

# JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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Volume 35

1981

Number 2

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*Journal of the Lepidopterists' Society*  
35(2), 1981, 81-93

## PRESIDENTIAL ADDRESS 1980 ON THE ACHROMATIC *CATOCALA*<sup>1</sup>

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Most of the nearly 100 species of *Catocala* Schrank (underwing moths, Noctuidae) that occur in North America are characterized by colorful, banded hindwings, which contrast strikingly with bark-like cryptic forewings. Some 20 species, however, have no trace of color or banding on the uppersides of the hindwings, these structures being entirely black (except for a contrasting white fringe in some species). The species having black hindwings (Table 1) are referred to as the achromatic (as opposed to chromatic) *Catocala*, and they have long held a special appeal to collectors. This appeal is reflected in the romantic, though doleful, names that many species bear—e.g., the widow underwing (*C. vidua* Smith & Abbot), the dejected underwing (*C. dejecta* Strecker), the inconsolable underwing (*C. insolabilis* Gn.) (Fig. 1).

There is general agreement that the achromatic *Catocala* are a series of distinct species that have evolved secondarily from species with chromatic hindwings (Grote, 1872; Hulst, 1880; Holland, 1903; Barnes & McDunnough, 1918; Forbes, 1954), but there has been considerable question as to the functional significance and mode of origin of the black hindwing pattern (Sargent, 1969, 1976, 1978; Kettlewell, 1973). I propose to explore these issues here, considering first the matter of function and then the origin of achromatic species from chromatic ancestors.

Kettlewell (1973, p. 215) contended that the *Catocala* with black

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<sup>1</sup> An abridged version of the Presidential Address prepared for the 31st annual meeting of the Lepidopterists' Society, Gainesville, Florida, June 1980.

TABLE 1. The achromatic *Catocala* of North America.

Group <sup>1</sup>	Foodplants	Species
III	Juglandaceae	<i>epione</i>
V	Juglandaceae	<i>robinsoni</i> , <i>judith</i> , <i>flebilis</i> , <i>angusi</i> , <i>obscura</i> , <i>residua</i> , <i>sappho</i> , <i>agrippina</i>
VI	Juglandaceae	<i>retecta</i> , <i>dejecta</i> , <i>ulalume</i> , <i>insolabilis</i> , <i>vidua</i> , <i>maestosa</i> , <i>lacrymosa</i>
XV	Ericaceae	<i>andromedae</i>
XVII	Rosaceae	<i>miranda</i> , <i>orba</i>

<sup>1</sup> Subdivisions of the genus, after Forbes (1954).

hindwings have “forfeited their flash coloration. . .” and so have “. . . abandoned a major mechanism of defence.” However, there is considerable evidence that achromatic hindwings, like chromatic hindwings, will elicit startle reactions in birds. The primary evidence for this startle effect is provided by *Catocala* specimens bearing crisp beak imprints on their wings (Type III damage—Sargent, 1973, 1976). Such specimens are regularly taken in large samples of these moths,

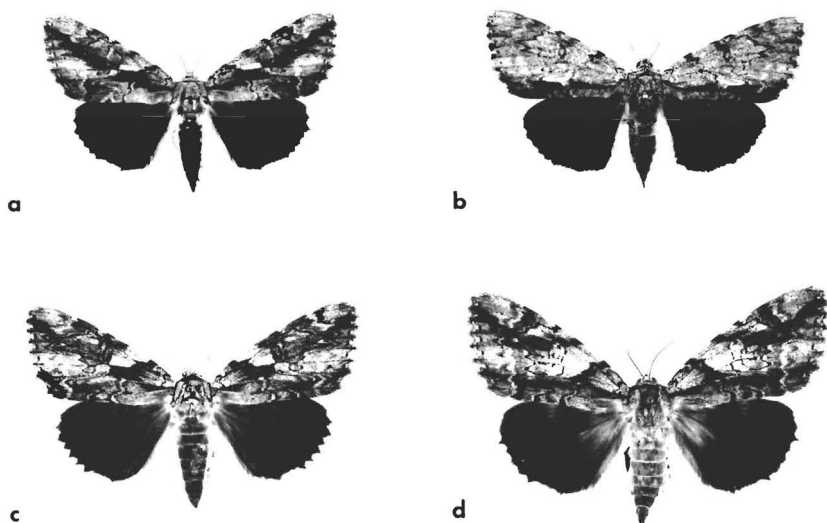


FIG. 1. Representative achromatic *Catocala* species. **a.** *flebilis*; **b.** *insolabilis*; **c.** *dejecta*; **d.** *vidua*. (ca. 0.55×)

