STUDIES ON THE CATOCALA (NOCTUIDAE) OF SOUTHERN NEW ENGLAND. VI. THE "PAIRING" OF C. NEOGAMA AND C. RETECTA

THEODORE D. SARGENT

Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003

ABSTRACT. The closely related, Juglandaceae-feeding *Catocala* species, *C. neo-gama* and *C. retecta*, have occurred in nearly equal numbers at the same time of year over several years at a single location in southern New England. These two species have very similar cryptic forewings, but their hindwings differ markedly. Prior studies have suggested that *Catocala* hindwings function as startle devices in instances of avian attack, and that specific differences in hindwing patterns between otherwise similar species serve an anti-predator function by interfering with avian habituation to startle stimuli.

Rearing studies with *C. neogama* and *C. retecta* indicated that the two species have no effects on one another's development rate or survival, though larvae of the two species have a somewhat stronger tendency to disperse from one another than do larvae of either species alone. Detailed analyses of light-trap data from Washington, Connecticut showed that *C. neogama* and *C. retecta* have occurred in equal numbers both across and within seasons at that location. However, the variance in the ratios between these species over years was greatest both early and late in the season when moth abundances were lowest, and this finding is interpreted as evidence for frequency dependent selection by birds on this species pair.

At least 40 species of the noctuid genus *Catocala* may co-exist at a single location in the northeastern United States. A number of these species have very similar life histories, including common foodplants and nearly identical flight seasons. In some cases, pairs of these species have similar bark-like cryptic forewings and resting behaviors on tree trunks (Sargent, 1978).

One of the closest pairings of this sort involves *C. neogama* (Smith & Abbot) and *C. retecta* Grote (Fig. 1), two closely related Juglandaceae-feeding species (Barnes & McDunnough, 1918; Forbes, 1954). These moths were sampled at a light-trap for 12 years by Sidney A. Hessel in Washington, Connecticut, and there the two species occurred in nearly equal numbers, exhibited parallel fluctuations in annual abundance, and had essentially identical flight seasons (Fig. 2). The two species also have very similar cryptic forewings, though they differ markedly with respect to their hindwings—*C. neogama* having orange and black banded hindwings, and *C. retecta* having entirely black hindwings with a prominent white fringe (Fig. 1).

Catocala hindwings are hidden beneath the cryptic forewings when the moths are at rest, and these colorful or boldly patterned structures apparently function as startle devices in instances of avian attack. The crisp beak-imprints found on the wings of many wild-



FIG. 1. Catocala neogama (Smith & Abbot) (above) and C. retecta Grote (below). Life-size.

caught specimens provide evidence for this startle function, indicating that birds sometimes release these moths when the hindwings are exposed (Sargent, 1973). There is also evidence that birds will habituate, i.e., learn to respond, to particular hindwing patterns (Sargent, 1973), and I have proposed that the interspecific hindwing diversity among the *Catocala* serves to interfere with this habituation process (Sargent, 1969, 1976). This apparent advantage of hindwing diversity might then account for the close co-existence of species with very different hindwings (Sargent, 1978, 1981).

Habituation may be defined as the "waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement" (Thorpe, 1963). This learning process requires a series of encounters with the specific stimulus in question, and while some generalization to similar stimuli may occur, encounters with sufficiently different stimuli are known to interfere with, or abolish, the



FIG. 2. The annual (**above**) and seasonal (**below**) fluctuations in abundance of *C*. *neogama* and *C*. *retecta* at Washington, Connecticut, based on specimens taken in a light-trap over 12 years. Abundances are expressed as percentages of the total number of individuals taken over the entire 12 seasons for each species (these totals given after the species names). The season half-months begin 1–15 July (1) and end 16–31 October (8).

development of an habituated response (Donahoe & Wessells, 1979). In the case of predators on *C. neogama* and *C. retecta*, it is assumed that habituation to the hindwings proceeds so long as only one of the two species is being encountered, and that under these circumstances the startle response eventually disappears, enabling a predator to capture individuals of that species. The number of successive encounters required for successful capture of one species, N_c, undoubtedly varies with many factors, including the species of predator and the time elapsing between successive encounters. However, evidence from

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prior studies of avian startle (Blest, 1957; Coppinger, 1969, 1970) suggests that this value lies somewhere between two and perhaps five or six encounters. The presence of a second species with very different hindwings serves to reduce the probability of N_c occurring by interspersing experiences which cause the startle response to reappear. Thus, by interfering with the habituation process, both species benefit by occurring together.

