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LIFE HISTORY OF THE BOG BUCK MOTH (SATURNIIDAE: *HEMILEUCA*) IN NEW YORK STATE

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ABSTRACT. The Bog Buck Moth (Saturniidae: *Hemileuca* sp.) occurs in wetland habitats in the Great Lakes region of North America and has been documented in fewer than 10 sites globally, of which 6 are in Oswego County, New York. The larvae feed on at least 10 species of plants at these sites, including the novel hostplants buckbean (*Menyanthes trifoliata* (Menyanthaceae)) and cranberry (*Vaccinium macrocarpon* (Ericaceae)). Details of the Bog Buck Moth's larval development, pupation, eclosion, flight behavior, and oviposition are presented. A censusing method tailored for the flight period is described.

Additional key words: Cryan's Buck Moth, Menyanthaceae, *Menyanthes trifoliata*.

In central and eastern North America, buck moths (Saturniidae: *Hemileuca*) occupy habitats ranging from pine barrens to wetlands (Ferguson 1971, Cryan 1985, Scholtens & Wagner 1994, Tuskes et al. 1996); presumably, glacial retreat left populations of buck moths in disjunct habitats throughout the Great Lakes region. While some of these populations have long been considered isolates of *Hemileuca maia* (Drury), others appear to be more like *H. lucina* Hy. Edwards or *H. nevadensis* Stretch, and their taxonomy remains enigmatic due to morphological, ecological, and behavioral variation (Ferguson 1971, Scholtens & Wagner 1994, Tuskes et al. 1996).

The Great Lakes populations of buck moths have adapted to wetland habitats. In fens around Ottawa (Ontario), in Oswego County (New York), and in Ozaukee County (Wisconsin), buck moth larvae feed on *Menyanthes trifoliata* L. (Menyanthaceae), an aquatic herb unrelated to other *Hemileuca* hostplants (Scholtens & Wagner 1994, Tuskes et al. 1996). Furthermore, the ability to feed on *M. trifoliata* appears to be limited to these scattered populations of *Hemileuca* (Scholtens & Wagner 1994, Legge et al. 1996, Tuskes et al. 1996). Although *M. trifoliata* occurs in more than half of the counties in New York State (New York Flora Association 1990), the Bog Buck Moth (BBM) only occurs in 6

sites in Oswego County (of 10 sites globally; Fig. 1). Two New York BBM populations were discovered in 1977 by John Cryan and Robert Dirig, hence their alternate common name, Cryan's Buck Moth (Legge et al. 1996).

Previous studies of the New York populations have included laboratory investigations of genetic traits and hostplant performance (Legge et al. 1996), preliminary surveys of potential habitats and captive rearing and cross-breeding experiments (Tuskes et al. 1996, J. Tuttle & D. Schweitzer, unpubl. data). However, little has been published on the BBM's natural history. Here I present details of its life history, feeding ecology, development, and oviposition behavior. I also provide data on egg rings, larvae, pupae, and adults, and describe a censusing method for monitoring these populations.

MATERIALS AND METHODS

I surveyed 6 BBM sites in Oswego County, New York from 4 May to 13 October 1995, and 1 May to 29 June 1996. The sites varied from rich shrub fens to a bog-like poor fen (Reschke 1990). Egg rings were found at 4 sites, larvae at 3 sites, and adult BBMs at 4 sites.

Egg ring data were recorded in May and early June 1995. Data included descriptions of the host plants (species, total height, stem diameter at height of egg ring), the egg rings (length, height from substrate, number of eggs per ring), and microhabitats (nearby plant species, microtopography, amount of water). Each egg ring was individually numbered and flagged.

Data were collected on larval behavior (feeding, moving, or stationary; response to conspecifics; relative position on vegetation), food plants, and larval lengths. If the larvae were clustered, the cluster size was recorded. In an attempt to document pupation and eclosion (i.e., to measure depth in substrate, pupa dimensions, microhabitat of pupation site, time required for pupation), and to collect a series of adult BBMs, I reared 100 larvae to pupation in the field. The larvae were reared in vertical sleeves placed around woody stems of *Spiraea alba* Duroi (Rosaceae). Occasionally I moved the larvae as a group to a fresh plant—approximately 25 larvae in each of 4 sleeves. Upon reaching late instar length (45–60 mm), larvae were placed in a fine mesh enclosure measuring 1 m × 1 m × 15 m. The enclosure transected open fen habitat which included the food plants *M. trifoliata* and *Vaccinium macrocarpon* Aiton (Ericaceae). The area inside the enclosure was cleaned of existing larvae before introducing the sleeve-reared larvae. By comparing the number of moths that emerged to the number of larvae that pupated, I intended to determine whether overwintering pupation occurs

