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M. Moynihan

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THE COINCIDENCE OF MIMICRIES AND OTHER
MISLEADING COINCIDENCES

In a recent note in *The American Naturalist* Barnard (1979) criticized the concept of social mimicry as described and interpreted by early workers (Moynihan 1960, 1962, 1968; Cody 1969, 1973*a*, 1973*b*). This concept was originally used to explain certain remarkable convergences of bright or otherwise conspicuous colors (including black and white) among not particularly closely related species of birds which often associate with one another in mixed flocks. It was hypothesized that the similarities of color facilitated the associations, and that they had been favored by natural selection because they had this particular effect.

Barnard proposed another explanation, apparently as an alternative. He suggested that the resemblances which have been ascribed to social mimicry are not only protective but that at least some of them are examples of Batesian and/or Müllerian mimicry. The suggestion is not entirely new since the possibility of such functions was mentioned in several of the papers cited above.

The hypothesis of social mimicry still seems to me to be plausible, insofar as it goes and if phrased in suitably cautious terms. Barnard's critique, however, does provide a convenient occasion to review some of the factors that influence or control divergence and convergence of superficial characters among associated species, and to comment upon the kinds of evidence that may or may not be pertinent in the context.

One should begin with a brief consideration of problems of communication (details and references in Moynihan 1970, 1978, 1979). Why are conspicuous colors selected for in the first place? The answer must depend upon the sensory capabilities of the animals involved, as well as on their biological and physical environments. Vivid colors can subserve a variety of functions, simultaneously or sequentially. In many species of birds they may appear, to a human observer, to have little to do with either interspecific gregariousness or predation. They may seem to be primarily concerned with intraspecific display (consider the peacock) or with the maintenance of reproductive isolation (e.g., the breeding plumages of the males of holarctic ducks). The colors must also, however, have multiple consequences. They can hardly fail to be noticed by predators and therefore to have eventual effects upon defenses against predation. They may also have repercussions upon other interspecific relations.

There are constraints upon the consequences. Resources are limited; both time and energy are usually in short supply. Any time or energy saved by a more efficient performance of one activity can be used to advantage for some other purpose, for rest and recuperation if nothing else. One animal always occupies or preoccupies some resource—space at least—which would otherwise be available for use by another animal. Neighbors are seldom irrelevant to one another. Thus, there will often be selection pressure in favor of making the interactions between any two animals as rapid and as definite, positive or negative, as possible in the

circumstances. This may help to explain why so many intraspecific encounters are stereotyped and also why some interspecific relations take the forms that they do in actual fact.

Animals apparently cannot perform an unlimited range of different kinds of social responses. Among birds, all or most interspecific social reactions seem to be extrapolations from intraspecific behavior. Again there are consequences. In many cases, once a species begins to react socially to other species, there is pressure for the sign stimuli used in intra- and interspecific relations to converge, to come to approximate one another. Why this should be so is debatable, but the phenomenon seems to have occurred repeatedly in the course of evolution. The crucial factor may be "economy". Most animals cannot cope effectively with sign stimuli of more than limited diversity. Approximation is, of course, a sort of simplification, a reduction of diversity. The process of approximation can go in one or several directions, depending upon the nature of the interspecific relations, whether they are unilateral or mutual.

Convergence of sign stimuli may be mimicry. The question is what kind(s)? Here it may be useful to insert some specifications and definitions. The concept of social mimicry probably should be extended beyond its original application. If the general arguments in favor of such mimicry are valid, they should apply to other animals in addition to birds, to other reactions in addition to flocking, and to other sensory modes in addition to vision. Cases of convergence in color pattern or voice to regulate hostile (agonistic) relations are known among Andean birds. There are more exotic examples. Thus, for instance, it must be supposed that some of the convergences of chemical stimuli, pheromones, in symbiotic associations of insects (many references in Wilson 1975) have been selected for because of their social effects. Some of the mutually beneficial relations among ants and their associates are difficult to interpret in terms of classical Batesian and/or Müllerian mimicry. The principal benefits secured are food and shelter from the elements.

Other cases of convergence in insect symbioses (descriptions in Hölldobler 1971) would seem to be "aggressive mimicry," more or less in the same sense of Brower et al. (1960). It is evident, and suggestive, that social and aggressive mimicry can be combined in some of the same animals and relations. The implications of such coincidences, and other possible or probable combinations of mimics, are considered below.

For the time being, it may be sufficient to note that a broad definition of social mimicry would include all convergences evolved to control or canalize social interactions among individuals of different species.

