

## NOTES AND COMMENTS

### THE PRINCIPLE OF METACHROMISM: A CRITIQUE

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A recent article by Hershkovitz (1968) concerning metachromism in mammals has aroused considerable interest in evolutionary trends of color change in mammals. The essential tenet of Hershkovitz's hypothesis is that saturation, bleaching, and elimination of pigments of the integument in mammals follow a unidirectional, similar, and irreversible pathway from agouti to albino. This trend was termed *the principle of metachromism*. A similar unidirectional change in loss and elongation of hair was also said to be correlated with metachromic processes. All mammals supposedly exhibit the trends, and any of them unfortunate enough to acquire albino pelage or hairlessness are considered to be doomed to extinction by Hershkovitz unless the animal "occupies or evolves into a niche where color and/or pelage have no survival value."

In my opinion there are four points of contention relating to Hershkovitz's arguments for a "principle of metachromism," namely, (1) the evolutionary relationship between the primitive hair pattern (agouti) and derived patterns is debatable; (2) evidence for "inadaptive" features of the integument given in his examples is insufficient; (3) there are no data to support the claim that color changes are irreversible; and (4) Hershkovitz's generalizations derived from observed color trends in marmosets are unwarranted. My evaluation of these four points follows.

Agouti tegumentary features are considered primitive by Hershkovitz (p. 556, 558, 573). Change from the basic agouti condition is considered derived ("progressive"), and he states that "Breakdown of the agouti pattern . . . is a character of progressive mammals, generally" (p. 558). From these comments it does not directly follow that "metachromism applies to all species whether terrestrial, arboreal, subterranean, aquatic or volant, and to all color changes in hair and skin, whether ontogenetic, phylogenetic, geographic, seasonal, sexual or individual," as Hershkovitz says it does. He declares (p. 573) that "Each of the various pelage types, including prenatal, juvenile, preadult and seasonal, is independently controlled genetically with respect to its growth pattern and color, and each evolves independently." The latter statement directly contradicts a substantial part of the former, since there are no means of unequivocally determining the sequence of evolutionary change from prenatal to

adult pelages if each pelage type evolves independently. Such generalizations are not supported by Hershkovitz's data. Moreover, his examples of marmosets demonstrate the sequences of color change only insofar as primitive (agouti), "advanced" (albino), and intermediate stages are defined on the basis of those animals, and in particular, *Saguinas fuscicollis*. The result often is a rather improbable scheme of color change in mammals, as exemplified by the hypothetical dispersal of prototypes in the marmosets of the *Saguinas mystax* group (Fig. 6, p. 563). Other phylogenies of marmosets can be constructed which are consistent with the data by assuming other color pathways leading from a primitive agouti condition. This does not seem unreasonable considering the complexity of color inheritance in mammals (see below), and since no evidence is provided to support his postulated sequences.

Hershkovitz implicitly creates an artificial dichotomy between physical and biotic environmental factors as they relate to adaptive features in mammals. The environment of an organism includes other components in addition to the physical factors to which it is exposed. It seems illogical to infer, as Hershkovitz does throughout the paper, that an animal is not adapted in its tegumentary characteristics when they are explained by "social selection," and not by parameters of the physical environment or by predation. Selection in a framework of social or other biotic factors (e.g., competition) is known to produce features that are adaptive. An example in mammals is aposematic coloration in skunks. Also, it seems completely reasonable that "social selection" or other selective factors may represent primary evolutionary forces responsible for change in rate or direction of pelage characters. The determinant as to whether selection is operating on the rate or direction of evolutionary change is directly related to the variance of genetic components and to the particular selective factors affecting the gene frequency. Hershkovitz cites no evidence to substantiate the claim that selection can "accelerate, retard and terminate metachromic processes but cannot alter, reverse or deflect them from their course" (p. 573).