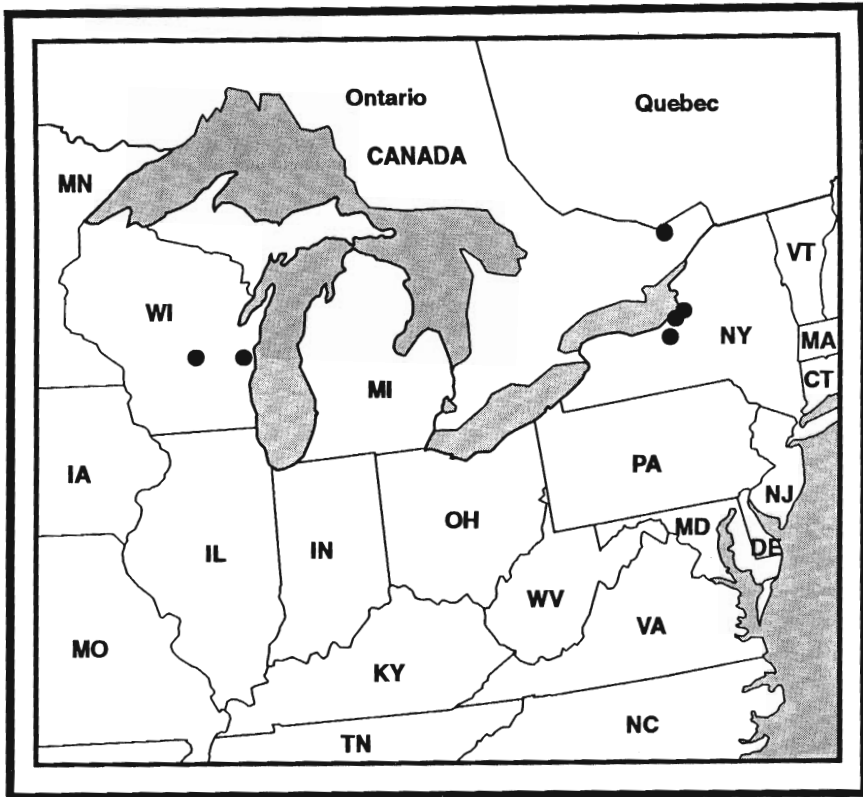


FIG. 1. Distribution of the Bog Buck Moth (*Hemileuca* sp.): populations that feed upon *Menyanthes trifoliata* and occur in fen habitats.

in this taxon, and if so, in what proportion. However, all pupae within the enclosure apparently were preyed upon (see Results).

In 1995, adult BBMs were first observed flying on 11 September, and the last were observed on 11 October. The flight period allowed censusing adult BBMs. I first determined the peak flight time for male moths i.e., between 1100 and 1400 h EST. I then determined the average "circling time" (the time required for a male to circle the fen once in search of females) i.e., approximately 10 min. Positioned at the center of the fen and looking outwards in one direction (along a radius), I then counted all moths that flew past that radius for 10 min. At each site, such a 10-minute count was made while looking north, followed by one looking south, then one looking east, and one looking west. The four 10-min counts were then averaged for an estimate of the number of moths

TABLE 1. Bog Buck Moth (*Hemileuca* sp.) egg ring data, collected spring 1995 from 3 sites in Oswego County, New York. Data expressed as mean with SD. Means followed by different letters are significantly different ($p < 0.05$) by Tukey HSD multiple comparisons.

Site	n	Egg ring height (cm)	Host height (cm)	Stem diameter (mm)	Ring length (mm)	Eggs/ring
A	10	17.9 (9.6) a	37.6 (16.7) a	3.8 (1.5) a	20.4 (3.8) a	142 (32) a
B	85	11.4 (6.1) b	35.1 (18.1) a	3.5 (1.2) a	19.1 (5.7) a	142 (44) a
C	7	27.0 (14.7) c	47.2 (15.2) a	2.7 (1.2) a	19.9 (4.5) a	131 (30) a

flying at that site during the peak flight period for that day. Several sites could be censused each day.