and beak imprints are at least as frequently found on achromatic as on chromatic individuals (Sargent, 1973).

The Type III damage pattern apparently results when a bird is momentarily startled by the appearance of a brightly colored or boldly patterned hindwing and relaxes its grip on a captured moth (Sargent, 1973). I have proposed previously that hindwing diversity, and particularly the contrast between chromatic and achromatic patterns, introduces the element of anomaly (the unexpected) into the predator-prey system involving birds and these moths. Anomaly then acts to interfere with the avian counteradaptation to startle effects-habituation. Habituation is defined as "the waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe, 1963). Habituation requires a series of encounters with a specific stimulus, and encounters with sufficiently different stimuli are known to interfere with, or abolish, the development of an habituated response (Donahoe & Wessells, 1979). This "dis-habituation" phenomenon provides, I believe, a selective basis for the evolution of hindwing diversity, particularly the distinctively different achromatic patterns, in the *Catocala* (Sargent, 1973, 1976, 1978, 1980).

As a specific example let us take *C. neogama* Smith & Abbot (orange and black banded hindwings) and *C. resecta* Grt. (black hindwings) (Fig. 2), two Juglandaceae-feeding species that are often encountered in the same habitats. It is assumed that habituation to the hindwings will proceed so long as only one of these two species is being encountered (say, *C. neogama*). At some point, perhaps after from 3 to 6 encounters, based on prior studies (Blest, 1957; Coppinger, 1969, 1970), the startle response will disappear and a bird would be able to capture individuals of that species. Now, however, if the other species (here, *C. resecta*), with its closely similar forewings, were encountered, the new hindwing would elicit startle again. Habituation to this new stimulus would again require a series of encounters, and this might or might not occur, depending on the frequencies of *C. neogama* and *C. resecta* in the environment. This situation has been analyzed in more detail elsewhere (Sargent, 1981), but it is apparent that the two species would substantially benefit one another with respect to startle as long as they were about equally common, and that the rarer of the two species would always derive a greater benefit from their co-occurrence. Birds would then exert frequency dependent selection on the moths, tending, thereby, to promote long-term stability of the two species at near equal numbers.

This reasoning has been based on the assumption that a bird cannot distinguish *C. neogama* and *C. resecta* in the resting (cryptic) state.

If that distinction were possible, then a bird might come to associate one forewing pattern with orange and black banded hindwings; another forewing pattern with entirely black hindwings; and habituate to both hindwings on the basis of these predictable associations. This possibility may explain why so many achromatic species in North America have forewings that are remarkably similar to those of certain chromatic species with which they co-occur. I have proposed previously (Sargent, 1969) that predator selection would favor the development of forewing similarities in species having very different hindwings, since, if the forewings were indistinguishable, they would provide no clue to the underlying hindwing patterns.

Examination of the *Catocala* fauna of North America reveals some striking forewing similarities between certain species having achromatic hindwings and others having chromatic hindwings. In some cases the species involved are known to be closely related (e.g., *C. judith* Strecker and *C. serena* W. H. Edw., *C. epione* (Drury) and *C. consors* (Smith & Abbot) (Fig. 2). In these cases the foodplants are the same, as are the patterns of seasonal occurrence, and often the behaviors associated with crypsis (selection of resting sites, orientation, etc.) (Sargent, 1969, 1976, 1978). One of the most remarkable pairings of this sort is that of *C. lacrymosa* Gn. and *C. palaeogama* Gn., where the two species occur in a striking, parallel series of forewing morphs (Remington, 1958) (Fig. 3). On the other hand, there are some cases of close forewing resemblance involving achromatic and chromatic species that are not closely related (e.g., *C. robinsoni* Grt. and *C. concumbens* Wkr., *C. maestosa* (Hlst.) and *C. marmorata* W. H. Edw.) (Fig. 4). The two species in these cases feed on very different foodplants, but there is some evidence to suggest that their patterns of seasonal occurrence and resting habits may be very similar (Sargent, 1976; J. Bauer, pers. comm.).

