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## STUDIES ON THE *CATOCALA* (NOCTUIDAE) OF SOUTHERN NEW ENGLAND. V. THE RECORDS OF SIDNEY A. HESSEL FROM WASHINGTON, CONNECTICUT, 1961-1973

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With the death of Sidney A. Hessel on 11 November 1974, lepidopterists lost one of their most enthusiastic and inspiring colleagues. This sad event also closed the pages on an unprecedented compilation of records on the moths of a single genus at a single location, for Hessel had faithfully noted all of the *Catocala* specimens taken at two light sources near his home on virtually every night of 12 seasons between 1961 and 1973.

These records, portions of which have been previously published (Sargent & Hessel, 1970; Sargent, 1976), are summarized and analyzed here, particularly with a view to assessing (1) the variability in *Catocala* populations from year to year, (2) the extent of seasonal separation among the various species, and (3) the degree of stability in hindwing diversity across seasons. I also hope to demonstrate the usefulness of such records for the development and testing of hypotheses relating to the ecology of these moths. Specifically, I will propose a mechanism for the maintenance of stability in the frequencies of certain hindwing patterns, drawing upon applicable data from Hessel's records.

I hope that this paper will illustrate the value of complete and detailed records that extend over several seasons and thus will encourage others to gather similar data at their own locations.

### METHODS

Washington is located in the Litchfield Hills of west-central Connecticut. The collecting site itself was at the bottom of a narrow north-south valley through which an all-season stream flowed southward. The

TABLE 1. Numbers of individuals (N) of all *Catocala* species taken over 12 seasons (1961-65, 1967-73) at Washington, Connecticut and the corresponding percentages (%) of the *Catocala* sample.

Species	N	%	Species	N	%
<i>palaeogama</i>	1795	17.45	<i>cara</i>	82	0.80
<i>residua</i>	1217	11.83	<i>ilia</i>	67	0.65
<i>habilis</i>	964	9.37	<i>crataegi</i>	47	0.46
<i>amica</i>	790	7.68	<i>dejecta</i>	46	0.45
<i>concumbens</i>	676	6.57	<i>parta</i>	45	0.44
<i>ultronia</i>	632	6.14	<i>subnata</i>	44	0.43
<i>grynea</i>	466	4.53	<i>unijuga</i>	42	0.41
<i>neogama</i>	446	4.34	<i>flebilis</i>	40	0.39
<i>antinymppha</i>	441	4.29	<i>blandula</i>	40	0.39
<i>retracta</i>	403	3.92	<i>coccinata</i>	39	0.38
<i>serena</i>	353	3.43	<i>praeclara</i>	38	0.37
<i>epione</i>	264	2.57	<i>relicta</i>	23	0.22
<i>obscura</i>	224	2.18	<i>similis</i>	21	0.20
<i>andromedae</i>	212	2.06	<i>amatrix</i>	7	0.07
<i>judith</i>	211	2.05	<i>innubens</i>	6	0.06
<i>mira</i>	201	1.95	<i>briseis</i>	3	0.03
<i>micronympha</i>	159	1.55	<i>piatrix</i>	1	0.01
<i>badia</i>	127	1.23	<i>vidua</i>	1	0.01
<i>gracilis</i>	114	1.11	<i>cerogama</i>	1	0.01

site was surrounded by hills, mostly of mixed deciduous woodlands, but including patches of earlier seral stages that result from the periodic establishment and abandonment of farms and pastures.

Most of the moths were obtained in a Robinson mercury vapor light-trap that was operated from dusk to dawn. The contents of this trap were checked each morning, and the number of specimens of each *Catocala* species was recorded. The majority of the specimens was released near the trap location after examination, so some individuals may have been captured and recorded on more than one occasion. However, studies of color-marked *Catocala* have shown that very few specimens are recaptured under such circumstances (Sargent, 1976). A few records were obtained at a 15-watt fluorescent black-light, which was checked periodically during the evening, and these records were combined with the Robinson trap data in Hessel's daily compilations. Both light sources were in operation from mid-March to mid-November each year (except for occasional 1-3 day absences).

The species of *Catocala* were identified as keyed and described in Forbes (1954), except that *gracilis* and *sordida* were not always distinguished; these species are considered together (as *gracilis*) throughout the present report.