RESULTS

Egg rings. Although egg rings were found at 4 sites, data from only 3 sites were analyzed due to low sample size ($n = 2$) at one of the sites. There were no significant differences in mean stem diameters, egg ring lengths, oviposition plant heights, or numbers of eggs per egg ring between the 3 sites (ANOVA, $p < 0.05$, Table 1). Mean egg ring height from the substrate differed among sites ($F_{2,99} = 17.3$, $p < 0.001$), particularly between sites A and C (Tukey HSD, $p < 0.001$; this was likely due to differences in microhabitat and dominant oviposition plant species). At site C, a rich shrub fen, all recorded egg rings were oviposited on *Myrica gale* L. (Myricaceae), a tall, woody plant that was sparse at sites A and B. Accordingly, the mean egg ring height was greatest at site C (27.0 ± 14.7 cm). At site B, a bog-like, open fen, most of the egg rings were oviposited on short, broken stems of *Anchistea virginica* (L.) J. E. Smith (Blechnaceae) and at the bases of *Alnus incana* ssp. *rugosa* (L.) Moench (Betulaceae). Thus, the mean egg ring height was lowest at site B (11.4 ± 6.1 cm). Egg rings from site A were found in a microhabitat that shared characteristics of sites B and C (i.e., site A egg rings were found in open, sedgy fen habitat, similar to site B, but most egg rings were on *M. gale*, the dominant oviposition shrub at site C). Furthermore, mean *M. gale* heights at sites A and C (35.8 and 47.2 cm, respectively) were not significantly different ($p = 0.220$), while the mean heights of egg rings deposited on *M. gale* were different between sites A and C (lower to the substrate at site A). The *M. gale* that bore egg rings at site C formed dense stands, whereas those at site A were isolated, individual plants in open habitat. Therefore, differences in habitat type and plant structure, not oviposition plant species *per se*, seem to explain the observed differences in oviposition sites.

Egg rings were found on 9 plant species: *Acer rubrum* L. (Aceraceae), *A. incana* ssp. *rugosa*, *A. virginica*, *Carex* sp. L. (Cyperaceae), *Chamaedaphne calyculata* (L.) Moench (Ericaceae), *M. gale*, *Salix pedicellaris*

TABLE 2. Bog Buck Moth (*Hemileuca* sp.) egg ring data, according to hostplant species. Data collected spring 1995 from Oswego County, New York, and expressed as mean with SD. Means followed by different letters are significantly different ($p < 0.05$) by Tukey HSD multiple comparisons.

<i>Myrica gale</i>	15	22.8 (12.4) a	42.5 (17.1) a	3.4 (1.6)	19.6 (3.8) a	132 (27) a
<i>Chamaedaphne calyculata</i>	18	13.5 (8.5) b	30.0 (12.2) a	2.9 (0.7)	21.0 (5.1) a	152 (42) a
<i>Alnus incana</i>						
ssp. <i>rugosa</i>	42	12.0 (4.6) b	40.6 (19.4) a	3.8 (1.4)	17.9 (5.9) a	136 (41) a
<i>Anchistea virginica</i>	20	6.9 (1.9) c	28.0 (18.2) a	3.6 (0.7)	19.1 (5.4) a	141 (50) a

Pursh (Salicaceae), *Spiraea alba* Duroi (Rosaceae), and *Cornus sericea* L. (Cornaceae). There were no significant differences among sites in mean number of eggs per egg ring or mean oviposition plant heights (Table 2). There were, however, significant differences in mean stem diameters of two plant species oviposited on, the mean egg ring lengths on the same two plant species, and the mean egg ring heights among all of the plant species oviposited on. Data for egg rings oviposited on *A. rubrum*, *Carex* sp., *S. pedicellaris*, *S. alba*, and *C. stolonifera* were not used in statistical analyses because of low sample size.