The extent to which N_c would be realized in sampling from a randomly mixed population of *C. neogama* and *C. retecta* would be a function of the frequencies of these two species. If N_c was 4, and *C. neogama* and *C. retecta* occurred in equal numbers (50:50), then the probability of a predator encountering four successive individuals of one or the other species would be ca. 0.06. The results of similar calculations, for values of N_c between 1 and 5, and for frequencies of either species ranging from zero to one, are depicted in Fig. 3. Examination of this figure reveals that for values of N_c above 3, there is a considerable advantage for either species when it is less common than the other species. This advantage remains substantial when the species are about equally common, but rapidly declines for either species.

These calculations are based on the assumption that predators cannot distinguish *C. neogama* and *C. retecta* in the resting (cryptic) state. If such a distinction were possible, then predators might come to associate the two distinguishable cryptic prey with their two very different startle patterns and eventually habituate to both. However, the forewing similarities of *C. neogama* and *C. retecta* may preclude the formation of such forewing-hindwing associations and so create a very difficult habituation problem. This possibility would provide a selective basis for convergence between the two species in cryptic characteristics.

Thus far we have considered only a possible advantage of the coexistence of *C. neogama* and *C. retecta*. However, these species do utilize the same foodplants and one might envision a disadvantage of their co-existence with respect to competition for food. I have suggested previously, however, that *Catocala*, particularly species like these whose larvae feed on the mature green leaves of large deciduous trees, may not be foodplant limited (Sargent, 1978, 1980). If this were true, and if, as previously described, each species benefited with respect to predation as the other species increased in abundance (Fig. 3), then there would be little basis for competitive interference between them, and the two species might come to share what is essentially a single ecological niche.

The first section of this report is an attempt to shed some light on



FIG. 3. The probability of a predator encountering the number of successive individuals of one species (e.g., *C. neogama*) necessary for startle habituation (N_c), when taking prey from a randomly mixed, two-species population (e.g., *C. neogama* and *C. retecta*) for various frequencies of the species in question (here *C. neogama*). Curves are plotted for values of N_c from 1 through 5. The probability of an encounter sequence other than successive individuals of the species (here *C. neogama*) is given on the right-hand ordinate.

possible competitive interactions between the larvae of C. neogama and C. retecta. These rearing studies were conducted in order to (1) corroborate, if possible, the identical phenologies reported from the field, (2) compare the survival and development rates of the two species when reared in pairs comprised of one or both species, and (3) describe any changes in larval behavior associated with the two-species as opposed to the one-species rearing condition.

The second section of this report is devoted to a detailed analysis of Hessel's field data, specifically to determine the extent to which *C. neogama* and *C. retecta* occurred in equal numbers over the season for the 12 years, 1961–1965 and 1967–1971, at Washington, Connecticut.



FIG. 4. The rearing situation for *C. neogama* and *C. retecta* larvae. Each container was supplied with leaves of the foodplant and a twig on which the larva(e) could rest (cover of the container not shown).

Finally, I will discuss the implications of the ecological correspondence of *C. neogama* and *C. retecta*, and speculate as to how their numerical equality might be maintained.

REARING STUDIES

Methods

One female each of *C. neogama* and *C. retecta*, wild-caught in Leverett, Franklin Co., Massachusetts during the summer of 1976, were induced to lay eggs in brown paper bags left hanging outdoors. The eggs were transferred to small glass jars with perforated lids and left in a sheltered, outdoor location to overwinter. Hatching of all the eggs occurred on 12 May 1977 for both species. The young larvae were immediately provided with leaves of shagbark hickory (*Carya*)



FIG. 5. The numbers of adult *C. neogama* and *C. retecta* eclosing over days (12–20 July) from larvae reared in single- and mixed-species pairs.

ovata) for feeding. On 24 May, the larvae were transferred from the glass jars and placed in pairs into pint-size plastic containers. Five containers with two *C. neogama* larvae, five containers with two *C. retecta* larvae, and 10 containers with one larva of each species were established. Each container was provided with a single hickory twig upon which the larvae could rest (Fig. 4). Fresh foodplant was supplied, and frass removed, on a daily basis.