A total of 10,288 *Catocala* specimens of 38 species was recorded over

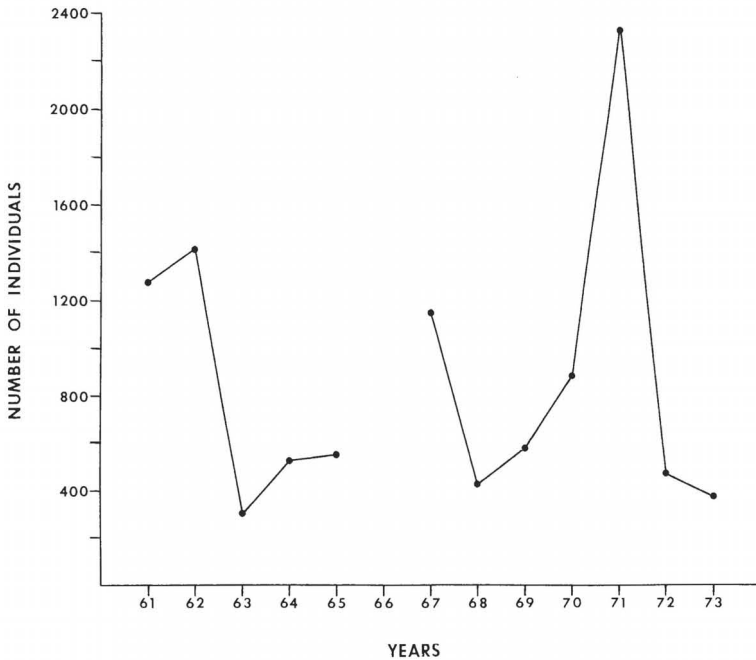


Fig. 1. Total number of *Catocala* taken each year at two light sources at Washington, Connecticut.

the 12 seasons, 1961–65 and 1967–73. The numbers of each species taken, ranked in decreasing order of abundance over the 12 seasons, are given in Table 1.

## RESULTS AND DISCUSSION

### Annual Variations

Analysis of Hessel's records revealed considerable variation in the *Catocala* samples from year to year, despite essentially identical collecting procedures. These variations included changes in (1) the total abundance of all *Catocala*, (2) the relative abundance of particular species, and (3) the overall pattern of species abundance.

The size of the *Catocala* sample fluctuated markedly from year to year, ranging from a low of 306 specimens in 1963 to a high of 2337 specimens in 1971 (Fig. 1). No long-range trend of increasing or decreasing *Catocala* abundance could be discerned against the erratic fluctuations in annual abundance.

In addition to changes in total abundance, there was also considerable

TABLE 2. The highest and lowest annual totals, with the corresponding percentages of total *Catocala* taken, for those species having at least 100 records over 12 seasons at Washington, Connecticut.

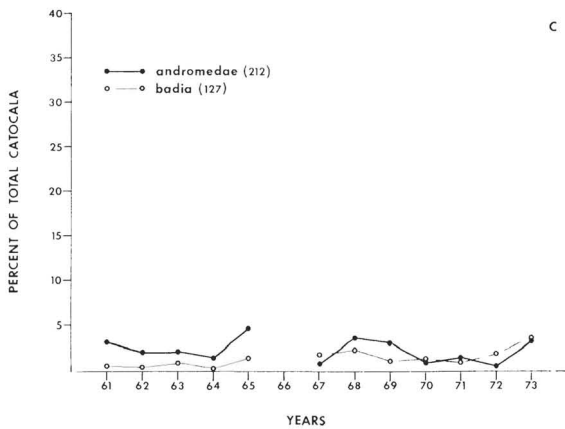
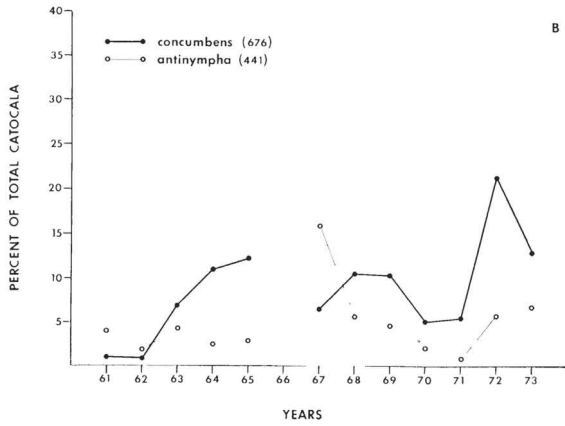
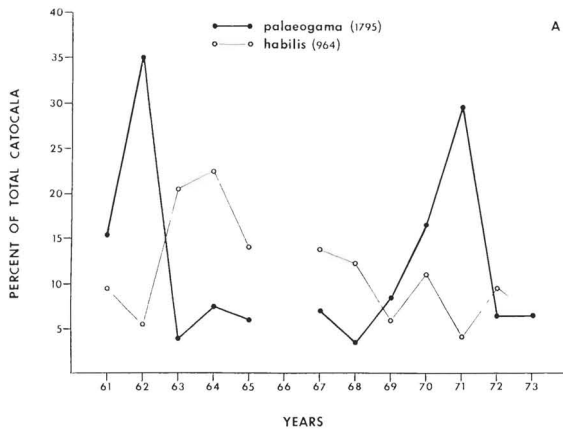
Species	Annual Totals			
	High		Low	
	N	%	N	%
<i>palaeogama</i>	690	29.53	12	3.92
<i>residua</i>	345	24.43	7	1.89
<i>habilis</i>	159	13.81	23	6.22
<i>amica</i>	281	12.02	10	3.27
<i>concumbens</i>	130	5.56	12	0.85
<i>ultronia</i>	220	9.41	14	4.58
<i>grynea</i>	72	5.65	8	2.61
<i>neogama</i>	97	7.61	4	0.86
<i>antinympha</i>	182	15.81	13	2.45
<i>retracta</i>	83	6.51	9	2.43
<i>serena</i>	124	5.31	0	—
<i>epione</i>	69	5.41	5	1.07
<i>obscura</i>	28	1.20	3	0.98
<i>andromedae</i>	40	3.14	3	0.64
<i>judith</i>	95	4.07	0	—
<i>mira</i>	76	3.25	2	0.17
<i>micronympha</i>	43	3.05	1	0.21
<i>badia</i>	27	1.16	2	0.38