Mean stem diameter of *C. calyculata* at the height of oviposition was significantly smaller (Tukey HSD, $p = 0.03$) than that of *A. incana* ssp. *rugosa* (2.9 ± 0.7 mm vs. 3.8 ± 1.4 mm). Generally, *C. calyculata* stems were thinner than those of *Alnus*. While the length of the egg ring changed with differences in stem diameter, the number of eggs per egg ring did not ($t = 2.04$, $p < 0.05$). Thus, it appears that the BBM lays an egg ring normally consisting of 100–180 eggs, and that the egg ring will be longer if the oviposition plant stem is thinner. This was supported by an isolated observation of oviposition on a slender stem of *Carex* sp. (1.8 mm diam.), in which the length of the egg ring (28 mm) was greater than the average on other oviposition plants (mean = 19.4 mm, $N = 95$).

Height of oviposition differed significantly among the hostplant species. Although egg rings were found on plants that ranged from 28 cm to >40 cm height, height of the plant did not appear to determine oviposition height. Differences in the height of the egg rings were attributed to differences in plant structure at the mean heights of oviposition (approximately 10–40 cm from the substrate). The density of foliage varied among the four main oviposition plants (*A. incana* ssp. *rugosa*, *A. virginica*, *C. calyculata*, and *M. gale*) at the time of oviposition. *Chamaedaphne calyculata* formed short, dense clumps of evergreen foliage on slender stems. *Alnus incana* ssp. *rugosa* exhibited thick, bare stems up to its sparse, wide leaves, which began at about 15 cm high. *Myrica gale* was sparsely-foliated with exposed stems its entire height, especially in

fall when the leaves began to curl and brown. *Anchistea virginica* died back with the first frost and essentially existed as a vertical stalk with some curled-up foliage. Often, this fern was broken off at a short height, and many old, broken stems bore egg rings. Thus, it appears that structural requisites (e.g., stem diameter, density of foliage), not oviposition plant species preference *per se*, determine the location and the height of egg rings in the field.

Larvae. BBM larvae hatched between 12 May and 14 June 1995. The side of the egg ring facing the sun tended to hatch before the opposite side. Upon hatching, the larvae (<4 mm long) circled the egg rings horizontally and joined into a cluster. The cluster then climbed the oviposition plant stem in a single travel line, investigated any foliage (and briefly consumed small portions of leaves such as *A. rubrum*), remained in the foliage feeding (especially *C. calyculata*, *Alnus*, and *Salix*), or returned down the stem if the oviposition plant was unacceptable. The larvae then formed a traveling line that fed mainly on *V. macrocarpon*, until approximately 12 days after the first egg ring hatched, at which point the leafing of *M. trifoliata* stimulated a switch in primary foodplants.

Throughout the summer, I observed the larvae feeding on *A. incana* ssp. *rugosa*, *Aronia melanocarpa* (Michx.) Elliott (Rosaceae), *Carex* sp., *C. calyculata*, *Ilex verticillata* (L.) A. Gray (Aquifoliaceae), *M. trifoliata*, *Quercus* sp., *S. pedicellaris*, *S. alba*, and *V. macrocarpon*. On 2 June 1995, 72% of feeding early instar larvae were eating *M. trifoliata*, 14% were feeding on *S. alba*, 6% were eating *A. incana* ssp. *rugosa*, 4% were feeding on *V. macrocarpon*, and 4% were eating *C. calyculata*. In contrast, on 5 July, at the same site, 54% of feeding late instar larvae were eating *V. macrocarpon*, 25% were feeding on *M. trifoliata*, 16% were eating *Carex* spp., 3% were feeding on *C. calyculata*, and 2% were eating *A. melanocarpa*. Thus, although *Menyanthes* appears to be the primary foodplant at earlier instars (Legge et al. 1996, Tuskes et al. 1996, pers. obs.), other foodplants are fed upon more heavily by mature larvae.

The number of larvae per cluster declined as larvae grew. Final instar larvae were typically seen alone, whereas solitary first instar larvae were seen only infrequently. On 2 June 1995, for example, the mean number of larvae per cluster was 23 ± 17 ($N = 175$ clusters). On 14 June, at the same site, the mean number of larvae per cluster was 7 ± 9 ($N = 36$ clusters). No significant differences in cluster sizes among 7 different host species were found. Larvae of different instars were sometimes in the same feeding cluster, suggesting that not all larvae in a feeding cluster were from the same egg ring, or that larvae developed at different rates.

Mature larvae reached a maximum length of approximately 60 mm before pupation (Fig. 2). On 11 July 1995 the mean length of larvae before pupating was 49 mm ($N = 60$ larvae). Many late instar larvae were

found dead on the surface of the sphagnum in July. While hot summer temperatures (maximum recorded surface sphagnum temperatures exceeded 38°C on several days in July) might have caused some larval mortality, NPV (nuclear polyhedrosis virus) should also be considered (Mitchell et al. 1985).

