Adaptation Can Be a Problem for Evolutionists

New terms are needed for describing useful features in organisms, because the traditional term, adaptations, can be misleading

Feathers are an adaptation for flight in birds. Right? Wrong. Birds undoubtedly cannot fly without feathers, but feathers very probably evolved initially as a heat insulation layer in a small predatory dinosaur. In which case, feathers are an "exaptation" for flight, not an adaptation, according to Stephen Jay Gould, of the Museum of Comparative Zoology at Harvard, and Elizabeth Vrba, of the Transvaal Museum, Pretoria, South Africa.*

The argument rests on the difference between current utility (in this case, flight) and historical genesis (in providing heat insulation, not in sustaining flight). It is, Gould and Vrba suggest, a general argument that goes beyond an obsession with semantics. The word "exaptation" is necessary, they say, because one thereby recognizes as important a phenomenon that modern evolutionary theory has neglected.

Briefly, the argument is this. An overemphasis on the power of natural selection to synthesize physical features that directly contribute to an organism's fitness has led to the view that virtually every aspect of an organism is a specific adaptation for some function. Gould has for some time been a critic of this so-called "adaptationist program," and he has pointed out, for instance, that constraints of embryological development contribute in an important way to morphological reconstruction through evolution.

Vrba joins Gould in the assault on the adaptationist program and they say that if you look at a feature with a particular current utility, the feature may have one of three derivations. It may have been directly constructed through natural selection, in which case the feature is an adaptation. It may simply have been coopted into its current use from a different previous use. Or it may have been coopted for its current use from a structure that previously had no function. These latter two would be termed "exaptations." The point that Gould and Vrba make is that it is folly to infer without caution the historical genesis of a feature from its current utility, and that structures without function represent an important, although little recognized, source of raw material in the origin of evolutionary novelty.

Some evolutionary biologists, notably Walter Bock, of Columbia University, New York, insist that anything that confers a survival advantage on an organism should be called an adaptation. Meanwhile, others, notably George Williams, of State University of New York, Stony Brook, have characterized some functionally important characteristics as lucky accidents. The unfused sutures in the skull of a mammal neonate are crucial for safe passage through the birth canal, for instance. But they cannot be described as adaptations for mammalian reproduction because they are to be found in the skulls of birds and reptiles, a fact that Darwin acknowledged. Nevertheless, in the absence of exaptation, there is no term to describe a structure that by chance performs an essential current role.

Gould and Vrba propose exaptation because such a structure, having been simply co-opted, is fit (*aptus*) by reason of (*ex*) its form, or *ex aptus*. This contrasts with a structure that has been pushed toward fitness, *ad aptus*, by natural selection, and this is an adaptation.

Now, there is another problem because the term adaptation is currently used to describe the static phenomenon of being fit. Gould and Vrba suggest that a more appropriate word would be simply, aptation, the modes of which would be adaptation and exaptation, depending on the historical circumstances.

Archaeopteryx

Were this animal's feathers adaptations or exaptations for flight? [Specimen from the Humboldt Museum of Natural History]

Students of evolutionary biology have long recognized the apparent co-optation of structures of one function for utility in another, of which feathers used for flight is a good example. This traditionally has been described as preadaptation, with the immediate rider that it is not meant to imply that a structure might evolve with the anticipation of a future function. The problem would be overcome, say Gould and Vrba, if preadaptation were dropped in favor of preaptation. Preaptations are potential, but as yet unrealized, exaptations.

Once a preaptation becomes an exaptation, there might follow some evolutionary modification. One might therefore have the following sequence of events: an adaptation becomes a primary exaptation and this is followed by secondary adaptation. In the case of feathers, there appears to have been relatively little secondary adaptation. But in the four-limbed locomotion of most land vertebrates, which is an exaptation from the four-finned condition of ancestral fishes, there has been considerable secondary adaptation in the detailed structure of the limbs, ranging from the human hand, to the bat's wing and the horse's leg.

If resolution of the embarrassment associated with the term preadaptation were the only benefit of Gould and Vrba's new terminology, then their effort would have been relatively modest. But an important aspect of their argument is the sharp focus turned on the role played by functionless, or rather nonaptive, structures in evolution. Two examples that are offered to illustrate the point are the sexual "mimicry" in the spotted hyena and the utility of apparently junk DNA.

Females of the spotted hyena are larger than males and dominant over them. The females also have an enlarged clitoris and labia majora which thus have the appearance of male external genitalia. These structures, like the male's true genitalia, are used in an important behavior known as the meeting ceremony. Students of hyena biology have speculated that these pseudogenitalia evolved as an adaptation in the meeting ceremony.

Paleobiology 8, 4 (1982).

Gould and Vrba suggest that their origin might simply be the result of the high levels of circulating androgens associated with the growth of the unusually large female body. The clitoris and labia majora, being homologs of the penis and scrotum, simply enlarge in response to the high levels of the hormone. Once present, the pseudogenitalia may then have been co-opted in the meeting ceremony, as exaptations. They arose initially with no function, and then assumed a role.