The fact that most small terrestrial mammals (e.g., most rodents, insectivores, rabbits) are rather uniformly drab in color suggests that selec-

tion has favored individuals in these groups that exhibit predator escape mechanisms such as concealing coloration. Alternatively, many other mammals (e.g., primates, many carnivores) are relatively free of predation, and therefore selection for mechanisms of predator avoidance is reduced or absent (as Hershkovitz suggests, p. 573). Consequently, experimentation with tegumentary coloration related to social activities would be favored by selection in individuals of those species if a reproductive or competitive advantage accrued. In highly social forms of the latter group, bright coloration often plays a prominent role in mate selection and group acceptability. Color of pelage in marmosets almost certainly is highly adaptive, not inadaptable as Hershkovitz states (p. 556). For if so, there should be little local variation in color, because local variation in secondary sexual or social-related features of highly social mammals would be selectively disadvantageous. Also, one would expect to observe discordant patterns of geographic variation in tegumentary features among different social species, since different species would not necessarily share common selective pressures geographically. These considerations provide an alternative explanation to Hershkovitz's interpretation (p. 556) of differences of the geographic relation of pelage coloration with the environment in the marmosets *Callithrix argentata* and *C. jacchus*.

If selection in marmosets has a social basis, one would predict that the body parts affected would involve principally the frontal region (chest, shoulders, and facial features). This is the case in all of the examples of marmosets Hershkovitz cites.

Variation in the brightly colored Amazon squirrels *Sciurus igniventris* and *S. spadiceus* differs from that in the marmosets. Hershkovitz records a broader range of individual and local variation for these animals, and suggests (p. 557), correctly I think, that this probably resulted from their different social structure and greater mobility. The reduction of such variation in the marmosets plus their high degree of social organization suggests that selection operates strongly to enforce rather uniform color patterns in these mammals. If so, the tegumentary features are adaptive.

Variation of tegumentary characters in marmosets probably does not occur independently of the environment. In any case, Hershkovitz never rigorously demonstrates that the color traits he describes are inadaptable, and the burden of proof rests with him.

There is no convincing evidence to substantiate the claim (p. 556, 557) that "degenerative" stages of color are irreversible. Further, no genetic evidence is provided for the "degenerative" nature of color change. Even if one assumes that agouti is primitive and that albino is "advanced," there is no demonstration by Hershkovitz that albino

and the intermediate color stages are irreversible as described.

There occur to me two ways in which reversibility of color change can be considered improbable. First, rates of reverse mutation, although not known for color traits, probably take place at a rate that is several orders of magnitude less than "forward" mutation. Thus, evolutionary reversals should be considered less probable than forward mutations but not ruled out altogether. Secondly, color reversal would be more unlikely in additive genetic systems that are highly canalized or otherwise buffered by genic or allelic modifiers than in a system regulated by simple dominance effects. The color trends Hershkovitz cites for marmosets may be due to such additive effects. Indeed, the evidence suggests that the traits are highly canalized in particular geographic areas. Both additive and dominance effects persist in known genetic systems affecting tegumentary color. A directional trend that could result from phenomena of the sort described here can easily be misinterpreted. For example, a phyletic color trend, each step of which was adaptive, would appear as an example of metachromism. Presently there is not sufficient evidence to determine the extent to which color change is reversible, but several lines of evidence are suggestive.

The five principle allelomorphous systems that influence coat color in mammals are the agouti, brown, albino, dilute, and extension series (Searle, 1968). All produce effects on intensity and distribution of melanins in the hair, although they differ functionally in certain respects. All of the loci affect both eumelanin and pheomelanin pigments. In laboratory strains of the house mouse, *Mus musculus*, a dozen alleles are known for agouti alone, and several have been reported for most of the other series (ibid.). It is not a valid argument to disregard genetics of laboratory animals simply because they likely would not survive in natural situations or because they represent "simulated regressions" of metachromic processes. The important fact remains that considerable allelic and genic variation does exist in forms that have been studied extensively.

The effect of several genes at the agouti locus is to dilute or magnify the intensity of the agouti band on the hair. Thus, a dark phase, such as that prevalent among certain populations of small mammals on lava beds (see below), can result from influence of alleles at different loci as well as from different alleles at the agouti locus. In *Mus musculus* there are at least six alleles (three dominant, three recessive) at different loci that produce a dark or completely black pelage (ibid.).

