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Systematics and Cognitive Ethology

Comments on Seyfarth and Cheney

Jeffrey H. Schwartz

Department of Anthropology, University of Pittsburgh

As a systematist invited by the conference organizers to comment on a paper by cognitive ethologists, I shall raise questions as they derive from the theoretical and philosophical concerns of my own discipline. My comments thus constitute not so much a critique of Seyfarth and Cheney's paper as an airing of questions which their paper provokes from an evolutionary biologist invested in problems of delineation of characters that might be phylogenetically revealing, the evaluation of the relative phylogenetic significance of those characters, and the generation of alternative, competing schemes of phylogenetic relatedness of taxa. The quotes below from Seyfarth and Cheney's contribution will serve as foci for these comments.

The goal of cognitive ethology is to determine precisely what these mental operations are and how they affect behavior.

European ethologists studied the behavior of animals in their natural habitats. For these scientists, an animal's mind was—like its skeleton or visual system—the product of evolution within a particular environment.

Anthropomorphism is a useful heuristic device because it draws our attention to those cases where natural selection seems to have produced the most impressive feats of animal intelligence.

Evolutionary theory, after all, holds that general skills—such as the ability to use signs as representations of objects—do not evolve unless they serve some adaptive function.

Drawing on our knowledge of the vervets' ecology and social behavior, we can also suggest why monkeys *need* such communication and hence why the cognitive abilities that

underlie it may have evolved. If different predators require different escape strategies, then the adaptive value of acoustically different alarm calls is obvious.

Even if rhesus and Japanese macaques are capable of distinguishing ignorance and false beliefs in others, however, their apparent failure to act on this knowledge is striking.

Research on chimpanzees offers hints that these apes, unlike monkeys, may possess a rudimentary theory of mind. Chimpanzees may recognize ignorance in others and take active steps to provide others with information they do not already have. Chimpanzees have been observed to deceive others.

Among the questions raised by Seyfarth and Cheney's contribution are the following. What is being selected for, i.e., what constitutes a trait (a question that permeated many of the contributions to this conference)? On what level or levels does selection act (also provoked by the conference at large)? And on whose (the animal under study or one of its ancestors) feature or features did selection act?

These questions all intersect on the subject and nature of hierarchy, i.e., hierarchical systems. For example, let us consider the questions of "on what" or "on what level" is selection supposed to act. Is it the organism or the gene—a question addressed in one way years ago by Lewontin (1970) in his discussion of different levels of selection. With regard to the gene, a question that was not broached outright was "which gene" or "which kind of gene?" Are we still at the level of one gene: one trait? But, for example, what about homeobox genes, or regulatory genes and structural genes? Are homeobox genes in fact a kind of regulatory gene? Are they all equivalent entities as far as selection and evolutionary explanation are concerned? And which, if any, of these are we talking about when we invoke selection—or is it some idealized construct of a gene, or just something genetic, that is being invoked? Much work—especially the derivation of formulae and mathematical models—in various areas identified as population genetics is done on the premise that the hard- or soft-tissue or behavioral morphology that one observes must be genetically based. And, therefore, we can talk about genes without knowing if there is a connection between a gene or genes and that which is measured, or even if there exists a specific gene at all for that morphology currently under scrutiny.

An organism, of course, is an amalgam of different kinds or levels of genes, but it is also an amalgam of the interactions and timings of interactions of different kinds of biotic elements.

Cells not only can create an environment with which they interact, but they often must interact with other cells in order for a structure to form (see review by Ten Cate 1989). In vertebrates, generic epithelial cells become differentiated into regions of organ-producing potential, but they need other cells (in conjunction perhaps with early innervation from a pioneer sensory nerve) to initiate structural differentiation (e.g., Lumsden 1980). In the vertebrate head, these "other cells" are sloughed off and migrate from the neural crest of the developing neural tube (the presumptive spinal cord) (Gans and Northcutt 1983; Hall 1988). In other parts of the body, the role of "other cell" is taken over by mitotically derived mesoderm. After the cells have been committed to form a certain structure, they will continue to produce this structure regardless of the environment in which they find themselves (as long as it is not a hostile environment) (DeMario et al. 1993; Kollar and Baird 1971).

