STUDIES ON THE CATOCALA (NOCTUIDAE) OF SOUTHERN NEW ENGLAND. III. MATING RESULTS WITH C. RELICTA WALKER

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Successful matings of *Catocala* moths have apparently been rarely achieved in captivity. I am aware of no published accounts of such matings in the North American literature. Considering, however, the many genetic, ecological, and evolutionary questions posed by this vast assemblage of moths, successful matings should provide results of wide interest. Consequently, I have begun attempts to mate *Catocala*, and this paper reports initial successes with *C. relicta* Walker.

C. relicta was selected for initial study, as its close European ally, C. fraxini Linnaeus, has been mated in captivity (e.g. Cockayne et al., 1937–38), and further, C. fraxini and C. relicta have been successfully hybridized (Meyer, 1952).

The present report is based on studies conducted from 1969-1971 in Leverett, Massachusetts. During that period a total of 541 adult *C. relicta* were reared from eggs, and 25 matings were observed.

METHODS AND MATERIALS

C. relicta occurs in three forms in the northeast (Beutenmüller, 1903; Forbes, 1954): typical, with clouding of black scales between am. line and base of forewing, and between pm. and st. lines (Fig. 1a, e, f); clara, with these areas largely white (Fig. 1c, d); and phrynia, with a nearly even dusting of black scales over the entire forewing (Fig. 1b). The present mating studies involved only typical and clara moths, although wild-caught specimens from Leverett have been approximately 30% typical, 60% clara, and 10% phrynia (1968–71, 43 records).

Rearing Procedures

The larval stages and pupa of C. relicta have been previously described in detail by Clark (1888) and Rowley & Berry (1910).

In the present study, eggs were obtained by placing wild-caught or mated adult females into paper bags which were hung outdoors for several days. The eggs were then transferred on small pieces of paper into baby-food jars which were left outdoors to overwinter. Larvae hatched in mid-May (initial hatch from 8–18 May over the three years) and were



Fig. 1. Specimens of *C. relicta*: a. P_1 wild-caught typical female; b. wild-caught phrynia male; c, d. lightest and darkest clara obtained in F_1 crosses; e, f. lightest and darkest typical obtained in F_1 crosses.

immediately supplied with fresh poplar leaves (*Populus tremuloides*). At 1–2 weeks of age the larvae were transferred individually into pint, plastic ice-cream containers. Herein each larva was provided with a poplar twig for resting and a dry, curled beech leaf (*Fagus grandifolia*)

Situation	No. Paired	No. Mated	Percent Mated
LOCATION			
Indoors Outdoors	$21 \\ 5$	$\frac{20}{4}$	$95\% \\ 80\%$
CAGE			
Small	6	5	83%
Large	10	10	100%
Cylinder	10	9	90%

TABLE 1. Mating success with C. relicta, 1969-70.

for pupating. Fresh poplar leaves were added, and frass removed, each day until pupation. Pupae were usually formed in the beech leaves and occasionally in the fresh poplar foliage (initial pupation from 15–22 June). Adults generally eclosed about one month later (initial eclosion from 15–18 July).

C. relicta did particularly well under these rearing conditions, with 80–90% survival from egg to adult being commonly obtained.

Mating Procedures

The plastic containers housing the individual pupae were checked each day for adults. When a male and female were available for pairing, they were transferred from these containers into one of three different types of cages: *small*, homemade of aluminum window screening on a wooden frame (approx. $20 \times 23 \times 23$ cm.); *large*, obtained from Ward's Natural Science Est. (14W 7500), made of nylon mesh on a plywood frame (approx. $28 \times 25 \times 41$ cm.); *cylinder*, homemade from aluminum window screening, rolled into a cylinder (18 cm. diam. \times 38 cm. high) and covered at both ends with cardboard pie plates. These cages were then either placed outdoors (on stumps, and hung from limbs) or indoors (basement, approx. 18° C., with small windows allowing some natural light). All paired moths were provided with an opportunity to feed from small pieces of sponge which were soaked daily with a honey and water solution.

The cages were checked by flashlight (covered with a sheet of red cellophane) at intervals during the night. At these times the behaviors of all moths were carefully noted, but prolonged observations of courtship were not attempted, as the flashlight seemed to distract and disturb the moths to some extent.

Mating was considered achieved only when a pair was observed in



Fig. 2. C. relicta pair in copulation on side of large cage-female above, male below (approximately natural size).

actual copulation. On the day following this observation the female was bagged for eggs and the male killed and retained as a specimen. When the female died she was also retained—male, female, and eggs being labeled with a common symbol.

RESULTS AND DISCUSSION

Behavior

Of 26 pairs of moths which were carefully observed during the summers of 1969 and 1970, 24 (92%) were observed in copulation, and 20 of these matings resulted in fertile eggs (i.e. produced larvae). Mating success was high in all three types of cages, and both outdoors and indoors (Table 1).