variation in the relative abundance of particular species from year to year. The highest and lowest annual totals of those species for which there were at least 100 records over the 12 years of collecting are given in Table 2. These data suggest that the more common species in the overall totals were more erratic in terms of annual abundance than were the less common species. This suggestion is supported by comparisons of the relative annual frequencies of certain more and less common species (Fig. 2). It is apparent that the most abundant species overall exhibited explosive increases in numbers from time to time, whereas the less common species maintained rather constant frequencies over the years. These differences in relative abundance across years suggest differences in the mechanisms by which populations of various species are regulated, and this possibility certainly warrants further study.

The 12-year totals of the *Catocala* species from this location (Table 1)

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Fig. 2. Fluctuations in abundance from year to year of several *Catocala* species at Washington, Connecticut. Abundance is expressed as a percentage of the total *Catocala* recorded each year. The species considered range in status from abundant (A) to common (B) to uncommon (C).



reveal a distribution of species abundance that is characteristic of most field samples of this sort, i.e., a few very common and many uncommon species. In this case, the five most common species comprised over 50% of the records, whereas the 20 most uncommon species comprised less than 7% of the total sample. However, the extent to which this pattern was developed did vary from year to year. For example, the most common species in 1962 (*palaeogama*) comprised 35% of the sample for that year, but the most common species in 1969 (*concombens*) comprised only 10% of the sample. At the other extreme, 15 species were recorded fewer than five times in 1963 (nine species occurred only once), whereas only six species were recorded fewer than five times in 1962 (only one species occurred only once).

These examples of annual variation in samples from a single location should illustrate the futility of making long-term assessments of *Catocala* populations on the basis of limited collecting. For even these records of Hessel, as extensive and complete as any known for the *Catocala*, will permit few conclusions regarding the status, or trends in the status, of the species at his location. This finding, however, is perhaps one of the most valuable to emerge from his records. As I have said elsewhere (Sargent, 1976), "Perhaps the lesson here is to view most general assessments of status in the *Catocala* as tentative."

#### Seasonal Occurrence

One of the most interesting questions regarding the *Catocala* concerns the nature of the isolating mechanisms that prevent hybridization among the many species which occur together at any one place. This problem has been discussed in detail elsewhere (Sargent, 1976), and it seems likely that many factors coact to isolate the various sympatric species. These factors include differences in daily and seasonal activity periods, and in courtship and mating behaviors. Here we will be concerned with only one of these factors—differences in seasonal occurrence.

Hessel's daily records, which cover the entire *Catocala* season for many years, are particularly useful for analyses of such differences; for his records, especially when summed across the years, provide the large sample sizes essential for the detection of relatively small seasonal offsets.

Hessel took adult *Catocala* over a four-month period (July–October), but most of his records fell between mid-July and mid-September (Fig. 3). A total of 33 species was taken during the second half of August, and as many as 21 species were recorded on a single night during that period (Sargent & Hessel, 1970). Clearly, many species had overlapping flight seasons.