Pupae. Larvae fed throughout the summer and passed through six instars before pupating. Only 10 pupae were discovered within the experimental enclosure, all of which had been bored into and hollowed out. After two exhaustive searches, no other pupae were found in the enclosure. No adult moths emerged within the enclosure. Outside the enclosure, pupae were found that had been preyed upon in similar fashion. Some pupae that had been preyed upon were found under 5 cm of sphagnum. Although predation of the pupae was not directly observed, damage to the buck moth pupae and the conditions of attack match descriptions of predation by beetles (Carabidae, Staphylinidae, and Elatidae) on pupae of the winter moth (*Operophtera brumata* (L.) Hydrimenidae) (Frank 1967; also J. Frank, pers. comm.).

Mean lengths of captive-reared BBM pupae (26.8 ± 2.6 mm, $N = 5$) were significantly different ($t = 2.97$, $p < 0.03$) from pupae discovered in the field (23.0 ± 1.2 mm, $N = 5$). However, mean widths of captive (9.2 ± 0.8 mm, $N = 5$) and wild (8.8 ± 0.4 mm, $N = 5$) pupae did not differ significantly ($t = 0.94$, $p > 0.5$). Significant differences in pupal lengths but not widths might be due to the relatively smaller size of the width measurements, or a small sample size. Mean depths of pupation in sphagnum were not significantly different between captive and field populations (4.3 ± 0.8 cm and 4.5 ± 0.4 cm, respectively).

Adult flight behavior. Upon eclosion, adult BBMs climb up the nearby vegetation to harden their wings. The moths were observed quivering their wings for short periods of time while grasping the vegetation. Presumably, this allows their flight muscles to warm up for the initial flight and for each subsequent flight after periods of inactivity. Flight records of BBMs at four sites are provided in Fig. 6. The total number of moths observed flying at each site during the fall 1995 flight season were: site A = 304, site B = 802, site C = 1369, and site D = 3.

No moths were observed flying during rainstorms, on cold days (temperatures $< 12^\circ\text{C}$), or during high winds. On such days, moths were dormant and clung to vegetation. Mean resting height for moths was not significantly ($t = -1.49$, $p > 0.05$) closer to the substrate in open fen habitat (35.2 ± 15.1 cm, $N = 16$) than in shrubby edge habitat (56.5 ± 39.0 cm, $N = 8$). However, resting height differed among plant species ($F_{7,16} = 5.09$, $p < 0.005$); these differences were attributed to differences in the heights and vegetative structure of the plants.

If approached or handled, moths were reluctant to fly and curled into



a defensive posture: wings extended outward dorsally, and the bright orange abdomen exposed and arched inward ventrally. When disturbed, the BBMs did not fall freely to the ground, as is described for other *Hemileuca* (Tuskes et al. 1996), but rather held tight to the vegetation (it was difficult to remove the moths without injuring them) or flew away.

Both sexes of BBMs flew early in the day (0900 h), but peak flights occurred between 1100 and 1400 h. Males and females were observed flying and resting throughout the day. Although I remained in the fens until dark on several occasions, the latest flight that I observed was just after 1600 h (moths were reported flying at 1830 h during the previous flight season; S. Bonanno, pers. comm.). Most moths flying during the peak hours were males, whereas most moths flying after 1400 h were females. Ovipositions occurred primarily in the afternoon hours from 1300 to after 1600 h.

Males and females differed in flight patterns and behaviors. Males flew in large, circular flight paths, covering the entire open area of the fen in about ten minutes. They flew for longer periods of time than females, which usually flew for only a matter of seconds (females made short but frequent flights in preovipositional searches). Males often flew around in small circles or even backtracked, while females beelined clumsily just above the vegetation. The weaving flights of the males indicated their characteristic search pattern: downwind approaches to pheromone trails and concentric circular flights that tightened around the calling and receptive females.