The larvae of *C. neogama* and *C. retecta*, like those of most *Catocala*, appear very bark-like from the third instar onward and usually rest by day on twigs of the hostplant (Sargent, 1976). For 21 days (26 May–16 June) during this period, the resting positions of the larvae in all of the containers having two larvae (i.e., in which neither larvae had died or pupated) were noted on one occasion, usually between 0700 and 0900 h. Data were recorded as to whether both, one, or neither larva(e) were on the twig in each container, with the species noted in those cases where both species were housed in the same container. Records were also kept of larval mortality and the dates of pupation and adult eclosion.

Results

The phenologies of *C. neogama* and *C. retecta* were essentially identical under these rearing conditions. The eggs of both species hatched on the same date (12 May) and their pupation periods commenced on the same date (9 June). The last pupa of *C. neogama* was formed on 16 June, and the last pupa of *C. retecta* was formed on 17 June. The adult eclosion dates overlapped completely, whether the moths were reared in single or mixed species pairs (Fig. 5). Thus, the



FIG. 6. The percentage of total daily observations when two, one, or no larvae were on the twig in rearing containers housing single-species (*retecta/retecta*; *neogama*/*neogama*) or mixed-species (*retecta/neogama*) pairs of larvae.

species were nearly perfectly synchronized and neither exerted an inhibitory effect on the development rate of the other.

All mortality occurred in the larval stage, but was restricted to *C. neogama*. This mortality was identical, however, in the single species and mixed species pairs (50% in both cases). Some aspect of the rearing conditions was less satisfactory for *C. neogama* than for *C. retecta*, but this difference was not related to the species with which a larva was reared.

The larvae of the two species exhibited rather similar resting behaviors in the single-species containers (Fig. 6). Both species preferred the twig (76.9% of the total observations in *C. neogama*; 71.7% in *C. retecta*), and the larvae often rested together on the twig (60.0% of the observed occasions when at least one larva was on the twig in *C. neogama*; 46.1% in *C. retecta*). Chi-square contingency tests indicate that the two species did not differ in their tendencies to utilize the twig ($\chi^2_{(1)} = 1.09$, P > .30), but that the *C. neogama* larvae had a greater tendency to occur together on the twig ($\chi^2_{(1)} = 5.44$, P < .02).

In the mixed-species pairs, both species exhibited a reduced tendency to utilize the twig (62.0% of the total observations in *C. neo*gama; 61.4% in *C. retecta*), and a reduced tendency to occur together on the twig (45.5% of the observed occasions when at least one larva was on the twig) (Fig. 6). Chi-square contingency tests indicate, however, that these changes in behavior from the single species situation were only significant for *C. neogama* ($\chi^2_{(1)'s} > 6.6$, P < .01).

The interspecific interactions seemed to involve mild aversion to one another's presence, particularly on the part of *C. neogama* to *C. retecta*. Neither species was clearly dominant on the twig, as the occasions when only *C. neogama* or only *C. retecta* was on the twig were equally frequent (Fig. 6). There was no evidence of increased aggression between species as compared to within species, though detailed behavioral observations were not carried out. However, whatever the interspecific behavioral interactions in this situation, they had no discernible effects on survival or development rates (Fig. 5).

FIELD DATA

Methods

The late Sidney A. Hessel of Washington, Connecticut recorded the number of individuals of all *Catocala* species taken in a mercury vapor light-trap on virtually every night of every season from 1961–1965 and 1967–1973. Details of the method employed, and many of the data gathered, have been presented elsewhere (Sargent & Hessel, 1970; Sargent, 1976, 1977). Here I will focus on details relating to the seasonal occurrence of *C. neogama* and *C. retecta* at this location.

Results

As previously reported, *C. neogama* and *C. retecta* were taken in nearly equal numbers in each of the 12 years of Hessel's sampling, and the two species also showed nearly identical flight seasons (Fig. 2; Sargent, 1978). Further analysis reveals that the 50:50 proportion of *C. neogama* and *C. retecta* also obtained across the flight season when the data are summed over years (Fig. 7). There was no tendency for increasingly close approximation to the 50:50 proportion as the flight season progressed. However, the variance in the *C. neogama*/ *C. retecta* proportions was greatest early and late in the season when the numbers of individuals taken were lowest, while this variance was least during mid-season when moth abundance was highest.

