

SHORT COMMUNICATIONS

Formalizing the Avoidance-Image Hypothesis: Critique of an Earlier Prediction

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Two papers on Parasitic Jaegers (*Stercorarius parasiticus*) that were recently published in this journal have reported tests of Paulson's (1973) avoidance image hypothesis: Arnason (1978) and Furness and Furness (1980). The authors of these papers, as well as Paulson (1973: 270), fail to distinguish the process by which apostatic selection operates from its end result—a frequency-dependent equilibrium between different morphs. The consequence of this confusion of process and result is that both of the contrasting (and seemingly contradictory) outcomes of these jaeger studies could be predicted from the avoidance-image hypothesis. Because either of the two possible outcomes of these studies would have been consistent with the avoidance-image hypothesis, the studies say very little about the validity of the hypothesis.

Paulson (1973) developed and tested the avoidance-image hypothesis to explain the remarkable intraspecific variability in coloration in raptors. Although many seem skeptical about the idea, it remains the only generally developed explanation of the repeated evolution of color polymorphisms in diurnal raptors. According to the avoidance-image hypothesis, a novel color morph may invade a raptor population if its prey have sufficient visual acuity and intelligence especially to avoid raptors that have attacked them previously. In short, the formation of avoidance images is hypothesized to cause prey more strongly to avoid hawks similar in color to those that have attacked them previously than other hawks whose coloration is novel.

The most cogent argument against this idea was put forth by an anonymous reviewer of an earlier version of this paper. He argued that the whole idea is nullified by the fact that most vertebrates avoid any strange stimulus, thus placing a rare invading color morph at a strong disadvantage. I doubt this argument for three reasons. First, it assumes that special avoidance is necessary for the operation of the avoidance-image hypothesis, but this need not be true. A prey lacking an avoidance image for a particular color morph may simply fail to *perceive* that hawk as rapidly as it could have done if it had had an avoidance image for that color morph. Second, the literature on the avoidance of strange stimuli seems inconsistent. In Chapter 3 of "The ethology of predation," Curio (1976) reviews a literature supporting this idea for predators exposed to novel prey ("novel" apparently meaning new species of prey),

but, in the following chapter, Curio reviews another literature showing that predators preferentially attack odd prey ("odd" apparently meaning unusual individuals, e.g. color variants, of the same species). Third, so far as I am aware, all of this literature relates to *predators* responding to unusual prey, but the avoidance-image hypothesis relates to *prey* responding to unusual predators. For prey the problem is rather different: to forage efficiently prey species must filter stimuli such that they do not madly dash for cover at every novel stimulus. In short, some discrimination causing them more strongly to avoid certain danger (e.g. hawks of a color that have previously attacked) than any novel stimulus could be advantageous, simply because novel stimuli must occur fairly frequently.

Paulson (1973), Arnason (1978), and Furness and Furness (1980) largely fail to distinguish between the mechanism by which a frequency-dependent effect is obtained and the resulting frequency-dependent equilibrium between the morphs. All of these authors assume that rarity *per se* is the issue. Consequently, all of them predict that the rare morph will always enjoy an advantage in encounters with experienced prey. This prediction is based solely on the mechanism by which a search image (or, by analogy, an avoidance image) is formed, namely, that a familiarity with objects makes them easier to recognize and respond to (see Curio [1976] for a review of the literature on the formation of search images). Predicting that the rare morph will always enjoy a higher prey-capture rate is valid under two conditions: either (1) both morphs are equally easy for prey to perceive (i.e. they are equally noncryptic), or, if they are not, then (2) the rare morph must be held below the equilibrium frequency that would be achieved solely by apostatic selection because of some disadvantage it suffers outside of interactions with prey.