Both "convergence" and "to" are key words. Some resemblances are not convergent (they may be inheritances from a common ancestor) and some convergences are not social (they may be similar adaptations to a common background). It is surprising how often these qualifications have been disregarded. Thus, for instance, any discussion of the possibility that the aardwolf, *Proteles cristatus*, is a mimic of the striped hyaena, *Hyaena hyaena*, must inevitably be inconclusive (Gingerich 1975). As the two species are related phylogenetically, and occur in the same habitats, the undoubted resemblances between them can be explained in too many (and not necessarily exclusive) ways.

The alarm calls of passerine birds in mixed flocks, cited by Barnard, are equally problematical. Many of these birds utter similar ventriloquial notes, but it is by no means certain that the shared character should be ascribed to mimicry. This type of note may be primitive in passerines. Similar notes are uttered by related species which do not usually associate in mixed flocks, and many nonpasserines which do associate in mixed flocks, e.g., coraciiform birds in West Africa, utter very different sounds in corresponding circumstances. Perhaps all that can reasonably be said on the subject is that there has been comparatively little selection for divergence in the evolution of the alarm calls of passerines.

Several other statements or suggestions by Barnard seem to me to be dubious for one reason or another. I simply do not understand what can be meant by the statement "The problems of associating are presumably similar wherever mixed flocks occur, but the pressures of predation are vastly different" (Barnard 1979, p. 616). It is difficult to imagine what factors, in the real world, could vastly affect one side of the equation without also, directly or indirectly, having appreciable effect upon the other side.

There is no cause to be surprised that social mimicry is "not more widespread" (Barnard 1979, p. 616). It is widespread enough. Perhaps the examples most likely to be noticed by human observers, i.e., convergences of visible characters, are more common in the tropics than in the north temperate zone. The fact that social mimicry was first invoked by biologists who have worked in the tropics may not be an accidental coincidence. The elaboration of interspecific relations may be diagnostic of the tropics (Dobzhansky 1950). It should also be noted, however, that "social parasitism" among insects, presumably with chemical mimicry, is supposed to be more common in cool climates than in hot ones (Wilson 1975).

More important is the question of the tastefulness or distastefulness of visually conspicuous birds. Barnard cites Cott and Benson (1971), but he extrapolates too much from their data. The data are slightly ambiguous or discrepant (they do not always agree with Cott 1946). They do seem to show that there is some variable positive correlation between distastefulness and conspicuousness. They do not show that conspicuous species which associate in mixed flocks are either more or less distasteful than equally visible species which do not associate in such flocks. There is even a hint that the conspicuous species which occur alone or in unmixed flocks are the most distasteful of all.

Barnard stresses that some experiments have shown that predators may preferentially select prey that appear to be "odd." In certain conditions in the laboratory, some hawks and falcons, given a choice among various kinds of prey (chicks, mice, or pigeons of the same or different colors), will often attack individuals of the prey species which look different from their companions, or from the prey to which the predators had forcibly been accustomed earlier. The experiments are convincing; this does not mean that they are relevant to interspecific mimicry in the field. Most of them are concerned with differences in color among individuals of the same species. One experiment compares chicks with mice—apples and oranges—in succession but not at the same times throughout a whole series of tests.

The only natural example cited, another hyaenid (another coincidence), the

spotted hyaena, *Crocuta crocuta*, reinforces the point. Kruuk (1972) and others have shown that spotted hyaenas choose their prey with discrimination. They seem to choose individuals which appear to be odd, but the chosen individuals probably appear to be odd because they are weak or sick, or otherwise vulnerable. Again, this has little to do with interspecific mimicry or natural selection against differences in appearance among different species.

There is, in fact, other evidence to suggest that differences in appearance can actually be protective in some circumstances. Many predators are known to form specific "search images" (Tinbergen 1960). The images seem to facilitate the discovery of similar prey but impede or delay recognition of different-looking prey. This may explain why there has been selection for "aspect diversity" in some assemblages of prey species (Rand 1967), and for other functionally equivalent adaptations such as Protean displays (e.g., Driver and Humphries 1970) and some kinds of polymorphism (references in Endler 1978). Obviously, selection for or against resemblances among individuals and species must be complicated. The result of conflicting selection pressures in any given area must depend upon many factors.

None of the evidence cited above would suggest that convergences among species that react to one another socially, as friends or rivals, are most likely to begin for Müllerian or Batesian reasons (perhaps an implication of Barnard's argument, if not stated as such). There is, on the other hand, much evidence from the field that such convergences really do work socially. Individuals of different species which look, sound, or feel alike do tend to interact with one another or with the same "third parties" more closely or more frequently, on the average, than do individuals of other species which do not resemble one another.

