2002

Adaptation for, Exaptation as

Nicholas S. Thompson
Clark University, nthompson@clarku.edu

Commentary/Andrews and Gangestad (target article authors)

Adaptation *for*, Exaptation *As*

Nicholas S. Thompson

Departments of Psychology and Biology

Clark University

Worcester, MA, 01610. nthompson@clarku.edu

[**Author correspondence**: Nicholas S. Thompson. Department of Psychology, Clark University, 950 Main St., Worcester, MA 01610. 508-793-7261]

Author acknowledgement: I am grateful to my honors students Rachael Falcon and Kelly Ku for our many discussions concerning the concept of exaptation.

Abstract: The expression *exapted as* is offered as a substitute for the target's *exaptation for* and *exaptation to* on the ground that *exapted as* is less likely to foster the pernicious intuition that natural selection designs for future consequences.

I am grateful for Andrews and Gangestad's clarifications concerning adaptionism, particularly for their point that the recognition of exaptations is secondary to and dependent upon the recognition of adaptations. I also endorse their conclusion that Darwinian explanatory stories should more frequently contain fortuitous consequences as steps in the evolution of traits. Our own preliminary theory of the evolution of babies' cries was a theory of that type, invoking the fortuitous consequences of the evolution of

the speech apparatus in babies as a determinate of the form of babies' cries and adults' sensitivities to them (Dessureau, Olson, & Thompson, 1998; Thompson, Dessureau, & Kurowski, 1998; Thompson, Olson, & Dessurerau, 1996; see also, Falcon, Ku, Elfenbein, Webster, Sokol, Stevens, & Thompson, 2002).

Because I think Andrews and Gangestad's article will have wide influence, I hope these authors will reconsider—perhaps even recant—their use of the expressions *exapted to* and *exapted for* in favor of the alternative *exapted as*. Different expressions afford different patterns of thinking. I fear that the expressions *exapted to* and *exapted for* will make much mischief in the years to come by fostering the idea that exapted traits are produced on account of their future utility.

"Natural selection" is a scientific metaphor or "model" (Thompson & Derr, 1995; Thompson, 2000). It is used to explain how organisms, as they have descended through time, have come to more or less match to the demands of the circumstances in which they have lived. The model is similar to the process by which breeders eventually create organisms matched to their needs by breeding some members of a herd, flock, or stand of organisms instead of others in the same herd, flock, or stand. In the model, breeders choose organisms for their properties—high-butterfat cows over low, good-flying pigeons over bad, sweet-tasting corn over bland. These choices determine the breeding future of the individuals chosen or not chosen. In nature, the survival and breeding of organisms is taken to occur for the same reason: because something selected them on the basis of their properties

Without both its parts, the formulation "Organism O has been selected for Property P" is dangerously incomplete. In the context of natural selection, it is meaningless to say what organisms we selected if we do not say what properties we selected them *for*. By itself, an individual-by-individual enumeration of the organisms that the breeder permitted to breed would tell us nothing much about how the selection regimen was going to change the flock. Furthermore, in an evolutionary context, to say that we selected organisms for P is useless if we fail to specify which sorts of organisms we obtained by that selection regimen. Selection claims display a sort of referential opacity. An organism that is selected for P may display a variety of other properties that the breeder (or nature) might not have selected, if he or she had the choice, because they had fortuitous consequences on the fitness of his/her stock. Understanding evolution as a historical process requires our knowing what sorts of other properties "came along" when we were engaged in our selection for P.

The philosopher of biology Elliot R. Sober (1984) has given much careful thought to this problem. He writes:

> [T]he idea of selection for and against characteristic...[may be understood in terms of] a toy my niece once enjoyed playing with before it was confiscated to serve the higher purposes of philosophy. [The toy is a transparent plastic cylinder with three horizontal layers.] Each horizontal layer contains holes of the same size. The holes on each level are larger than those on the level below. The balls also vary in size. If the balls are at

the top, shaking the toy distributes them to their various levels. This is a selection machine. Balls are selected for their smallness. The smaller a ball is, the more successful it is at descending. Balls of the same size happen to have the same color. The smallest balls, and only they, are green. So the selection process selects the green balls, because they are the smallest.

There are *two* concepts of selection that we must pry apart. There is *selection of objects* and there is *selection for properties.* The smallest balls are the objects that are selected; it is equally true that the green balls are the objects that are selected. However, the concept of selecting for properties is less liberal. There is selection for smallness, but there is no selection for being green.