Contrasting with this mechanistic prediction is a prediction based on the relative fitness of the two morphs when they are at their equilibrium frequency. This prediction assumes that nonforaging aspects of fitness are unrelated to color. When this is the case and when the morphs are near their equilibrium frequency, then the per-individual foraging success of the morphs should be nearly equal. In the case of a light-dark color polymorphism, such as that of the jaegers, the assumption of equal visibility of the morphs is almost certainly false: one or the other of

the color morphs must be easier for prey to perceive. That morph which is least cryptic should be easier to avoid and also may be easier to incorporate into an avoidance image (see Gittleman and Harvey, 1980). In jaegers it is not obvious which morph will be less cryptic: light-phased jaegers are probably more cryptic when their victims see them against the sky, but dark-phased jaegers may be more cryptic when their victims see them against sea cliffs or the surface of the sea. To simplify discussion I shall assume from here on that, when the morphs are not equally easy to perceive, light individuals are more cryptic to prey than dark, a situation that probably holds for many open-country *Buteo* hawks. When the dark morph is more conspicuous, the fundamental problem for the avoidance-image hypothesis is to identify conditions under which dark individuals could be favored when they are rare. I do this below with the consequence that new and testable predictions are derived from the avoidance-image hypothesis.

The equilibrium frequency between the light and dark genotypes will occur when the effects of color on nonforaging, X , and on foraging, F , aspects of fitness are equal for the light, L , and dark, D , morphs:

$$f(X_L, F_L) = f(X_D, F_D). \tag{1}$$

To simplify arguments, I shall assume that $X_L = X_D$, that is that color is only affecting foraging success. Relevant to the avoidance-image hypothesis are the factors affecting F_L and F_D , which I shall write as the probability of capturing an individual prey that has or has not had experience with the predator morph times the frequency of that prey type.

$$F_L = P(L|N) \cdot n + P(L|ED) \cdot d + P(L|EL) \cdot l + P(L|EB) \cdot b \tag{2}$$

$$F_D = P(D|N) \cdot n + P(D|EL) \cdot l + P(D|ED) \cdot d + P(D|EB) \cdot b \tag{3}$$

In equation (2) $P(L,N)$ is the probability of a light-phased predator capturing a naive prey (naive prey hold avoidance images for neither morph); $P(L,ED)$ and $P(L,EL)$ are the probabilities of a light predator capturing prey that are experienced with dark and light predators, respectively; and, $P(L|EB)$ is the probability of a light predator capturing a prey having avoidance images for both light and dark predators. The probability terms in (3) are defined analogously. Frequencies of prey that are totally naive or are experienced with dark, light, or both predator morphs are symbolized by n , d , l , and b , respectively, and $n + d + l + b = 1$.

If light and dark predators were equally easy for prey to perceive, then $P(L|N) = P(D|N)$, $P(L|EL) = P(D|ED)$, and $P(L|EB) = P(D|EB)$. If it is also true that avoidance images are equally as easy to learn for light and dark morphs, then the foraging aspects of fitness for light and dark morphs will be equal when $P(L|ED) \cdot d = P(D|EL) \cdot l$. This will occur when $d = l$,

which will occur when the frequency of dark-phased predators is equal to the frequency of light-phased predators. It is exceedingly unlikely that all of these assumptions would hold and, therefore, that the equilibrium frequency for the light and dark morphs would be 1:1. Most implausible is that light and dark forms would be equally easy to perceive, an assumption implicit in each of the preceding three conditional equalities.

Now consider the situation where light predators are more cryptic. In this situation, predicting the equilibrium frequency becomes an empirical problem for which no relevant data exist. The theoretical problem is why a conspicuous dark morph should ever invade a population of lights. Here, I address the conditions required for the increase of a dark morph when it is rare. As before, I simplify arguments by assuming that prey form avoidance images with equal ease for either morph, even though the dark morph is presumed to be more conspicuous. If light predators are more cryptic, this implies that $P(L|N) > P(D|N)$, $P(L|EL) > P(D|ED)$, and $P(L|EB) > P(D|EB)$. When these inequalities hold, the necessary condition for the invasion of a dark morph is that $P(D|EL) > P(L|EL)$. This is the essence of the avoidance-image hypothesis. It is not, however, a sufficient condition for the invasion of a conspicuous dark morph. The sufficient condition for invasion occurs when

$$P(D|N) \cdot n + P(D|EL) \cdot l > P(L|N) \cdot n + P(L|EL) \cdot l \tag{4}$$

or, when

$$l \cdot [P(D|EL) - P(L|EL)] > n \cdot [P(L|N) - P(D|N)]. \tag{5}$$

These inequalities follow from equations (2) and (3) because, on invasion, d and b are nearly 0; therefore, $n + l \approx 1$. Whether or not (5) will be true depends on the relative frequency of prey that are experienced, l , or inexperienced, n , with the light morph. If l is very small, then invasion by the dark morph cannot occur unless $P(L|N) - P(D|N) \approx 0$. From this relationship it follows that a shortage of naive prey is required for the invasion of a dark morph when dark is more conspicuous than light.