Often, males circled within a meter of the female for several minutes, then landed nearby and walked around. Failing to locate the female, they eventually flew away. The females were usually well-hidden in vegetation while releasing pheromones. When discovered by a male, the female would sometimes climb up out of the foliage to an exposed stem where copulation proceeded (Fig. 3). Staying concealed may reduce exposure to predators, but often appeared to reduce the success of enticing a male. Mate-finding in the BBM appears to be based mainly on pheromone attraction rather than visual cues. For example, when I enticed males in the field with captively-reared females, the males rapidly swarmed about, but could not readily find the females' cage. Instead,

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FIGS. 2-5. **2**, Late instar Bog Buck Moth larva (*Hemileuca* sp.) feeding on *Menyanthes trifoliata*. Its red head capsule resembles the caranberries (*Vaccinium macrocarpon*) that abound in its habitat. **3**, Male (left) and female (right) *Hemileuca* mating on exposed stem of *Myrica gale*. **4**, Two seamlessly joined *Hemileuca* egg rings on a single stem of *Anchistea virginica*; unhatched, recently oviposited eggs (above, darker) and hatched egg ring from the previous year (below). **5**, Spider (*Argiope aurantia*) predation on *Hemileuca*.

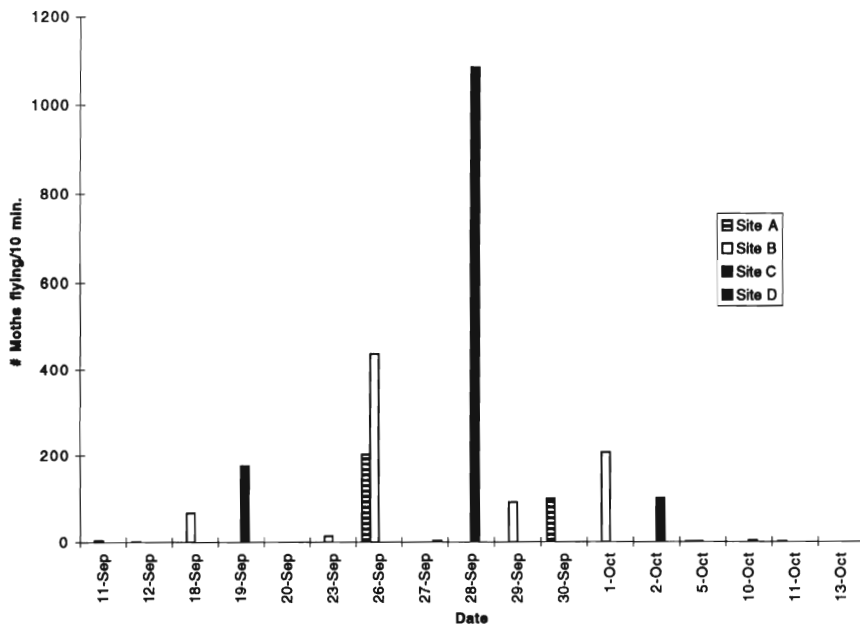


FIG. 6. Flight records of the Bog Buck Moth (*Hemileuca* sp.) from 4 sites in Oswego County, New York, fall 1995.

the males would alight on my head or body, then walk around until locating pheromone on my hand or on the cage.

Both sexes usually flew with the abdomen hanging straight down or curved slightly inward (ventrally). Males tended to fly with the abdomen arched up and back (dorsally) when homing in on the females' pheromones.

No migration between sites was observed, although the presence of a few adult moths in one submerged fen (in which no egg rings or larvae, and only sparse food plants were found) indicated this possibility. Four of the 6 documented sites were completely surrounded by upland deciduous forests. The other 2 sites were separated from each other by a creek and were buffered from surrounding forests by marshes. No moths were seen flying above the treeline surrounding their respective fen. Most moths flew lower than 1 m above the vegetation, although some individuals were observed flying up to 2 m above the fens.

Oviposition. Female BBMs flew hastily and awkwardly, low against the shrubs and open fen habitats. The females landed in clumps of shrubby vegetation (as opposed to the open fen), where they backed down each of the stems around them. The moths fluttered their wings while climbing up and down the stems. At each descent, a female flew

briefly to another stem or crawled across to another plant. Usually only a few centimeters were tested per stem. Occasionally the females flew a few meters away to repeat the process.

The females seemed to choose stems of a particular diameter by using their ovipositor and legs. The chosen site for oviposition tended to be unobstructed by leaves or adjacent stems. The height of oviposition generally was low and probably dictated by low oviposition plant height and the low heights of available, unobstructed stems. Oviposition plant species did not seem to matter *per se*, other than an aversion to the aromatic *Larix laricina* (Duroi) K. Koch (Pinaceae).