One well known example of heritability of naturally occurring genetic variants is an agouti polymorphism in *Peromyscus maniculatus* (Blair, 1947). Two alleles, buff and gray, of a major color gene affecting the agouti band on the hair

are known from certain populations. The buff allele is dominant. The relative frequency of each allele is dependent on the color of the substrate where the mice occur. The most likely interpretation in view of the evidence is that selection is responsible for determining frequencies of the buff and gray alleles in populations on differently colored substrates. Numerous other examples of color polymorphisms are known in natural populations (e.g., in muskrats, foxes, bats, other rodents).

Hershkovitz (p. 571) states that, despite the improbabilities ("Transition from the agouti to the saturate blackish or brown grade is extremely perilous and odds against survival in a terrestrial but non-subterranean niche are overwhelming."), an albinotic race of the pocket mouse, *Perognathus apache*, arose on the White Sands of New Mexico. He suggests that this form is irrevocably confined to the White Sands, and that the race cannot survive beyond its range. I trust that no one would deny that the race, as presently defined, would disappear if the White Sands turned brown, and that the race by definition is confined there. He suggests that the form may have resulted from colored invaders of the sands that mutated directly to the pale condition. In any event, the process is suggestive of the adaptability of color change. There is no *a priori* reason to believe that dark color mutations (reversals?), if present, would not be favored in the event the sands did, in fact, turn brown. Finally, the fact that a pale form of mouse does exist on the White Sands indicates to me that the color transition to white in this case was anything but perilous; in fact, it obviously was highly adaptive.

Certain mammals (e.g., weasels, snowshoe hare) exhibit seasonal changes in color of the pelage. In winter the coat is wholly or partially white, and in summer it is brownish. Seasonality of color change is absent in populations of weasels in North America that occupy warmer areas (Hall, 1951). The ability to change color with season also varies geographically and it is heritable (*ibid.*). In the hare, *Oryctolagus cuniculus*, the Himalayan allele at the albino locus induces color change and is temperature dependent. Rabbits exposed during ontogeny to low temperatures show increased darkening of the skin and fur. Color changes induced by photoperiod are known in mink, weasels, and the snowshoe hare (Rust et al., 1965). Apparently these developmental and seasonal changes result from hormonal responses to light intensity, temperature, or other environmental cues (*ibid.*). In any case, the adaptive significance of such changes seems clear, and the flexibility of color pattern in these forms is evident. Also, the developmental control of color change in *Oryctolagus* contradicts Hershkovitz's assertion that ontogenetic changes in color are always independently evolved (p. 573).

The observations of hybrid marmosets are not unexpected in view of the unpredictable nature of subspecies and species crosses. They do not provide unequivocal evidence for metachromism. Also, when Hershkovitz states (1) that each pelage type (age- or season-related) is independently controlled genetically with respect to color and growth pattern (p. 573), (2) that each evolves independently (*loc. cit.*), and (3) that hybrids are intermediate (*loc. cit.*), he clearly delineates a means for reversibility of chromatic succession.

The important aspects of the comparative genetics of coat color may be summarized as follows: (1) gene action at a number of different loci can lead to formation of such pelage colors as black and white, as well as others; (2) color genes usually are epistatic and often pleiotropic; (3) similar color expression may result from a dominant allele at one locus or a recessive allele at another; (4) the evolution of coat color involves both major allelic substitution and gradual multifactorial change; and (5) dominance evidently has evolved at the same and at different loci for different color traits. Furthermore, it seems clear that there have been different alleles incorporated into the genomes of different species, so that wild-type alleles in one species are mutant in another. The evidence indicates that irreversibility is not characteristic of the inheritance of tegumentary color in mammals. The processes discussed above indicate to me that color inheritance is not necessarily a unidirectional phenomenon, but rather that color change, although often complex, operates within a framework of mutation, natural selection, and adaptation. The latter processes would be directional in the case of adaptation of an organism to environments changing in a directional manner. Clearly, color traits evolve in different ways. The particular phenotypic manifestations of color may result from either different allelic or genic combinations. Although it is doubtful to me, the marmosets may have evolved in the way Hershkovitz describes. In view of the genetic evidence, however, there appears to be no support for Hershkovitz's arguments or demonstrations for a *principle of metachromism*.