These arguments should make it clear that the two requirements for the invasion of a conspicuous color morph are, first, that the conspicuous morph is more successful than the cryptic morph at capturing prey that have formed an avoidance image for the cryptic morph, and, second, that there is a shortage of naive prey. The requirement of a shortage of naive prey suggests that, among species of predators, those that are most successful on a per attack basis will be less likely to evolve color polymorphisms than those that often miss prey. Could it be that the Peregrine Falcon (*Falco peregrinus*), a species that preys almost exclusively on birds, is not color polymorphic because it has an unusually high ratio of captures per chase?

A shortage of naive prey or victims seems quite

plausible for hawks of temperate areas in winter and for jaegers hunting around breeding seabird colonies. Naive prey accumulate either by new recruits entering the population of prey or by experienced individuals forgetting previously held avoidance images. Because most polychromatic raptors prey on higher vertebrates (Paulson 1973), memory may be long enough to contribute substantially to a shortage of naive prey and thus facilitate the invasion of rare and presumably less cryptic dark-color morphs. If the invasion of a conspicuous, dark morph is permitted by a shortage of naive prey, then the fitness of dark individuals will decline as their frequency increases, because an increasing proportion of the prey will form an avoidance image for the dark morph. This frequency dependence should be sufficient to produce a stable equilibrium between the light and dark morphs.

At the risk of redundancy let me restate how these arguments affect the prediction drawn by Paulson (1973), Arnason (1978), and Furness and Furness (1980), namely that the rare morph should have a higher per encounter rate of prey capture. This prediction is based solely on the mechanics of avoidance-image formation and makes the implicit assumption either that the morphs are equally visible or that the rare morph suffers a disadvantage in activities unrelated to foraging. If either of these assumptions is true, the prediction should hold, because fewer prey will hold an avoidance image for the rare than for the common morph. Note that the assumption that fewer prey will hold an avoidance image for the rare morph includes the assumption that many attacks, even by the cryptic and presumably more common morph, are unsuccessful and, thus, that many "educated" prey exist.

In contrast, it may be assumed that success in prey capture largely or entirely determines the equilibrium frequency, and that most populations are near equilibrium. In this case, neither morph will have an advantage. This is so because selection should have balanced the opposing advantages (1) of surprise enjoyed by the more cryptic morph and (2) of a frequent lack of special avoidance on the part of experienced prey that is enjoyed by the more conspicuous, but less abundant, morph when it attacks.

At Arnason's (1978) study site, jaegers of the rare light phase were significantly more successful as kleptoparasites than were dark-phased individuals. Furness and Furness (1980) employed the victim's speed of reaction to light- and dark-phased pursuers as an inverse measure of hunting success. They found no difference in response times to attacks by light- and dark-phased jaegers at a different locality where, again, light-phased individuals were rare. By the mechanics of apostatic selection and its attendant assumptions, Arnason's results support the avoidance-image hypothesis and those of Furness and Furness do not. In contrast, by the equilibrium frequency ar-

gument and its attendant assumptions, the results of Furness and Furness support the avoidance-image hypothesis and those of Arnason do not. Clearly, more and better data are required for an adequate intrapopulation test of this hypothesis.

I shall end by making two suggestions for future fieldwork in this area, both of which follow from the preceding considerations. First, simple observations on unmanipulated populations are unlikely to affect the credibility of the avoidance-image hypothesis strongly unless naive and experienced victims can be distinguished. Such might be possible if attacks by jaegers of the different color morphs were separately tallied for adult and for immature seabirds. If naive and experienced victims could somehow be distinguished, then two predictions follow: (1) the more common (more cryptic) morph should be more successful in attacks on naive prey, but (2) the rarer (less cryptic, but less often avoided) morph should be more successful in attacks on experienced prey. This test might be particularly feasible on Eleonora's Falcon (*Falco eleonorae*), because at certain colonies most prey (fall migrant birds) may be assumed never to have been attacked previously and because several falcons of either or both color morphs often repeatedly attack a single prey (Walter 1979). Thus, the relative success of light and dark falcons on *first* stoops would measure their relative crypticity and the relative success of attacks by like color morphs preceded by like and opposite color morphs preceded by opposite would estimate the advantage a novel morph would experience in attacks on experienced prey.

