

mates with more resources, or be more attractive to such potential mates, or form more permanent pair-bonds, or something. How does coyness confer such an advantage? In short, what is the functional significance of coyness?

If some distinctive behavior actually has a phylogenetic origin, then we may suppose that it has (or has had) some functional significance, and that it has benefited those who had it. But if we find some distinctive behavior that has a cultural origin, then it may or may not be functionally important; it could be just a cultural ritual that does neither good nor harm to anyone. It is hazardous indeed to suppose that a particular ritual reflects some continuing adaptation to the cultural niche, or that it confers any advantage upon those who practice it. E-E describes a ritual dance performed by young couples in New Guinea, which is said to play a role in mate selection. Do young people there really select mates on the basis of this dance? Or do they pair off the same way every one else does it, on the basis of propinquity and availability?

Or consider the eyebrow flash. The author had convinced me with his earlier writings that the eyebrow flash is as characteristic a human behavioral trait as having hairy eyebrows is a morphological trait. Now he tells me that the Japanese learn to suppress it. I am puzzled. I now have to wonder about all the non-Japanese cultures: is it possible that we all learned it? I worry about the Japanese, how could they forego such a beautiful, expressive gesture? And why don't they see it as beautiful and expressive? Worse yet, are they likely to become extinct because they no longer have whatever advantage the eyebrow flash conferred upon all the rest of us (it must have been advantageous or we would not all have it, right)? But how can 100 million Japanese become extinct? For that matter, how could there be 100 million Japanese if they have such a handicap? The answer must lie in different selection pressures. The unique Japanese response must be an optimal adaptation to a unique environment (or there would not be 100 million of them), just as having the eyebrow flash must have been optimal for everyone else in the common environment that shaped everyone else. What was that unique environmental pressure that made nonflashing so successful? What does the eyebrow flash have to do with fitness, anyway? What are we talking about? Let us get on with the business of ethology.

**by Gerald Borgia**

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**Levels of selection and human ethology.** The first part of this commentary focuses on the last section of E-E's paper in which he describes his views on the relation of the various levels at which natural selection might operate and the study of human behavior. Although this represents a very small part of the material presented, this information is critical to my subsequent evaluation of the overview of human ethology he presents.

E-E correctly rejects the "survival of the species" notion which "ethologists have for a long time used" and he nominally embraces the inclusive fitness model as a means for explaining "altruistic" behavior. There is, however, some confusion in his presentation of this model, and, together with his inordinate reliance on models of group selection, he provides a rather curious view of patterns of benefit transfer in which "investment should pay off to any group member and not just immediate kin." What he views as man's tendency toward self-sacrifice, and a problem in the common interpretation of the inclusive fitness model, are the reasons he cites for this tendency toward group-wide altruism. But there are other means of explaining apparent self-sacrifice that are more likely and involve individuals maximizing inclusive fitness without relying on differential group extinction. This is significant because Williams (1966) provided cogent arguments concerning the unlikelyhood of group selection as a source of adaptation when it conflicts with individual interests. Moreover, individual competition for mates, wealth, and status dominate social interactions in most human groups (Murdock, 1949). Such behavior implies much less within-group harmony than intimated by E-E and could be expected had group selection molded patterns of social interaction.

Although E-E accepts the inclusive fitness model, there appears to be a basic misunderstanding about how it operates. He cites a study which gives it strong support (Massey, *op. cit.* 1977) but then argues that "To reckon only on the 50 percent of genes that a person shares with his full sibling, or parent, or child . . . is to oversimplify matters . . . the majority of a person's genes are shared with any other member of the group." There is a flaw in this argument which comes from the suggestion that the absolute level of genetic overlap between individuals should be used as the criterion of optimality for distributing benefits, rather than the relationship as calculated by identity in terms of descent. Hamilton (*op. cit.* 1964) pointed out that ordering benefit-giving priority according to identity by descent gives the most evolutionary stable pattern for beneficent behavior.

Alleles specifying different patterns of beneficence are assumed to be in competition. Those that follow the pattern Hamilton specified gain most, on the average, from the combined effects of likewise beneficent copies of themselves while not wasting aid on potential competitors, and therefore become dominant in natural populations. (Seemingly indiscriminate beneficence within breeding units might also evolve were alleles able to recognize and direct benefits toward identical copies in other individuals, but such a pattern seems unlikely; see Hamilton, 1964; Alexander and Borgia, 1978.)

These considerations suggest that, contrary to E-E's suggestion, individuals commonly discriminate in aid-giving within social groups, and group selection cannot be considered the dominant force in shaping patterns of behavioral adaptation in human populations.

Consistent application of E-E's view that all members of a group exchange benefits without regard to differences in relationship leads to some curious predictions about intragroup behavior. For instance, one is disposed to assume that aggression within groups is initiated because of anticipated advantage to the aggressor which ultimately allows him to gain control of some scarce resource. However, strict adherence to the notion that human behavior is a product of group selection causes us to surmise that this behavior occurs for an entirely different reason. We might guess, for instance, that aggression functions to equalize the distribution of resources among group members. The lack of discussion of the functional significance of many supposed adaptations, together with ambiguity caused by E-E's assumptions about levels of selection, prevent the reader from correctly understanding his intent, particularly where there are several possible explanations for a behavior. Such problems intensify if one attempts to test some of the proposed models.

E-E uses common ethological terms such as appeasement, canalized aggression, and agonistic buffering, which were in use before the concept of inclusive fitness was generally applied to behavioral models. These were defined in terms of species or group level adaptation, and may hence refer to functions that were of putative benefit to the group or even to mechanisms whose existence would not be predicted if selection were considered only at lower levels. The use of these terms leads to ambiguity in the discussion of the adaptive basis of behavior.

For example, when E-E says that smiling or gaze aversion "blocks aggression," does he mean that expression of these facial gestures by a girl toward a boy who had previously hit her makes that boy *incapable* of hitting her again? We have to consider how this gesture might cause the boy not to strike her. Does he refrain from attack because the gesture communicates (1) that she is not a threat and has nothing he wants; (2) that she will report the attack to a higher authority and he will be punished; or (3) that she has been harmed and he has been programmed to avoid harming other group members? Unless we know why the boy refrains from hitting her, the term "blocks aggression" is meaningless, assuming that we are concerned with determining the evolutionary consequences of this act. Perhaps the only way to remove such ambiguity from behavioral analysis is to drop, or at least carefully redefine, much of the common ethological jargon.

E-E shows some concern about Wilson's (*op. cit.* 1975) claim that ethology will be incorporated as part of a new science to be called sociobiology. What we label the study of behavior seems relatively unimportant compared to the need to produce a discipline that develops testable predictive models of behavior. The continued use of ethology as a label for the study of behavior will depend on how successfully those who call themselves ethologists apply advances in selection theory to the study of behavior.

**by William R. Charlesworth**

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**"It's true, but we don't know why:" Problems in validating human ethological hypotheses.** E-E's paper represents in summary form a great portion of his total effort in the field of human ethology: the themes, arguments, illustrations, and photos will be familiar to those who have kept up with his work over the past ten years. During this time, E-E has logged at least 15,000 hours in the field filming human behavior in many different cultures, and he has spent at least twice that much time analyzing films. This vast and singular effort qualifies for serious consideration his claim as to the universality of certain behavior patterns.

In my opinion, there is no question that E-E has identified universal human behaviors. I recognize them on film and in vivo, and am confident that because of such universal behaviors people manage, despite great cultural and linguistic differences, to get along with each other at tourist resorts, in United Nations assemblies, and in close quarters on transcontinental trains. Actually, it is odd

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