Examination of data on small mammals from lava beds and the White Sands in the Tularosa Basin, New Mexico, suggests an entirely different interpretation than that of Hershkovitz's (p. 570, 571). All of the forms that exhibit definite concealing features of the pelage are ecologically isolated to a large extent from nearby populations of those forms. I refer to populations of the species *Spermophilus variegatus*, *Perognathus intermedius*, *Peromyscus difficilis*, *Neotoma albigula*, and *N. mexicana* on the lava flow; and to *Perognathus apache*, *Spermophilus spilosoma*, and *Peromyscus maniculatus* on the White Sands (Benson, 1933). In effect, these populations are geographically isolated. Species not exhibiting a distinct

population on the sands or lava beds are representative of contiguous populations adjacent to and including those areas. My interpretation of the available data is that the degree and duration of isolation are determinants of the extent to which the forms inhabiting the White Sands and the Malpais have differentiated. Gene flow between populations occurring on and adjacent to either the lava or sands may tend to obscure any change toward concealing coloration. The effectiveness of gene flow is dependent on the selection coefficients involved, the rate of gene flow, and the relative size of the populations in and outside the lava beds and White Sands. Differences in these factors could account for the differences of "chromatic adaptability" (p. 571) between the mammals in the two areas noted by Hershkovitz. The importance of gene flow at these places also was recognized by Benson (1933), and by Hooper (1941) in his comparison of mammals occurring on lava beds in Valencia County, New Mexico, and on the Malpais of the Tularosa Basin.

A notable exception to the pale forms that inhabit the White Sands is the endemic pocket gopher, *Geomys arenarius brevirostris*, which is darker than individuals from nearby populations of the species. Benson (1933) attributes the darkened condition to the gopher's occurrence in wet washes where the soil is consistently wet and darker than the surrounding dune sand. Blair (1943) suggested that the form has only recently been isolated in the White Sands.

The difference in "chromatic adaptability" between forms on the Malpais and on the White Sands is best described as the result of differences in the degree of similarity of the habitats in each of those places from those of the surrounding areas. Ecologically, the habitats of the White Sands and adjacent areas differ less than the habitats in and outside the lava beds. Consequently, forms on the Malpais have differentiated to a greater extent. The amount of differentiation in forms on the White Sands resembles closely that observed in populations on lava beds studied by Hooper (1941). In the latter it was noted that most of the habitats adjacent to the lava beds were ecologically similar to those on the lava flow, and the mammals there have become little differentiated.

The contention (p. 574) that a trend toward albinism inevitably leads to extinction unless the pelage has no survival value is not founded on any evidence known to me. All integumentary features that are favored by natural selection would have a relatively high survival value. The polar bear is not a "geographically peripheral animal which, as a dominant predator, evolved beyond the need for a particular pelage in order to survive." Rather, it seems to me that it is a dominant predator in its environment because it evolved a particular color of pelage, namely, a

concealing white (or nearly white). Nor is there any evidence that the African mole rat, *Heterocephalus glaber*, "having lost both color and pelage, except for a few vibrissae, evolved into an underground habitus for survival" (p. 574).

Generalization to other mammals from one or a few examples of color change in marmosets is unwarranted on the basis of the foregoing evidence. Given that color patterns in the marmosets examined do reflect the sequences of color change postulated by Hershkovitz, it does not follow unequivocally that other mammalian species or even other marmosets also exhibit the same or similar trends as Hershkovitz infers. This is so because of the complexities of the genetics of tegumentary features. This kind of fallacious extended reasoning is clearly demonstrated by Hershkovitz's explanation of color phenomena in polar bears and in lava bed and White Sands rodents.

In view of the above considerations, it is my contention that (1) the supposed trends of color change in marmosets and in other mammals sponsored by Hershkovitz are not adequately supported by the examples he presented; (2) his hypothesis is too simplistic in view of the known complexities of color genetics and of evolutionary processes of mutation, natural selection, and adaptation; and (3) his hypothesis is insufficient for explaining evolutionary change in mammalian tegumentary features in view of alternative explanations that, in my opinion, are more parsimonious and better supported by the evidence.

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