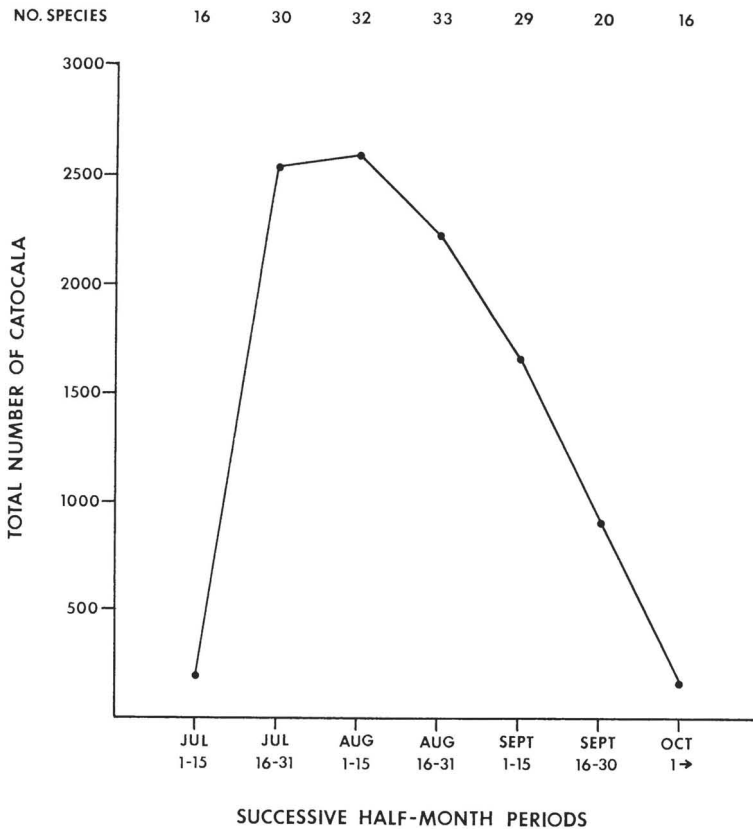


Fig. 3. The total number of *Catocala* recorded during successive half-month periods of the season at Washington, Connecticut, summed over 12 years. The number of species taken during each half-month period is given at the top of the graph.

However, if one compares the median dates of capture of those species for which there were 24 or more records (Fig. 4), some interesting seasonal offsets between certain species become apparent. Thus, for example, approximately a month separates the median dates of capture of *dejecta* (3 August) and *retecta* (2 September), and *serena* (11 August) and *habilis* (14 September). In these cases, three-quarters of the records of the earlier species occurred before the first quarter of records for the later species. Other closely related species pairs exhibiting marked differences in median capture dates include *blandula* (13 July) and *mira* (1 August), *subnata* (10 August) and *neogama* (6 September), *residua* (19 August) and *obscura* (6 September), and *concupbens* (25 August)

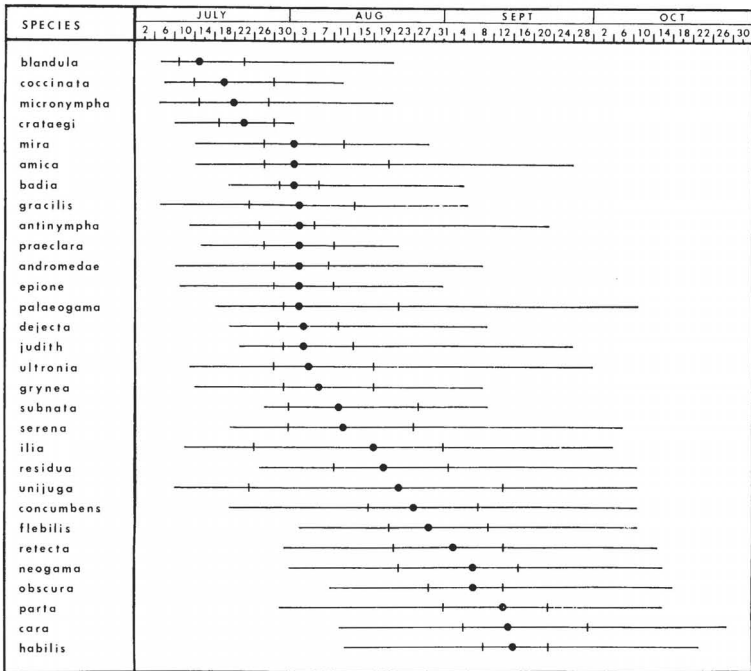


Fig. 4. Seasonal occurrence of *Catocala* species at Washington, Connecticut based on records summed over 12 seasons. The lines run from the earliest to the latest dates of capture, and quartile dates are indicated by a dot (median) and dashes (first quarter, third quarter). Only species for which there were 24 or more records are considered, and these are arranged in descending order on the basis of a seasonal sequence from early to late.

and *cara* (13 September). Assuming that most matings occur near the beginning of the flight season of a species, it seems likely that seasonal offsets such as these must contribute to the reproductive isolation of the species involved.