Courtship behavior, though not observed in detail, seemed generally similar to that described for other noctuids (e.g. Shorey, Andres & Hale, 1962; Birch, 1970). The females almost invariably adopted a "calling" posture shortly after dusk, and maintained this posture (unless mating occurred) for most of the night. In this calling posture a female elevated the abdomen (from either a horizontal or vertical surface) above the plane of her partially spread wings (the wings being vibrated rapidly



Fig. 3. Time of mating (Eastern Daylight Savings Time) for 25 pairs of C. relicta observed during the summers of 1969–71.

during high intensity calling), and protruded the pheromone-producing gland beyond the tip of her abdomen. Just prior to mating, considerable male activity (walking and flying about the cage) was noted, presumably involving behaviors similar to those described by Birch (1970). Copulation then quickly ensued, usually on the side of a cage (on three occasions under the roof), with the female the uppermost moth. After initial contact the hindwings of both moths were visible beneath their partially spread forewings, but shortly thereafter the wings were closed as in the resting posture, with the female's forewings overlapping those of the male (Fig. 2). Pairs remained in copulation for from 2–13 hrs., a longer period than that reported in other noctuids (Shorey et al., 1962; Birch, 1970).

Visual stimuli were apparently not required for courtship and mating, as successful copulations were achieved in essentially total darkness (basement). This agrees with prior observations on other noctuids (Shorey, 1964; Shorey & Gaston, 1970).

Although females were observed in the calling posture during all hours of the night, matings were initiated during a relatively short period (Fig. 3). These observations suggest that males were chiefly responsible for the timing of mating; and although daily cycles in male responsiveness



Fig. 4. Night following pairing during which mating occurred in 25 pairs of C. *relicta*. Actual ages of the moths from night of eclosion are given within each box (male/female).

to female pheromone are known in noctuids (Shorey & Gaston, 1964, 1965), the timing of mating is chiefly controlled in these species by a circadian rhythm of female pheromone release (Sower, Shorey & Gaston, 1970, 1971). The possibility then of chiefly male timing in *C. relicta* would seem to warrant further investigation.

The night during which mating occurred following pairing of the moths varied widely, and fertile eggs were obtained from matings involving males and females ranging from 1–16 days of age (Fig. 4). Some variability in the occurrence of mating was expected in view of prior studies on reproductive age in noctuids (Shorey, McFarland & Gaston, 1968; Shorey, Morin & Gaston, 1968), but I am not aware of prior reports of delays in mating extending to two weeks or more in caged moths which are apparently capable of mating much earlier.

A totally unexpected result obtained in this study was the failure of calling females to attract males to their cages. This occured even though *C. relicta* were being captured in the study area at bait and in light traps, and despite the release of scores of unmated (marked) males into the study area. While many factors are known to reduce the effectiveness of pheromone attraction (Saario, Shorey & Gaston, 1970; Sharma, Shorey & Gaston, 1971), none of these would seem to account for the present total failure. Variable numbers of caged females were observed calling

every night over one-month periods during the summers of 1969 and 1970, and these periods included considerable variation in environmental factors such as humidity, temperature, wind, and moonlight. In addition, the height of the cages was varied between 0 and 6 ft. above the ground, and on occasion fresh poplar foliage was added to the cages (in the event that the female pheromone *plus* a chemical from the foodplant was necessary to attract males—as reported for the saturniid, *Antheraea polyphemus* (Riddiford & Williams, 1967)).

One possible explanation for this situation would involve postulating a non-chemical communicating stimulus which attracts males from a distance and which caged females are incapable of producing. Such a stimulus could conceivably be auditory (perhaps produced in free flight), and be analagous to the visual stimuli known to initiate courtship behaviors in butterflies (e.g. Magnus, 1963; Brower, Brower & Cranston, 1964). A significant role of auditory stimuli in directing the approach of courting moths has recently been reported in *Achroia grisella* (Fabr.) (Pyralidae) (Dahm et al., 1971). Perhaps the males caged with the females in the present study were in close enough proximity to bypass any long-distance communication and to proceed immediately with chemically mediated courtship stages. Whatever the explanation, this matter warrants close study in the future.

Genetics

All *C. relicta* discussed in this report are descendents of a wild-caught female taken in Leverett in 1968 (Fig. 1a). This **typical** female produced 90 eggs, from which 85 progeny (F₁) were reared: 42 **typical** (20 & &, 22 \heartsuit \heartsuit) and 43 **clara** (27 & &, 16 \heartsuit \heartsuit). This 1:1 phenotypic ratio suggested that a single Mendelian factor was responsible for the difference between the **typical** and **clara** forms, and that the cross had involved a homozygote \times heterozygote for that factor. This suggestion was confirmed through subsequent crosses of the F₁, the **typical** allele proving to be dominant (Table 2).