Second, an experimental field test of the avoidance-image hypothesis could be achieved by comparing the average hunting success of individuals of different color morphs before and after their relative frequencies were altered by removals. Breeding Parasitic Jaegers that forage around alcid or larid colonies should be ideal for such a test because their numbers are sufficiently low that their relative frequencies could be altered easily by removals. After a substantial proportion of the individuals of one morph had been removed, the remaining individuals of that morph should enjoy a gradual increase in foraging success. The change might be slow if most potential victims had already been attacked by individuals of both morphs, because some time would be required for previously established avoidance images to be forgotten. Over time, however, the average success of the remaining individuals of the reduced morph should increase, while that of the unmanipulated morph should decrease. A hidden weakness of this test, as well as the preceding one (if applied to jaegers), is the assumption that the color polymorphism is relevant to the time over which the observations are made. Because Eleonora's Falcon preys primarily on insects in its nonbreeding season but exclusively on birds in its breeding season, this hidden testing assumption certainly holds for this species.

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Kirtland's Warbler, Victim of Its Own Rarity?

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The recent history of the population of the Kirtland's Warbler (*Dendroica kirtlandii*) presents some baffling questions. The population declined from about 500 singing males in 1961 (Mayfield 1962) to about 200 in 1971 (Mayfield 1972) under intolerable pressure from nest parasitism by the Brown-headed Cowbird (*Molothrus ater*), which has expanded its breeding range to include that of the warbler only in the last 100 yr (Mayfield 1960). The cowbird has continued to increase. In the late 1960's it parasitized 70% or more of all Kirtland's Warbler nests and depressed the production of young to less than one fledgling per pair of adults per year (Ryel 1981). Measures to control the cowbird started in 1972 and are continuing with remarkable success, reducing parasitism to negligible levels (Shake and Mattson 1975). The production of young warblers immediately rose to rates never seen before and has remained at these high levels (Walkinshaw 1977, Nicholas L. Cuthbert unpubl.), setting to rest any doubts about the fecundity of the species. The decline in the population was arrested, but the number of adults has not increased as expected. The number of singing males has remained nearly level from 1971 to 1982, fluctuating between 167 and 243 (Ryel 1982).

What factors hold the population down in spite of excellent nesting success and survival of adults? Plainly, some combination of factors has been operating selectively against the young with special force in the last two decades. I will consider several possibilities, beginning with problems in the breeding season.

Intuitively, most biologists turn first to the breeding habitat. Indeed, this is restricted and specialized, consisting of extensive homogeneous stands of young jack pines (*Pinus banksiana*) on poor sandy soil in northern lower Michigan. This habitat is a transitory

phase in the forest succession occurring naturally after forest fire and in a modified form after cutting and planting. We suspect the habitat was most extensive in historical times during the 1880's and 1890's in Michigan and perhaps also in Ontario, Wisconsin, and Minnesota at the height of lumbering in the region, when forest fires were frequent and unretarded. At that time Kirtland's Warblers were found on their wintering grounds in the Bahama Islands much more frequently than today (Mayfield 1960). Jerome Weinrich (unpubl.) has calculated that suitable habitat also declined 40% from 1961 to 1971 along with the recent decline in warblers. Thus, a probable maximum and a recent minimum in population have corresponded with gross trends in the extent of suitable habitat. Without doubt, at some level of population, the available habitat would limit the number of birds, and, therefore, efforts to increase the habitat would be a wise conservation measure, but field study has not turned up evidence that the present habitat is inadequate.

Nesting success is good. Unmated individuals are rare. In nesting "colonies" the area used by each pair always seems much smaller than the space available to them. Measured territories have a mean area less than 4 ha (Mayfield 1960), but the area available on occupied tracts usually amounts to more than 12 ha per pair. When mapped, the territories are rarely contiguous on all sides as though crowded. In addition, many tracts of young pines that appear suitable to human eyes are not used by warblers. An example is a large cutover tract in Oscoda County that held the following numbers of singing males in the years beginning in 1975: 0, 6, 0, 1, 1, 10, 14, 22. If it was suitable in 1976 when it held six males, it was surely not less so in the next three years when it had virtually none. In 1980 it became more productive.