On the other hand, certain other pairs of closely related species had nearly identical median dates of capture. Among such pairs were *badia* (1 August) and *antinympha* (2 August), *gracilis* (2 August) and *andromedae* (2 August), and *praeclara* (2 August) and *grynea* (6 August). Clearly such species pairs must depend on isolating mechanisms other than seasonal separation.

Complete understanding of the complex of factors that isolate all of the *Catocala* species at any one location must await much more study. But these records of Hessel suggest that seasonal separation is one of the factors involved in certain cases.



TABLE 3. Distribution of *Catocala* in five hindwing groups at Washington, Connecticut (1961-65, 1967-73).

Hindwing Group	Species	Number	%
1	<i>relicta</i>	23	0.22
2	<i>epione, judith, flebilis, obscura, residua, relecta, dejecta, vidua, andromedae</i>	2618	25.45
3	<i>piatrix, antinympha, badia, habilis, serena, palaeogama, subnata, neogama, cerogama, gracilis, crataegi, mira, blandula, grynea, praeclara, similis, micronympha, amica</i>	6048	58.79
4	<i>innubens, ilia, parta, briseis, unijuga, coccinata, ultronia</i>	834	8.11
5	<i>cara, concumbens, amatrix</i>	765	7.44

### Hindwing Diversity

The forewings of many *Catocala* species are strikingly variable (polymorphic), but the hindwings are essentially invariable (monomorphic) within any species. However, hindwing diversity across species is substantial, and this matter has been the subject of considerable prior study (Sargent, 1969, 1973, 1976; Sargent & Owen, 1975). The records of Hessel provide an opportunity to analyze the occurrence of various hindwing types at a single location in considerable detail. This analysis in turn prompts some speculation regarding the apparent maintenance of stability in hindwing diversity at this location.

Dr. Denis Owen and I recently analyzed the frequencies of various hindwing types occurring in large *Catocala* samples taken at mercury vapor lights at four localities in eastern North America (Sargent & Owen, 1975). For purposes of our analysis, the hindwing patterns were arbitrarily divided into five groups: (1) black and white, banded; (2) black, unbanded (on upper surface); (3) yellow to yellow-orange and black, banded; (4) orange-red to red and black, banded; and (5) pink and black, banded. The frequency distribution of these hindwing types was remarkably similar at each of the localities we considered, despite marked differences in species composition. These frequencies closely resembled those obtained at Washington, Connecticut, as compiled from Hessel's total records (Table 3).

This apparent stability in hindwing diversity at different locations was more simply expressed by combining the hindwing groups into an achromatic assemblage (groups 1 and 2) and a chromatic assemblage (groups 3, 4, and 5). This division emphasizes the most obvious hindwing dichotomy in the *Catocala*, i.e., the presence or absence of color. And the

frequency of occurrence of these two hindwing types was nearly constant across localities, with achromatic individuals consistently comprising ca. 20% of the total *Catocala* samples (Sargent & Owen, 1975).

We interpreted the apparent stability in hindwing diversity at various locations as a result of selective predation, especially by birds, and argued that the observed frequencies function to "confuse" predators, presumably by introducing the element of anomaly (the unexpected) into the overall predator-prey system (Sargent & Owen, 1975). Thus, for example, achromatic hindwings might serve as effective startle devices only if they comprised no more than ca. 20% of the total *Catocala* hindwings encountered. At higher frequencies, predators might come to expect such a hindwing pattern, and predation would increase until the frequency was again returned to 20% of the total. Presumably, such selection pressure would eventually result in stabilization of the different hindwing types at optimal frequencies with respect to predation.

In further analyzing Hessel's records, I will consider only the achromatic and chromatic hindwing groups, since these are the most easily defined and perhaps most meaningful categories with respect to *Catocala* hindwing diversity. And since most of the species with achromatic hindwings feed as larvae on the Juglandaceae (hickories, *Carya*, and walnuts, *Juglans*), particular attention will be devoted to the species that utilize those foodplants.