The alleles were given the symbols C (dominant) and c (recessive), with CC and Cc representing respectively homozygous and heterozygous **typical** individuals, and cc representing homozygous **clara** individuals. Homozygous and heterozygous **typicals** were not phenotypically distinguishable with certainty, there being considerable and rather continuous variation among the **typical** progeny of all $Cc \times Cc$ crosses. However, the darkest **typicals** were obtained in these crosses (e.g. Fig. 1f), and these may have been homozygous individuals. The extent of variation among **typical** and **clara** moths in the progeny of all F_1 crosses is illus-

Matings		Prog						
Brood	clara		tyı	typical		Totals		
Number	Male	Female	Male	Female	clara	typical		
clara \times clara (a	$c \times cc)$							
08-70	23	19	-	-	42	-		
09-70	8	5	-	-	13	-		
11-70	5	2	-	-	7	_		
02-71	10	12	-	-	22	-		
Totals					84	0		
$clara \times typical$	$(cc \times Cc)$)						
01-69	27	16	20	22	43	42		
01-70	8	7	4	7	15	11		
03-70	8	6	6	8	14	14		
05-70	9	11	10	7	20	17		
06-70	5	8	4	9	13	13		
07-70	9	7	6	6	16	12		
01 - 71	5	5	8	6	10	14		
04-71	6	10	9	6	16	15		
Totals					147	138		
clara \times typical ($cc \times CC$)								
03-71	_	-	39	51	0	90		
typical \times typica	$(Cc \times C)$	Cc)						
02-70	4	2	12	12	6	24		
04-70	6	2	6	12	8	18		
10-70	5	6	13	2	11	15		
Totals					25	57		

TABLE 2. Summary of C. relicta crosses, 1969-71.

trated in Fig. 1 (c, d and e, f)—no intermediates between the forms were obtained.

All F_1 crosses produced phenotypic ratios which did not differ significantly from those expected in one-factor crosses involving autosomal alleles and complete dominance (chi-square goodness-of-fit tests). However, the totals in $Cc \times Cc$ crosses actually fitted a 2:1 (typical:clara) ratio better than a 3:1 (chi-squares of 0.29 and 1.33 respectively), suggesting that the homozygous dominant genotype may have been lethal in some cases (perhaps in the presence of certain modifiers). Close examination of the data reveals a marked deficit of typical females in brood 10-70 (Table 2). The two typical females obtained in this brood were rather light, whereas five of the 13 typical males were extremely dark. It may be that lethality here is similar to that described in situ-



Fig. 5. Percentage of males eclosing over successive three-day intervals of the eclosion period for each brood (summed over 16 broods, 1969–71). The number of individuals eclosing is given above each point on the graph.

ations involving the sex-limited "alba" gene in *Colias* butterflies (Remington, 1954), but the present numbers are rather small, and further study is needed.

Sex Ratios

The over-all sex ratio in moths from 16 broods (Table 2) was 275 && and 266 &&&, with only one brood (the previously noted 10–70) departing significantly from a 1:1 ratio (chi-square 3.84, P = 0.05 in that case).

There was a consistent tendency for females to eclose before males (Fig. 5), with the sex ratio for eclosion days 1–10 summed for all broods being 188 & & and 211 \Leftrightarrow \Leftrightarrow (47% male), and for eclosion days 11–20 being 87 & & and 55 \Leftrightarrow \Leftrightarrow (61% male). These ratios are significantly different (chi-square, 2 × 2 contingency test, 8.03; P < 0.01).

In most Lepidoptera, males tend to eclose before females, and this certainly is true in C. fraxini (Cockayne et al., 1937–38). The significance of the present reversal of the usual trend is not yet apparent.

SUMMARY

Twenty-five matings were observed in caged pairs of C. relicta during the summers of 1969–71 in Leverett, Massachusetts. All of these matings

were initiated between 2100 and 2400 EDST, and it appeared that males were chiefly responsible for this timing. Successful matings were obtained with males and females ranging from 1–16 days of age. Progeny reared from these matings revealed that the expression of the **typical** and **clara** forms in the adults is largely controlled by a single gene, with the allele for the **typical** pattern being dominant. The possibility of some lethality among homozygous **typical** individuals was suggested. Over-all sex ratios were close to 1:1, but females tended to eclose before males.

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OBSERVED MATING BETWEEN PIERIS RAPAE AND PIERIS PROTODICE (PIERIDAE)

Late in the afternoon of 5 July 1971, I explored a weed-infested lemon and avocado orchard in Goleta Valley (Santa Barbara County, California), looking for Nathalis iole (Boisduval). N. iole had once been locally common in lemon groves in rural areas around Santa Barbara, but apparently had not colonized this orchard. The only butterflies sighted that afternoon were Danaus plexippus (Linnaeus), Vanessa carye (Hubner), Pieris rapae (Linnaeus) and Pieris protodice (Boisduval & LeConte). The latter two species were flying around the wild mustard in great abundance, fluttering close to the ground, and often landing—obviously getting ready to settle down for the night.

At approximately 1700 I noticed a copulating pair of *Pieris* land a few feet in front of me. Upon closer observation, I noticed that they were two different species, a male *P. rapae* and a female *P. protodice*. The female *protodice* was the flying partner. They were netted, pinched and carefully placed in an envelope. Still in copulation, I later mounted them on a piece of cardboard and placed them in my collection.

When two close species are found together in abundance, such interspecific matings are possibly not as rare as one might suspect. I have previously observed mating between these two species in the Santa Barbara area. About a decade ago, in a field across from Arroyo Burro Beach State Park, I noted a pair in copulation. Considering that these species are very common throughout the United States, and are usually ignored by local lepidopterists, many such matings could go unnoticed.

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