DISCUSSION

The co-existence of *C. neogama* and *C. retecta* in nearly equal numbers should confer a substantial advantage to both species with respect to deterring predators that tend to habituate to specific startle patterns (Fig. 3). And we have seen that these species may actually occur in nearly equal numbers over many years at a single location (Figs. 2 and 7). The question then is, what mechanism might maintain this seemingly advantageous numerical relationship of the two species?

The facts that *C. neogama* and *C. retecta* are closely related species that utilize the same foodplants at the same times suggest that they



FIG. 7. The percentages of *C. neogama* and *C. retecta* totals (N) made up by *C. retecta* during successive weeks of the season (30 July-14 October) at Washington, Connecticut (solid dots), and the standard deviation for each point (open dots). Data are summed over 12 years, 1961–1965 and 1967–1973.

may be exposed to very similar selection pressures. These same facts also suggest that the two species are intense competitors for food. However, the results of the rearing studies reported here lend some support to prior suggestions that *Catocala* are not food-plant limited. When the two species were reared together, there were some changes in larval behavior (Fig. 6), but these seemed to reflect a mild interspecific aversion that resulted in an increased tendency of the larvae to disperse. There was no evidence of detrimental aggressive interactions under these conditions, as neither species exerted an inhibitory effect on the survival or development rate of the other (Fig. 5).

Even if one were to grant, however, that food is not limiting for these species, it does not follow that they should occur in nearly equal numbers over long periods of time. Other factors (e.g., diseases, parasites, climatic variables) would almost certainly favor one or the other species at different times. Thus, the extremely close and continuous 50:50 proportion between *C. neogama* and *C. retecta* at Washington, Connecticut (Figs. 2 and 7) suggests the operation of a rather precise regulatory mechanism.

A number of mechanisms that are known to promote stable polymorphisms within species (e.g., heterosis and certain types of nonrandom mating) (see Sheppard, 1959) could not operate in this twospecies situation. However, one extrinsic mechanism, frequency dependent selection, could operate here and warrants closer examination. Frequency dependent selection, or "apostatic" selection (Clarke, 1962), occurs when each member of a pair of morphs or species is at an advantage with respect to predation when rarer than the other, but at a disadvantage when more common than the other (see Cain & Sheppard, 1954; Haldane, 1955; Clarke & O'Donald, 1964). Such a situation would seem to hold in the present case (see Fig. 3). Thus, if *C. neogama*, for example, comprised 25% of a *C. neogama/C. retecta* population at some point in time, then *C. retecta* should be more heavily predated until its numbers were roughly equal to those of *C. neogama*. If *C. neogama* became more common than *C. retecta* then *C. neogama* should receive more predation, and so on. In this way, predator selection would tend to promote and maintain a 50:50 proportion of the two species.

There is some evidence suggesting the operation of frequency dependent selection in the C. neogama/C. retecta situation at Washington. Connecticut. If one assumes that there is some threshold abundance of these moths below which they do not attract significant predation, and above which predation is significant (i.e., that this predator-prev relationship fits the so-called Type III function) (Holling, 1959, 1965, 1966), then the effects of predation should be maximal at mid-season when prey density is highest, and minimal or non-existent at the extremes of the season when prey densities are lowest. The C. neogama/C. retecta proportions at Washington, while averaging 50:50 across the entire season when the data are summed over vears, do show less variance at mid-season (Fig. 7). This finding may be evidence that predators drive the system to equilibrium when the moths are abundant, but exert little influence when the moths are scarce. And this, in turn, could explain why C. neogama and C. retecta may not show the 50:50 relationship at locations where they are relatively rare (e.g., Leverett, Massachusetts; unpubl. data).

In summary, there is substantial evidence that *C. neogama* and *C. retecta* may occur in nearly equal numbers at a given location while occupying very similar ecological niches. This situation is seen as a consequence of several factors, including (1) a presumed close phylogenetic relationship between the two species, (2) an abundance of resources such that food is not limiting, and (3) predator selection that (a) promotes convergence in all characteristics associated with crypsis, (b) simultaneously promotes divergence in startle characteristics, and (c) acts in a frequency dependent manner with respect to these startle characteristics.

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