Humans, as mammals, share with fish and insects a homeobox gene that causes segmentation, starting anteriorly (Melton 1991). The fundamental segmentation of our human brain happens to be a consequence of this embryonic and primitive level of organismal differentiation (Holland 1988). What distinguishes vertebrates from insects, mammals from other vertebrates, primates among vertebrates, and so-called higher primates from other primates are different levels of derivedness of a tripartite brain whose basic structure is determined by a homeobox gene not specific to any of these potential clades. Additional homeobox genes cause further differentiation, or simplification, especially among mammals, of skeletal and associated soft tissue elements. Humans have, for example, a large occipital bone which results from fusion of many bones, seven cervical vertebrae, and maximally two sets of functional teeth, not because they are humans, or even primates, but because they are mammals. Thus, if we wanted to ask an evolutionary question regarding, say, the selection of or for these latter features or a tripartite brain with large cerebral cortex, it would not be appropriate to direct the question to the level of extant humans, or the last common ancestor of humans and other hominids, or even the last common ancestor of hominids and other primates. Rather, we would have to direct the inquiry at the level of the last common ancestor of extant mammals.

And this is the crux of the hierarchical nature of the biological system. An organism is the composite not only of features that

are unique to its own species, but of features that were inherited from a series of ancestors it shared with a series of increasingly phylogenetically distant relatives. The same is true of each ancestor: Each would have been distinguished by at least one feature or trait that was unique to it, whereas the bulk of its biological being would, in turn, have been inherited from a series of ancestors. One can extend this reconstruction as far as one would like.

The point is, of course, that very few features or traits are specific or unique to any particular organism; (in phylogenetic, specifically cladistic, terminology, features unique to an organism are referred to as derived features or apomorphies or evolutionary novelties). Related organisms might share features because of inheritance from a common ancestor, but the important question is: How many of the features shared by related taxa were evolutionary novelties at the level of the last common ancestor and how many were inherited from their last common ancestor because it had merely inherited them (i.e., as primitive retentions)? Thus, if one is speculating about selection of or for a particular feature or trait, or the selective advantage of a feature or trait for a particular species, one must first try to reconstruct the evolutionary relationships—both close and broad—of the taxon under scrutiny and delineate primitive and derived features, both for the taxon under scrutiny and its series of ancestors. Surely, it should make a difference if the feature or trait that one is focusing on was relevant at the level of some ancestor rather than at the level of the taxon under scrutiny. It is in this context that we must deal with the issues in cognitive ethology raised by Seyfarth and Cheney.

With regard to primates—and accepting the hypothesis that these mammals do constitute a monophyletic group—we are all familiar with the diversity of studies that have focussed on the development, mass, neural-glial ratios, etc. of the primate cerebral cortex. Among primates, the catarrhine primates (Old World monkeys, apes, and humans) are distinguished further (presumably by virtue of their last common ancestor being so distinguished) by an absolute as well as a relative increase in volume of cerebral cortex (Stephan and Andy 1969). Also, and although all mammals display some degree of cerebral asymmetry, catarrhine primates are more cerebrally asymmetric than other primates (Galaburda et al. 1978). But volume of cerebral cortex and degree of cerebral asymmetry are another order of

magnitude more marked among the large-bodied hominoids (humans, orangs, chimps, and gorillas). And, at least in humans, these features have been claimed to be correlated with handedness and language (*ibid.*).

How can we explain this sharing by extant large-bodied hominoids of these apparently derived features of cerebral morphology? We could suggest that the large-bodied hominoids possess these features because their last common ancestor did—that these were among those evolutionary novelties that distinguished their last common ancestor from other primates. We could, of course, also suggest that these features (and their apparent correlates) were selected for independently in the evolution of each extant taxon. In the former case, the uniquenesses generate a theory of phylogenetic relatedness: *i.e.*, the reason large-bodied hominoids possess these features is because their last common ancestor did. In the latter case, an explanation of independent derivation of these features of the brain is demanded by some other (unspecified but assumed) information.