These examples of forewing similarities in species with chromatic and achromatic hindwings, particularly when considered in light of the evidence that such species commonly co-occur in the same environments, strengthen the argument that achromatic hindwings function as startle devices on the basis of their contrast with chromatic hindwing patterns. Now, however, we are faced with a most perplexing question. If some species benefit by co-existing with other species having different hindwing patterns, why has no species adopted what would seem a simpler means of ensuring that co-existence, i.e., by becoming polymorphic with respect to the hindwings?

A few trivial hindwing variants have received names, e.g., form "normani" of *C. ilia* (Cramer), which shows some extension of black scaling along the veins, or form "sinuosa" of *C. coccinata* Grt., show-

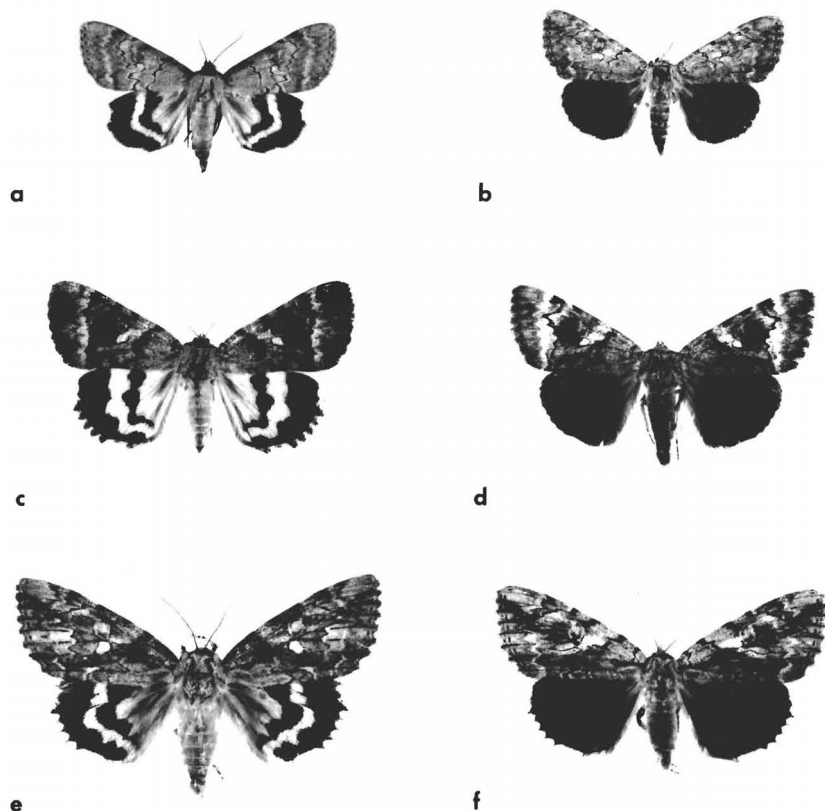


FIG. 2. Pairs of Juglandaceae-feeding *Catocala* species having similar forewings, but chromatic and achromatic hindwings. **a, b.** *serena* and *judith*; **c, d.** *consors* and *epione*; **e, f.** *neogama* and *resecta*. (ca. 0.55 $\times$ )

ing a reduction in the width of the inner band, characteristic of southern specimens. And occasional mutants with very aberrant hindwings do occur. Even an entirely black hindwing may turn up in a species whose hindwings are normally chromatic (e.g., ab. "fletcheri" of *C. unijuga* Wlk., or the recently described ab. "sargenti" of *C. micronympha* Gn. (Covell, 1978) (Fig. 6). These exceptions are exceedingly rare, however, and constancy is certainly the rule with respect to the hindwings within any species. What selective factor(s) would promote such constancy?