Molecular biology of recent years has revealed many new and intriguing categories of DNA, some of which appear to have no role. One explanation of this has been that the nonaptive sequences provide raw material for future evolution. But the logic of natural selection does not allow for selection for future use. More likely is that the accumulation of nonaptive DNA is a consequence of the innate property of repeated sequences of nucleic acid to replicate and move around the genome. Later it may be recruited to perform some role, in which case it becomes an exaptation.

"The ultimate decision about whether we have written a trivial essay on terminology or made a potentially interesting statement about evolution must hinge upon the importance of exaptation, both in frequency and in role," write Gould and Vrba. Evolution depends on the raw material presented to selection, and this typically has been thought of in terms of genetic variation. Gould and Vrba say that phenotypic variation, in contrast to genotypic variation, has not adequately been considered. "Flexibility lies in the pool of features available for exaptation," they state. "The paths of evolution—both the constraints and the opportunities—must be largely set by the size and nature of this pool of potential exaptations."

In addition to placing the phenomenon of genetic redundancy in the realm of exaptation, Gould and Vrba suggest that most of what the human brain now does is unrelated to its original adaptation, and are there for exaptations. With examples like these, they assert, the subject cannot be deemed unimportant.

"The codification of exaptation not only identifies a common flaw in much evolutionary reasoning—the inference of historical genesis from current utility. It also focuses attention upon the neglected but paramount role of nonaptive features in both constraining and facilitating the path of evolution."—ROGER LEWIN

Solar with a Grain of Salt

Salt gradient solar ponds are the simplest, cheapest way to collect large amounts of solar energy and should be the first to find wide use

Modern solar energy technology often seems to deviate sharply from the age-old engineering dictum that simpler is better. High-tech photovoltaic cells, computer-controlled arrays of heliostats focusing sunlight on high-temperature boilers, and even solar power stations in space are all contenders for shares of the solar energy pie. In the midst of this technological clutter, it seems somehow refreshing that the technique most likely to find the first wide use for collecting solar energy for industry and electrical generation is also the simplest.

Salt gradient solar ponds, which carry the uneuphonious acronym SGSP's, are already in operation in the United States, Israel, and Australia. Several others are already under construction, and at least three much larger projects are on the drawing board. These developments were reviewed at the recent American Chemical Society meeting in Las Vegas and at an April workshop on salt gradient ponds sponsored by the U.S. Department of Energy.

The immediate precursor of the SGSP, the shallow solar pond, has been viewed as a potential energy source since at least the turn of the century. The theory behind it is simple. A shallow bed of water is exposed to sunlight, which heats it to a temperature as high as 60°C. The heated water can then be used directly or the heat energy can be extracted. Small shallow solar ponds are in use at several sites around the world, but they have important limitations, the most crucial being that heated water is brought to the surface by convection. At the surface, a significant proportion of the stored energy is lost through evaporation and radiation, particularly at night. Investigators at several laboratories are exploring ways to retain heat. New ways include pumping the warm water into insulated chambers at night, covering the pond at night with foam, covering the pond with plastic to retard evaporation, and enclosing the water in plastic bags.

As long ago as 1960 Harry Zvi Tabor and his colleagues at the National Physical Laboratory in Israel found that heat loss could be limited by establishing a salt gradient. Their SGSP has three distinct zones: a convective upper layer, a nonconvective middle zone, and a bottom storage zone. The upper zone, says Robert L. French of the Jet Propulsion Laboratory, "is not a designed component but something that is formed naturally as a result of rain, runoff, and other natural occurrences."

The middle zone is the most important, says French, because it traps the heat. It is generally about 1 meter thick, with a density ranging from 1.0 at the top to about 1.2 at the bottom. The density gradient is produced by dissolved salts such as sodium carbonate, sodium chloride, magnesium chloride, or sodium sulfate. This layer is relatively transparent to incident solar radiation, but is opaque to the infrared radiation from the hot water below. Most important, the gradient prevents hot water in the bottom zone from circulating to the surface.

The bottom zone is generally 1 to 4 meters thick and has a high, uniform density produced by concentrations of salt as high as 20 percent. The amount of salt required can be as much as 900 kilograms per square meter. This zone absorbs most of the incident sunlight and stores heat. Because the heat is trapped, the bottom zone can easily boil if heat is not removed.

The work in Israel was abandoned in the early 1960's because petroleum was so cheap then. It did not resume until after oil prices skyrocketed in 1973. The second wave of work was spearheaded by Tabor, the Israeli Ministry of Energy and Infrastructure, and Ormat Turbines, Ltd., one of the largest manufacturers of Rankine cycle turbines for generation of electricity. Rankine cycle turbines are similar to conventional steam generators, but operate with organic fluids whose boiling points are lower than that of water. They can thus be used with low temperature heat sources.

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