The percentage of specimens with achromatic hindwings at Washington, Connecticut ranged from 16.76% in 1973 to 36.24% in 1961 and averaged 25.67% over the 12 years. However, a more striking constancy of achromatic hindwings can be demonstrated when only those *Catocala* whose larvae feed on the Juglandaceae are considered. This analysis excludes only two achromatic species from Hessel's totals (*relicta*, a Salicaceae feeder; and *andromedae*, an Ericaceae feeder), leaving eight achromatic (*epione*, *judith*, *flebilis*, *obscura*, *residua*, *relecta*, *dejecta*, and *vidua*) and six chromatic species (*piatrix*, *habilis*, *serena*, *pala-eogama*, *subnata*, and *neogama*). All of the chromatic species in this case have yellow-orange and black, banded hindwings.

The percentage of individuals with achromatic hindwings among these Juglandaceae-feeding *Catocala* was remarkably constant from year to year, despite considerable variation in the species composition and the number of individuals taken each year (Fig. 5). Such stability in the occurrence of achromatic hindwings suggests the operation of a control mechanism related in some way to predation.

Two possibilities immediately come to mind: (1) predators consistently select *Catocala* such that trapped samples will reveal a constant

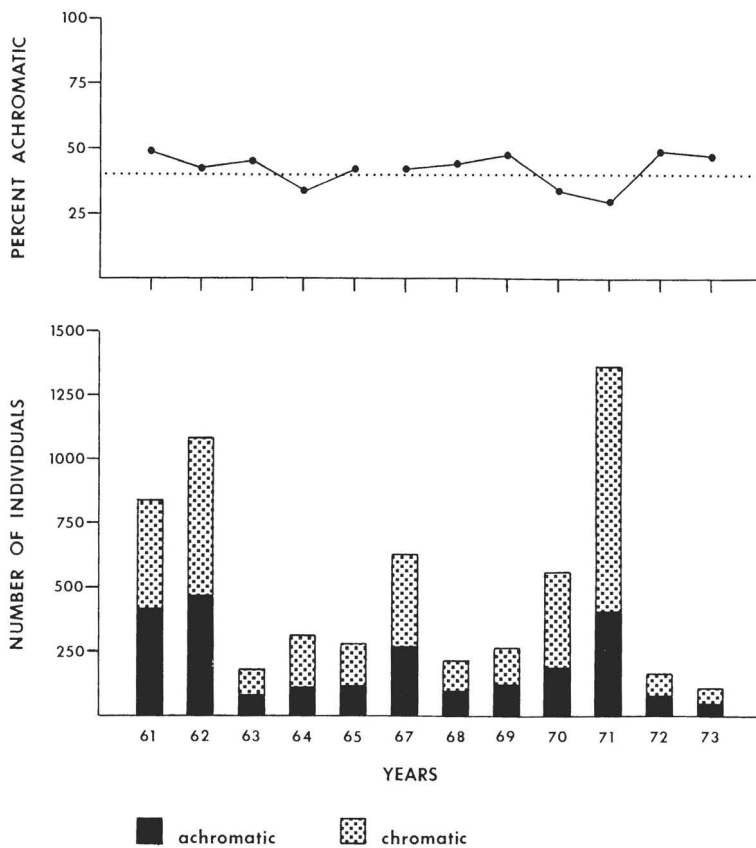
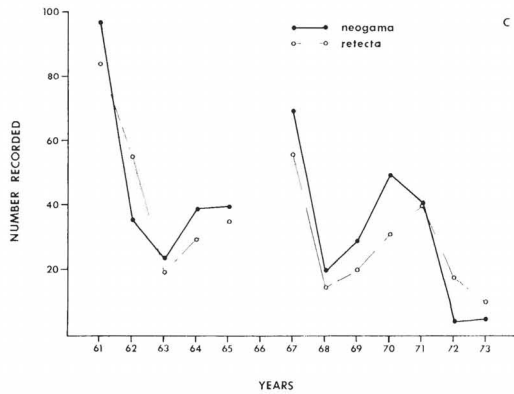
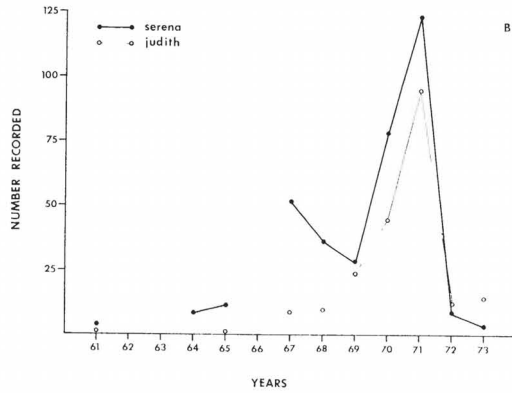
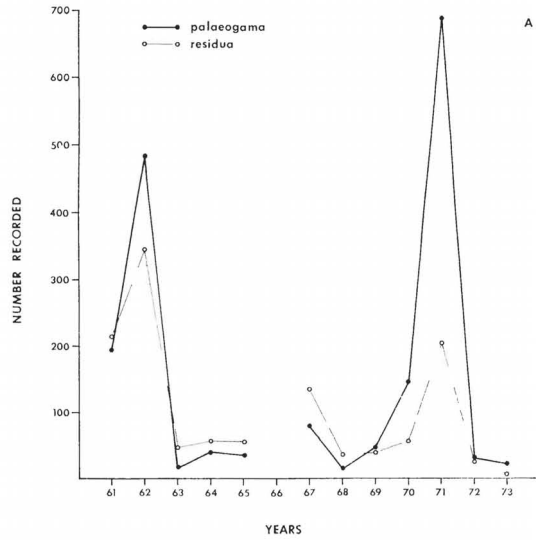