One might suggest that the hindwings are mimetic in some way

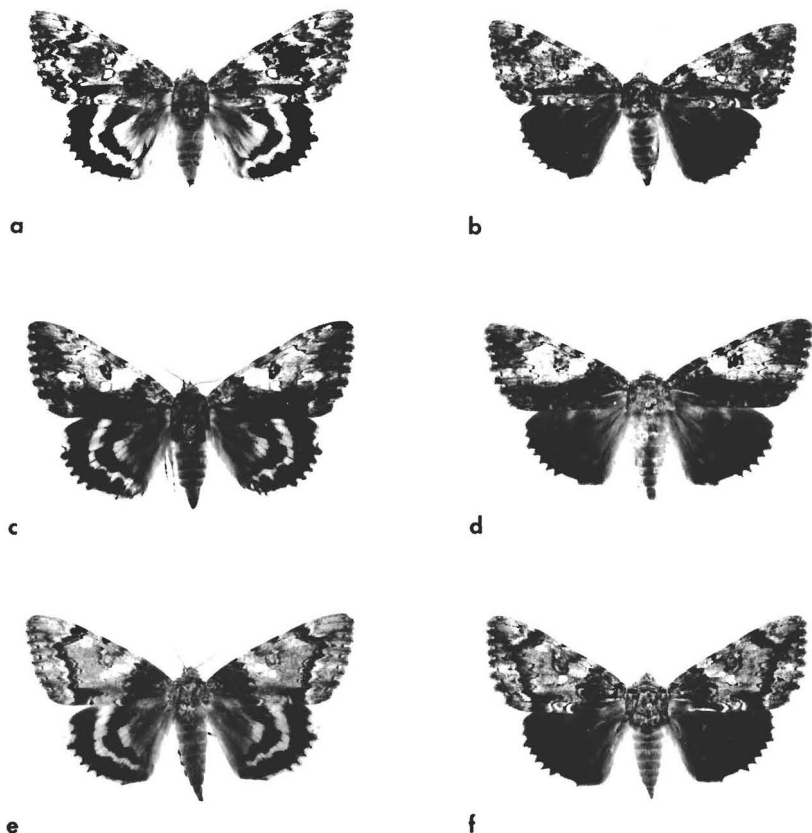


FIG. 3. Parallel forewing morphs in *C. palaeogama* (left) and *C. lacrymosa* (right). a, b. typical, typical; c, d. "annida," "evelina"; e, f. "phalanga," "zelica." (ca. 0.55 $\times$ )

and have been selected for closeness of resemblance to various models. However, *Catocala* hindwings bear no clear resemblance to known noxious or unpalatable prey items or to dangerous or threatening predators; rather, the hindwings seem to function simply as startle devices in anti-predator contexts. It is possible that this startle function will account for some of the uniformity we see. Certain combinations of colors, contrasts, and edges may, because of operational properties of the visual and nervous systems of predators, produce a maximal startle effect. It may be that the banded and entirely black *Catocala* hindwing patterns are particularly effective startle stimuli. This, however, will not explain the lack of intraspecific variation in

