to be food.

Nature is full of items which are not artifacts at all but which nevertheless are prized by one organism or another for performing some function. The gravel in a hen's gizzard is not designed for its grinding role, or for any other role; hens may be quite picky, though, about what bits of gravel end up in their gizzards. Or consider salt, which plays such a life-enhancing role in the lives of us all, to say nothing of the air we breathe (try living without it) and the very ground we stand on, for that matter. If hemoglobin molecules have the function of transporting oxygen molecules around in the blood stream, what is the function of the oxygen molecules? These items maintain their aptness for their functional roles independently of any shaping by natural selection of *their* properties; natural selection designs the surrounding systems to take advantage of them. How shall we apply the concept of exaptation to this ubiquitous feature of evolution? Shall we call all these cases exaptations? If it were not for Preston's attempt to keep Gould and Vrba's concept of exaptation from evaporating under scrutiny, these problems with it might have gone unnoticed.[7]

[7] In a long footnote, Preston claims that I make "a rather elementary mistake in moving from 'every adaptation developed out of an exaptation' to 'every adaptation is an exaptation'." As she points out: "We do not say that because every bird developed out of an egg, every bird is an egg" (243 fn. 31). True indeed. I make a similar point in *Darwin's Dangerous Idea* (p. 206). But in the context in which I make the claim (quoted above), my meaning is clear: every adaptation is an exaptation at some point in its career, just as every bird is an egg at some point in its career. Contrary to what Preston says, I do not "repeat the slogan that all adaptations are exaptations at intervals," though it is true that the many adaptations I discuss all start out as exaptations, as I sometimes note. I do say (once, p. 390) that all exaptations are adaptations, and Preston attempts to rebut this claim as well, by finding me (and Millikan) guilty of a fatal equivocation: "in the case of exaptation, 'selec-

Preston is right to deplore the paucity of work on artifacts by philosophers, but the lacuna is not quite so gaping as she supposes. Some, but not all, of the good points in Preston's essay are made by me in my various discussions of "artifact hermeneutics."[8]

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tion' means adoption for a particular use on a particular occasion regardless of whether that use is successful or is repeated" (243 fn. 31). I doubt if this is what Preston meant to say, since it licenses a profligacy of function beyond all imaginable theoretical interest. On this definition of exaptation, "selection" is so leniently defined that every stone a creature stepped on would become a stepping stone, even if the creature stumbled on it. Since this was probably not her intention, her objection to Millikan and me remains unclear.

[8] "Beyond Belief," in A. Woodfield, ed., *Thought and Object: Essays on Intentionality* (New York: Oxford, 1982); "Evolution, Error, and Intentionality," in *The Intentional Stance* (Cambridge: MIT, 1987); and "The Interpretation of Texts, People, and Other Artifacts," *Philosophy and Phenomenological Research*, L, Supplement (1990): 177-94.