Fig. 5. Number of Juglandaceae-feeding *Catocala* taken each year at Washington, Connecticut with achromatic and chromatic hindwings distinguished (bottom); and the corresponding percentages of individuals with achromatic hindwings (top).

frequency of achromatic hindwings; and (2) the moths themselves, in response to long-term predator selection, have evolved the means of maintaining a constant frequency of achromatic hindwings. Both possibilities pose difficulties, but it seems particularly unlikely that the stability of achromatic hindwings in trapped samples is entirely a product of immediate predator selection; for this would assume that few moths are trapped prior to their exposure to intense predator selection, and such an assumption seems clearly unreasonable.

Thus, the possibility that the moths themselves are maintaining a constant frequency of achromatic hindwings must be examined. This possibility is rendered particularly perplexing in view of the fact that



none of the species involved are polymorphic with respect to hindwing types, and, consequently, mechanisms that would maintain a balanced polymorphism within a species (Ford, 1964) cannot be operating. How, then, is a stable relationship between two hindwing types to be achieved in a complex of species, each monomorphic with respect to hindwing type, and each highly variable with respect to abundance from year to year?

One theoretical possibility in a system wherein each species regulates its own density by assessing and responding to the density of every other species present. Such density regulation might be envisioned for a single species (Wynne-Edwards, 1962) but seems entirely implausible for an assemblage of species, given the complex social behaviors required in such a control system.

It may be, however, that an overall stability in the relationship between achromatic and chromatic hindwings could be achieved on the basis of simpler interactions between or among certain species. If, for example, the achromatic and chromatic species were paired and the members of each pair exhibited parallel fluctuations in annual abundance, then a stable relationship between the two hindwing types would result.

That such pairings of species may exist is suggested by the nearly identical fluctuations in annual abundance of certain achromatic and chromatic species (Fig. 6). These similarities suggest that the two species involved in each case are responding to environmental variables in the same fashion and thus may have identical, or nearly identical, ecological niches. This suggestion, however, seems to raise problems with respect to the so-called *competitive exclusion principle*, i.e., the ecological dictum that two species cannot share the same niche, since competition between them should eventually exclude the less well-adapted species (see discussion in any ecology text, e.g., Ricklefs, 1973). This principle clearly assumes that the two species compete for some limiting resource, usually food. The *Catocala*, however, may be limited by predation rather than the availability of food, and in that case the competitive exclusion principle would not apply.

The fact that many *Catocala* species may utilize the same hostplant suggests that food is not generally limiting for these moths. Many of the

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Fig. 6. Numbers of individuals of three pairs of Juglandaceae-feeding *Catocala* species taken each year at Washington, Connecticut. The species are paired on the basis of similarities in abundance across years, and each pair includes a species with achromatic hindwings (open dots) and a species with chromatic hindwings (solid dots).

Juglandaceae feeders under consideration here, for example, are known to feed on shagbark hickory (*Carya ovata*) (Sargent, 1976). On the other hand, the fact that the ova, larvae, and adults of most *Catocala* are highly cryptic implies that predation has long been substantial on these insects. There is some evidence for heavy bird predation on the adults, since beak-damaged individuals may comprise as much as 4% of trapped specimens (Sargent, 1973). Such beak-damaged individuals have escaped from their predators, but presumably many more individuals are actually eaten by birds. I have shown that naive blue jays (*Cyanocitta cristata* (L.)) will quickly learn to capture *Catocala*, rarely losing individuals after 12–15 experiences with these moths (Sargent, 1973).