'Selection of' pertains to the *effects* of a selection process, whereas 'selection for' describes its *causes.* To say that there is selection for a given property means that having that property *causes* success in survival and reproduction. But to say that a given sort of object was selected is merely to say that the result of the selection process was to increase the representation of that kind of object.

When the green balls reach the bottom more frequently than the blue ones, we think that there must have been a reason why green balls were

> selected; so they must have had some property that was selected for. But the property in question was not their color. There was *selection of* green objects, but no *selection for* greenness. I offer the following slogan to summarize this logical point: '*selection of' does not imply 'selection for'* (pp. 99-100).

In a later passage, Sober insists that we extend that convention to the expression *adaptation for*:

> [T]he concept of adaptation needs to be understood in terms of the idea of *selection for properties;* the idea of *selection of objects* will not suffice...If a neutral trait is pleotropically linked to an advantageous one, it may emerge because of a process of natural selection. It was selected, but this doesn't mean that it is an adaptation. The reason is that although it was selected, there was no selection *for* that trait.
>
> The main idea here is to contrast adaptations with fortuitous benefits. After [stegosaur] dorsal fins became prevalent in the species, they may have performed any number of functions. Perhaps they served as cooling systems. Perhaps they helped stegosaurs attract mates. But if these additional benefits did not play a causal role in the emergence of the trait, it would be a mistake to describe the fins as adaptations for temperature control or mating (p. 197).

Here Sober is making exactly the same distinction between adaptations and fortuitous effects as the target authors are making between exaptations and adaptations when they write, in section 2.2.1:

> [Adaptations] are traits that have been constructed by a process of phenotypic modification by natural selection for a particular gene-propagating effect...[A]n exaptation is a pre-existing trait that acquires a new beneficial effect without modification to the phenotype by selection.

Sober is determined to limit the selection-for-Property-P attribution to those P's that are causally efficacious in determining the greater reproduction of the organisms that bear them. The target authors, however, seem to blur that distinction by coupling the prepositions *to* and *for* with both adaptation and exaptation. Thus, in their terminology, a trait is exapted *to* (approximately 27 times) or *for* (approximately 7 times) its effects, even though the authors acknowledge that it is neither selected *by* them nor *for* them.

I have spent nearly a lifetime trying to expunge my students' intuitions that natural selection somehow manages to sniff out the future and generate traits that will be suitable to it. I fear that the moment we accept either *exapted for* or *exapted to* as standard usage, my students will begin to demand to know how it is that natural selection is prescient in designing exaptations. I urge that, following Sober, we reserve the use of *adapt for* to the "relation between a trait and its selecting consequences," and then use *exapt as* to refer to "the relation between a trait and its fortuitous nonselecting consequences." In so doing, we would be following the verbal practice implicit in such ordinary-language sentences

as, "I bought the tool for turning screws, but when I got it home, I found I could use it as a chisel."

Thus, if speaking of the stegosaur and believing that the fins on its spine are selected by their capacity to ward off the bites of predators, but also believing that these fins had the fortuitous beneficial effect of disseminating body heat, we would write that the stegosaur's fins are adaptations *for* protection that are subsequently exapted *as* heat disseminators. This exaptation might later lead to selection *for* increased surface area in the fins or *for* their vascularization, and these further changes would be adaptations *for* heat dissemination

References

Dessureau, B.K., Olson, C., & Thompson, N.S. (1998). A reassessment of the role of pitch and duration in adults' responses to infant crying. *Infant Behavior & Development*, 21(2), 367-371.

Falcon, R. G., Ku, Y.L.K., Elfenbein, D., Webster, K. L., Sokol, R.I., Stevens, D.A., & Thompson, N.S. (2002) Adult perception of infant cries: A multidimensional analysis identifying salient features and associated acoustic characteristics. Manuscript submitted for publication.

Sober, E. R. (1984) *The nature of selection*. Chicago: Chicago University Press.

Thompson, N.S. (2000) Shifting the natural selection metaphor to the group level. *Behavior and Philosophy, 28*, 83-101.

Thompson, N.S. & Derr, P.G. (1995) On the use of mental terms in behavioral ecology and sociobiology. *Behavior and Philosophy*, 31-37.

Thompson, N.S., Dessureau, B., & Kurowski, C. (1998) Infant cries as evolutionary melodrama: Extortion or deception? *Evolution of Communication, 2*:1, 25-43.

Thompson, N.S., Olson, C., & Dessureau, B. (1996) Babies' cries: Who's listening? Who's being fooled? *Social Research, 63*:3, 763-784.

Williams, G.C. (1966) *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.