Certain convergences among flocking birds may not be protective at all. Others may be indirectly protective in non-Müllerian and non-Batesian ways. Barnard is inclined to discount impressionistic evidence, e.g., the observation that conspicuous individuals in mixed flocks in Panama behave as if they were vulnerable to predation (see also Buskirk 1976). Of course, impressions are merely indicative, but they may be the only pertinent data obtainable outside the artificial conditions of the laboratory. (In the particular case of the Panamanian flocks, I might add that their conspicuous members are much less confident and bold than the African drongo, *Dicrurus adsimilis*, which does seem to be distasteful and to be the model for at least one Batesian association frequently cited by Barnard and others in discussions of avian mimicry. The difference in behavior leaps to the eye.)

One further point deserves to be made. There is an aspect of some convergences which is not discussed by Barnard (nor by most other authors) but which may still be of considerable evolutionary significance. It is quite possible, even probable, that mimicry is often used to a variety of effects. How or why should this occur?

I think that it may be assumed that social mimicry does exist. Most people would accept that Batesian and Müllerian mimics exist. There probably are other kinds of mimicry in existence (Wickler 1968). They are distinguishable in logic, but they can be combined in practice.

Some possible developments may be illustrated by hypothetical examples. It

has already been mentioned that bright colors may begin to be favored by natural selection for various reasons. One would expect the same to be true of other conspicuous characters. A conspicuous character may subservise only one function at first. Sooner or later, however, there should be pressure for the character to acquire other, additional functions, partly for economy. Thus, for instance, if the character is effectively social in one context, it is quite likely to come to be used socially, perhaps in new ways, in other contexts (*viz.* the relations between intra- and interspecific patterns).

There may be other cumulations of functions. Any conspicuous character that has been selected for must be advantageous on the whole, somehow, somewhere. Yet it can hardly fail to have some entailed disadvantages, of lesser but not negligible importance, such as increased exposure and vulnerability to predators or competitors. In these circumstances, the animals exhibiting the character should strive for the best possible ratio. They should try to minimize the disadvantages. This may be difficult or impossible to carry very far without sacrificing too much (*i.e.*, the character itself). They should also attempt to maximize the advantages. One way of maximizing is to multiply uses. Thus, again for instance, there should be pressure, in many cases, for a species which has developed a conspicuous character for social reasons to go farther, to develop some repellent quality (*e.g.*, distastefulness) to discourage enemies, and then to use the existing character to advertise (to different respondents) the disagreeable as well as the agreeable aspects of its personality or being. The species might, in other words, add Batesian and/or Müllerian mimicry to social mimicry. The principle is simple. One might as well be hanged for a sheep as a lamb.

Of course, there may be variations in the sequences of cumulations. One can easily imagine circumstances in which social mimicry could be added to Batesian or Müllerian mimicry. (It is unfortunate that so little is known of, or published about, the social behavior of the brightly colored tropical butterflies which are distasteful themselves or live in the same areas as distasteful forms of similar appearance. Do they interact with one another, positively or negatively, directly or indirectly?)

Coincidences of different kinds of mimicries may be common. There are reports of intergrades and overlaps between the classical Müllerian and Batesian types. Other types, aggressive, "Mertensian," "Peckhamian," etc. (Wickler 1968), apparently can be combined with one another and/or with social mimicry and/or with any one or all of the various convergent resemblances which have evolved for protection against predators.

The last sentence is suggestive in its awkwardness. Mimicry is not always, perhaps not often, an "either . . . or" proposition. The awkward and deceptively noncommittal "and/or" does seem to be a more appropriate combination of conjunctions for many contexts.

The assumption that coincidences may be common can help to identify new problems, or to put old problems in new perspective. Consider the Panamanian flocks again. The fact that the bright colors of some members are not conspicuously Batesian or Müllerian may be more remarkable, from an evolutionary point of view, than their obvious social effectiveness. This, in turn, should tell us

something about the local environment, and especially about predation. The most dangerous predators of these flocking birds may be animals (mammals, snakes?) that do not make much use of color vision. The possibility is at least worth investigating.

There is a moral to be drawn in conclusion. Social characters may have more than one function. One type of mimicry does not necessarily preclude others. Combinations of different types of mimicry might even be expected in many circumstances. They do not seem to occur in all circumstances. Both combinations and apparent absences of combinations need to be understood and explained. They are not likely to be fully understood without careful observation in the field as well as in the laboratory.

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M. MOYNIHAN

SMITHSONIAN TROPICAL RESEARCH INSTITUTE
P.O. BOX 2072, BALBOA, PANAMA

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