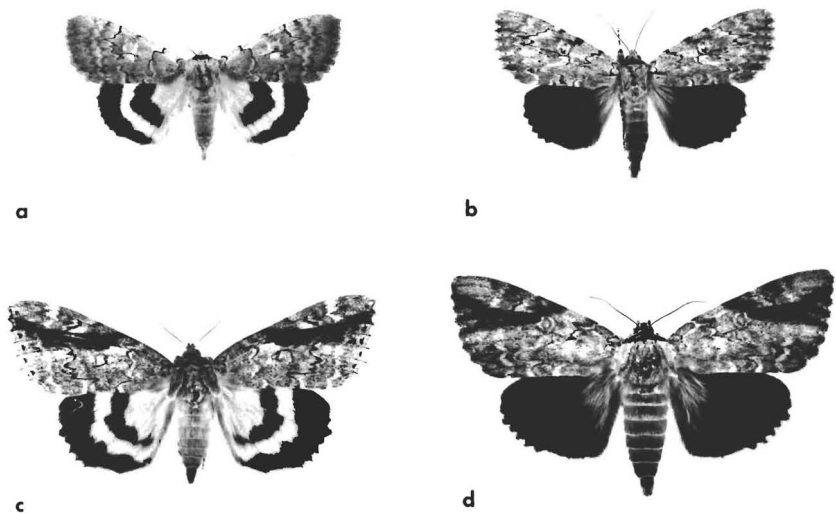


FIG. 4. Pairs of *Catocala* species having similar forewings, but chromatic and achromatic hindwings, and feeding on different foodplants. **a, b.** *concumbens* (Salicaceae) and *robinsoni* (Juglandaceae); **c, d.** *marmorata* (Salicaceae) and *maestosa* (Juglandaceae). (ca. 0.55 $\times$ )

the hindwings, as there are many variations across species, each of which is presumably an effective startle stimulus.

Actually, this problem of interspecific hindwing diversity plagues any effort to explain hindwing uniformity within species in terms of effects on predators. We are forced, I believe, to consider a selective factor that would operate *within* each species to promote an invariant

TABLE 2. The numbers and frequencies of chromatic and achromatic Juglandaceae-feeding *Catocala* in Robinson Trap samples taken over one or more entire seasons at several locations (1961–1979).

Locations (no. years)	Chromatic		Achromatic	
	Species	No. (%)	Species	No. (%)
Washington, CT <sup>1</sup> (12)	6	3603 (60)	8	2406 (40)
Leverett, MA (10)	4	473 (39)	7	728 (61)
W. Hatfield, MA <sup>2</sup> (10)	5	960 (49)	8	998 (51)
Sturbridge, MA <sup>3</sup> (2)	4	73 (46)	6	85 (54)
Geo. Reserve, MI <sup>4</sup> (1)	4	138 (34)	6	268 (66)
Amherst, MA <sup>5</sup> (1)	6	93 (46)	7	110 (54)
Totals	6	5340 (54)	9	4595 (46)

Data courtesy of S. A. Hessel<sup>1</sup>, C. G. Kellogg<sup>2</sup>, C. C. Horton<sup>3</sup>, D. Owen<sup>4</sup>, and F. A. Vaughan & L. P. Brower<sup>5</sup> (two traps).

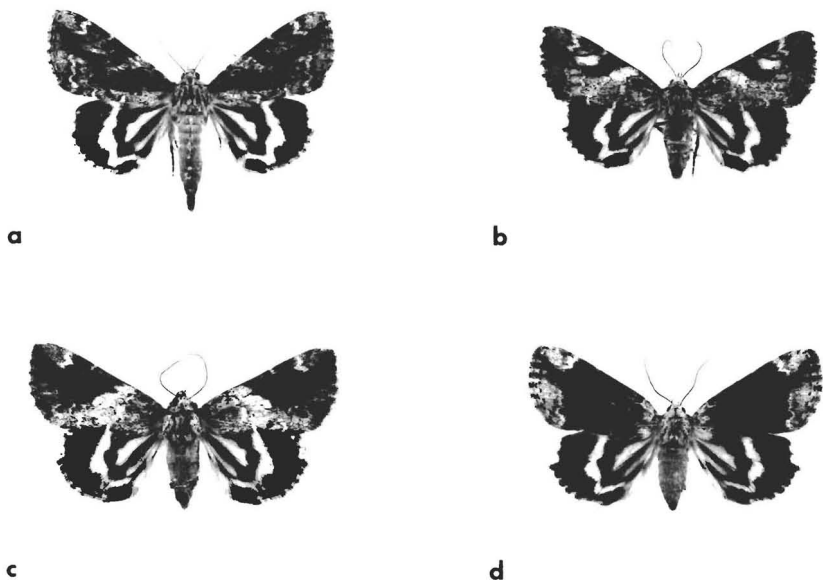


FIG. 5. Forewing morphs of *C. micronympha*. a. typical; b. un-named; c. "hero"; d. "grisela." (ca. 0.80 $\times$ )

hindwing pattern. Such selection would occur if the hindwings function as specific recognition devices, playing a role in courtship and mating, and so serving as isolating mechanisms within the genus.