But even these features of the brain are apparently not independent attributes. Only in large-bodied hominoids do pregnant females excrete the steroidal hormone, estriol—which is a reflection of these primates' being distinguished among primates in having relatively larger fetal adrenal glands and zones—and fetal adrenal secretion is directly correlated with encephalization (Czekala *et al.* 1988; Graham 1988).

Also among primates, large-bodied hominoids have the longest gestations periods—both absolutely and relative to female body size (Cross and Martin 1981). Is this, too, as has been suggested for humans, related to large relative brain size, and all the behavioral and other attributes that are supposed to go hand-in-hand with large brain-body ratios? On purely cladistic grounds, one could suggest that the development of a long gestation period (absolute as well as relative) in large-bodied hominoids is a feature that distinguishes them as a clade among primates because it had been an evolutionary novelty in their last common ancestor. And if this feature is indeed correlated with increased brain growth, size, and other brainy attributes, then, again, questions about the evolution of the human brain, the orang-utan brain, the chimpanzee brain, and the gorilla brain are, at some fundamental level, actually questions about the brain of the last common ancestor of these primates. As such, this is the level at which (at least some) questions of selection should be addressed.

So when studies suggest, as do those reviewed by Seyfarth and Cheney, that chimpanzees, unlike monkeys, may possess a rudimentary theory of mind—that these hominoids may recognize ignorance in others of their species, and that individual chimpanzees take active steps to provide other individuals with information they do not already have and even deceive others—are these observations of something specifically adaptive in the evolution of chimpanzees, or are these observations of something that was adaptive for the last common ancestor of all large-bodied hominoids? Perhaps a rudimentary theory of mind could arise only because of an enlarged cerebral cortex, marked cerebral asymmetries, relatively enlarged fetal adrenal gland and zone, prolonged gestation period, and production in the female of estriol. And, like these seemingly more tangible morphological and physiological features, a theory of mind (or the capacity to form a theory of mind) has come to be retained by the chimpanzee from the last common ancestor it apparently shared with other large-bodied hominoids.

To reiterate, the question should be: On whom does or did selection act, and for whom is or was something adaptive? Was it the living species or one of its ancestors? Furthermore, for those chimpanzees we find enacting a theory of mind, can we assume that the "settings" (for want of a better term than niche, econiche, environment, or something like this) in which we find these chimpanzees, or the selective pressures we believe are acting on these chimpanzees, are the same as those that would have impacted the ancestor in which a theory of mind first appeared? A trait that may have been adaptive for an ancestor, may *not* be in its descendants, who may retain that trait merely by virtue of phylogenetic accident.

But if chimpanzees have a rudimentary theory of mind because of primitive retention from an earlier hominoid ancestor; what can we say about the apparent lack of a theory of mind in the vervets, rhesus macaques, and Japanese macaques also discussed by Seyfarth and Cheney? If there are some developmental, physiological, or other fundamental aspects of the brain underlying why chimpanzees, the large-bodied hominoids as a group, and/or the last common ancestor of the extant large-bodied hominoids have a theory of mind and these Old World monkeys do not, the answer could be simple: A theory of mind is a derived trait for large-bodied hominoids; lack of a theory of mind is primitive for Old World monkeys. If there are not, then, things

about communication in Old World monkeys that they as catarrhine primates share specifically with hominoids to the exclusion of other primates, then it is not necessarily relevant that we say something about communication in any Old World monkeys in particular. Rather, instead of contrasting Old World monkeys with chimpanzees, we could just as easily discuss, for example, diurnal lemurs—who also have calls for predators and have been described as having escape strategies—as examples of primates lacking a theory of mind. Because the lack of a theory of mind would be primitive among primates, any primate example should do.

One should not, and in reality cannot, discuss adaptation (and function, for that matter), and consequently invoke evolutionary explanation regarding a certain taxon (such as a selection-explanation), without first embracing a hypothesis of its relatedness to other taxa. Often, however, a phylogeny is presumed or taken for granted, but without it being overtly acknowledged or the reason for choosing it over an alternative being specified. In order to enact the comparative approach, a phylogenetic scheme must exist before an evolutionary explanation can be generated in its details. But, as we know, hypotheses of relationships are not unimpeachable.

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