It seems likely that the simultaneous presence of two species with different hindwing types would be advantageous to both species with respect to the effectiveness of their hindwings as startle devices, for birds are clearly less effective predators when confronted with the novel or unexpected in their prey (Sargent, 1976). And since novelty and anomaly are functions of scarcity, the advantage of any one hindwing type should increase as the numbers of the other hindwing type increase.

Thus, it follows that two species with different types of hindwings might share the same niche, and the advantage of each species with respect to predation would increase as the other species increased in abundance. In such a situation, neither species should act to exclude the other from the niche, and each should become as abundant as other limitations (climate, parasites, etc.) permit. Given that the two species are closely related and are adapting to the same niche, it should not be surprising to find them occurring in approximately equal numbers, as seems to be the case in several instances at Washington, Connecticut (Fig. 6).

The system envisioned here would result in stable relationships between pairs of species with achromatic and chromatic hindwings and would not require intrinsic mechanisms for the assessment or adjustment of population densities. One species would need only to adapt to a niche already occupied by a species with a different type of hindwing. If such pairs of species comprised a substantial portion of the total of species under consideration, then a stable overall relationship between the different hindwing frequencies would be expected.

There remains the question of why hindwing diversity, if it is such an advantage with respect to predation, has not developed *within* any species. The answer must be that there is an even greater advantage associated with hindwing monomorphism at the species level. This suggests that the hindwings function as specific recognition devices, per-

haps serving as releasers during courtship and mating behaviors, and thus act to isolate various species. If the hindwings do serve as isolating mechanisms, it seems possible that sympatric speciation on the basis of hindwing differentiation might occur on occasion in the *Catocala*. Sympatric speciation might then account for the phenological similarities we have seen in certain pairs of species with different types of hindwings.

These ideas regarding the maintenance of stability in hindwing diversity, though often quite speculative, are based on data that Hessel acquired over many years at Washington, Connecticut. I hope that other workers will be stimulated to test these ideas by acquiring additional data and conducting further studies on the *Catocala* at their locations. Whether such studies support or refute the ideas developed here, the results can only advance our understanding of these moths. And in this way, the records of Hessel will make their most important contribution.

#### SUMMARY

The late Sidney A. Hessel of Washington, Connecticut recorded all of the *Catocala* taken at two light sources near his home over 12 seasons (1961-65, 1967-73). Totals of 38 species and 10,288 individuals were recorded.

The *Catocala* populations at this location varied considerably from year to year. These annual variations included changes in the total number of *Catocala* taken, the relative abundance of particular species, and the overall pattern of species abundance. The more common species exhibited more erratic fluctuations in annual abundance than the less common species. It is concluded that limited collecting will not permit long-term assessments of status and trends in *Catocala* populations.

The *Catocala* season at Washington extended from July-October, and most of the species had overlapping flight seasons. However, detailed analyses, including comparisons of the median dates of capture of various species, suggested that certain closely related species might be isolated in part by seasonal offsets.

The frequency distribution of various hindwing types at Washington is summarized. The percentage of individuals with achromatic hindwings, particularly within the group of Juglandaceae-feeding species, remained remarkably stable over the years. A possible mechanism for the maintenance of that stability is proposed, based on observations of nearly identical fluctuations in annual abundance of certain pairs of species that included one member with achromatic hindwings and one

member with chromatic hindwings. It is suggested that the species in each of these pairs may share the same ecological niche, and may have arisen sympatrically.

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#### MELITAEA SAXATILIS MOD. "SASSANIDES" (NYMPHALIDAE) IN IRAN: CONFIRMATION OF AN OLD RECORD

On 5 July 1974 I took eight adult specimens of *Melitaea saxatilis* mod. "sasanides" (Higgins) in Alborz, Mount Damavand, northern Iran. The butterfly was restricted to the height of 4000 m, near the third mountaineer's shelter where a steep rock slope was covered by a few scattered species of Cruciferae, Labiatae and grasses. The adults were feeding on the few Labiatae flowers that existed. No early stages were found.

Higgins (1941) in his "An illustrated catalogue of the Palearctic *Melitaea*" (Trans. Roy. Ent. Soc. London 91: 175-365) mentioned that the only specimens he saw were amongst the ex. coll. Grum-Grshimaile collection at the British Museum. They were collected on 29 June 1894 and no additional record has ever been published. Personal contact with Dr. Higgins and the literature confirm this claim. Unfortunately, due to the change of the weather and the dangerous location of the butterfly habitat, I was not able to collect a sample of the vegetation or investigate farther.

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