The contention that *Catocala* hindwings may play a role in the sexual interactions of the moths themselves seems unreasonable in some ways. *Catocala* are nocturnal, as far as is known, and visual communication, particularly if colors are involved, seems prohibited at night. Furthermore, *Catocala* males presumably locate females by chemical signals (pheromones), and it seems likely that the males also elaborate pheromones (Bailey, 1882) which could be the basis for acceptance or rejection of the males by the females.

On the other hand, very little is actually known regarding courtship and mating in these moths. Only *C. relictata* Wlk. has been mated in captivity (Sargent, 1972), and while these moths were reported to mate at night, it was also noted that courtship involved considerable male activity ("walking and flying about the cage") and that the hindwings of both partners were exposed when the moths came into sexual contact. Perhaps some courtship activities of the *Catocala* are restricted to bright, moonlit conditions? It is also possible that court-



FIG. 6. *C. micronympha* "gisela" (**above**) and an aberration, "sargenti," with achromatic hindwings (**below**). (ca. 0.80 $\times$ )

ship activities in some species are initiated during crepuscular periods or even during daylight. David Baggett has reported instances of males of *C. insolabilis* Gn. aggregating about a female during the late afternoon in Florida (pers. comm.).

Certainly we need more information on the reproductive behaviors of the *Catocala*. For the moment, however, I think we cannot rule out the possibility that the *Catocala* use their hindwings as species-specific visual signals during courtship. Such a possibility would provide the intense stabilizing selection that seems required by the hindwing uniformity that exists within each *Catocala* species.

Let us now return to the achromatic hindwings and consider specifically the question of their origin. My discussion to this point indicates that the black hindwing pattern is an effective startle device, at least when present along with chromatic hindwings, but that it might be selected against in mating. Yet, there are some 20 *Catocala* species with black hindwings, most of which appear to have evolved independently from chromatic ancestors. How have these speciation events occurred?

We have seen that the achromatic hindwing pattern can arise in a single step, since occasional specimens of normally chromatic species have all traces of hindwing color obliterated by black scaling. Such

specimens are exceedingly rare, but they must represent a first step in the sort of speciation process that we are considering. Usually, no doubt, such specimens die without leaving progeny, but they must occasionally persist. And when they do persist, they must rapidly achieve species status, as the black hindwing pattern does not occur as a morph in any extant species.

The classical allopatric model of speciation seems entirely inadequate to account for this situation. Certainly, it seems most unlikely that achromatic hindwings arose in isolated subpopulations and that these subpopulations remained isolated long enough to acquire genetic differentiation sufficient to enable their members to re-invade the ranges of the parent populations as full species. Why would isolated populations acquire achromatic hindwings in the first place, especially in view of the evidence which suggests that achromatic hindwings are most effective as startle devices when they co-occur with chromatic hindwings? And if one postulates the founding of these isolated populations by individual females, who happened to be mutants with black hindwings, is it conceivable that this event could have occurred on several separate occasions, given the great rarity of such mutants in chromatic species? And even if that were granted, is it likely that each of the achromatic subpopulations would by chance remain isolated until species status was achieved?

Another allopatric scenario might be based on the assumption that achromatic hindwings arose as anti-hybridization devices after speciation, and re-invasion events had led to the co-occurrence of similar chromatic species. But is it likely that this particular anti-hybridization device would arise by chance on so many occasions? And how would one account for the spread of the achromatic trait into areas of non-overlap of the hybridizing species?

It seems more likely to me that individuals with achromatic hindwings have become new species while co-occurring with their parental species with chromatic hindwings. This, however, is sympatric speciation—a controversial concept indeed (see Mayr, 1963; Maynard Smith, 1966; Bush, 1975). In this case, we must posit some mechanism which restricts the matings of individuals with achromatic hindwings to other achromatic individuals (homogamy).

We might invoke a second, coincidental mutation that would affect some aspect of the mate selection process such that individuals with achromatic hindwings could only mate with one another. However, this would require the simultaneous occurrence of two individuals of opposite sex, both of whom had the mutation for achromatic hindwings *and* the mutation for altered mating preferences, and this un-

likely event would have had to occur many times over in order to account for the present achromatic species.

A pleiotropic effect of the mutation for black hindwings on some aspect of mate selection would strain credulity a little less, for in this case every individual with black hindwings might only be able to mate with another black-hindwinged individual. This pleiotropic effect could conceivably involve a change in hindwing preference, though a change in something like the timing of emergence or mating readiness would seem more likely. In this way, a mating between siblings with black hindwings might occur, even with the seeming impediment of inappropriate hindwings, given that no other mates might be available at a changed mating time. An initial sib mating of this sort might provide sufficient progeny to initiate selection for an altered hindwing preference in mating.

This scenario is essentially a case of instantaneous speciation, a concept that has been extensively criticized by many evolutionary biologists (see Mayr, 1973, p. 432 ff.). Mayr has pointed out (1973, p. 472) that, "... a species would lose all the advantages of improved utilization of the environment through adaptive polymorphism if it were to split into a series of narrowly specialized species." Yet, in a sense, the *Catocala* have done just that. Many species occur as "narrowly specialized species" (differing in hindwing patterns) in the same environments. Hindwing polymorphisms would seem to be a more efficient and adaptive means of creating the diversity we see, but hindwing polymorphisms do not occur.

Thus, unlikely as the sympatric speciation model may be, I believe that it provides a more plausible explanation of the existing *Catocala* situation with respect to achromatic hindwings than does an allopatric model. Plausibility, however, like beauty, may lie in the eye of the beholder. Is there any evidence we might obtain that would enable a better judgment of the arguments I have advanced?

I would like to conclude by suggesting two lines of investigation that might provide such evidence. The first of these involves mating these moths. We must find the secret to obtaining this behavior in captivity. Once done, we should be able to determine whether the hindwings do play a role in mate selection, and if so, what kinds of alterations interfere with that process. We should also be able to determine whether the species with achromatic hindwings have different pheromones or courtship behaviors than their closely related chromatic species, or whether they differ only with respect to the time of day at which they mate. If such studies indicated that the achromatic species are isolated from their chromatic relatives by a consistent,

single characteristic, this might support the argument for their origin by a series of similar sympatric speciation events, rather than by a number of separate allopatric events.

The second line of investigation I would recommend involves the technique of protein electrophoresis (for a lucid discussion of this method and the rationale underlying its use and application, see Futuyma, 1979). Use of this technique might reveal extremely close relationships between certain achromatic and chromatic species; closer, perhaps, than any other relationships within the genus. Such a finding would again support the sympatric hypothesis, regarding the origin of the achromatic species. Also, since the sympatric speciation process could occur anywhere within the range of a parent population, then speciation might occur more frequently than allopatric models would predict. This could be reflected in electrophoretic data suggesting close groupings of species having one chromatic member and two or more achromatic members.

These sorts of investigations may permit some assessment of the rather unconventional ideas that I have advanced. I would stress, however, that many other kinds of studies should be carried out as well. The life histories of a number of species have not been recorded (see Sargent, 1976). We know almost nothing of the competitive interactions among larvae of species feeding on the same foodplants. Recorded observations of predation on the moths, either under field or captive conditions, are virtually non-existent. In short, we need more information on all aspects of the biology of the *Catocala*. And as our knowledge of these insects increases, so too must our understanding of their patently complex evolutionary history. I suspect that many exciting discoveries await our closer attention.

I wish to thank Victoria Borden Muñoz for the photographs of the moths.

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