Upon choosing a stem, females promptly began laying eggs: facing the stem, they curled their abdomens in towards the stem, felt for a site with the ovipositor, and deposited a single egg perpendicular to the stem. The eggs were grey-brown when deposited and turned light green in about a minute. After laying an egg, the abdomen returned to a relaxed, hanging position (parallel to the stem). The female remained in this position until ready to lay another egg, from a few seconds to a few minutes later. The eggs were not always laid immediately next to another. The females laid eggs in empty spaces, between two eggs, or next to a single egg. One row usually was completed before eggs were laid in the next row up on the stem. Oviposition proceeded in all cases from the bottom up. All observed females laid egg rings with their backs to the sun. Oviposition was concealed by downfolded wings, but the females would respond with the typical defense posture if handled.

One female failed to successfully adhere her initial eggs to an *Aronia* stem. The first three eggs stuck to each other and then came off the stem, attached to her abdomen. She proceeded to lay eggs, and the initial clump of eggs fell to the ground. All subsequently laid eggs adhered to the stem.

Another female was interrupted while laying an egg ring on an *Aronia* stem. A small (approx. 5 mm long) jumping spider (Salticidae) moved up the stem and investigated the freshly-laid eggs. The spider then jumped onto the moth's wing, whereupon the moth twitched her wings and the spider fell. After laying approximately 25 eggs, a male BBM then located the same female moth and proceeded to copulate (at 1515 h). After copulation, the female laid another distinct egg ring of about 30 eggs, 3 cm above the first. Five days later the stem was chewed off less than 2 mm above the upper egg ring, and scattered droppings and a neat trail of nipped-off chokeberry stems suggested feeding by an eastern cottontail rabbit (*Sylvilagus floridanus*) (J. A. Allen).

One fresh egg ring was discovered on *A. virginica* immediately above a hatched egg ring from the previous season. The two egg rings were adjacent and seamlessly joined; the only observable differences were the

color and the hatched/unhatched status of the rings (Fig. 4). I observed old egg rings immediately beneath new egg rings, and instances where the two occurred nearby on the same stem. Bog Buck Moth egg rings are clustered at each site, sometimes 8 on a single shrub. Frequently, old egg rings are found within a meter of new egg rings. I also discovered an egg ring on a stem of *S. alba* that was sleeved off and held larvae for captive rearing experiments in the field. No other egg rings were deposited on the abundant nearby *S. alba* that had not harbored larvae. Some conspecific frass remained attached to this particular stem. Presumably, conspecific larval silk also remained on this stem.

Oviposition did not appear to be cued by proximity to *Menyanthes trifoliata*. Egg rings were found that >20 m from the nearest *M. trifoliata* plant. Some egg rings hatched a week or more before the emergence of *M. trifoliata*, and upon hatching those larvae fed upon *V. macrocarpon*. In September and October 1995, when female moths oviposited, *M. trifoliata* was uncommon or senesced in areas where it was abundant during the summer months.

Predation. Egg rings are susceptible to a variety of predators, including small mammals and invertebrates, and they may accidentally be ingested by white-tailed deer (*Odocoileus virginianus* (E. A. W. Von Zimmermann)) and rabbits (*Sylvilagus floridanus*) that consume the host plant stems. I observed predation on eggs by velvet mites (Trombididae) in spring and fall (12 May and 13 October at site A). An unhatched egg ring that I collected on 24 June 1996 subsequently yielded Hymenoptera (Chalcidoidea: Eupelmidae) from each of the 200 or so eggs in the ring. Buck moth larvae were preyed upon by true bugs (Hemiptera). Other parasitoid Hymenoptera and Diptera surely occur in these sites and also parasitize the larvae. As described earlier, beetles and their larvae (Carabidae, Staphylinidae, and Elatidae) may have been responsible for heavy predation of BBM pupae.

Adult BBMs were also subject to predation. Three paper wasps (Vespidae) were observed stinging a male buck moth in flight and devouring it alive, from the thorax out, once it fell to the sphagnum. Paper wasps had nests in at least four of the sites, and preyed in similar fashion upon migrating Monarchs (*Danaus plexippus* L.) that flew over the fens.

Two species of araneid spiders, *Araneus diadematus* Clerk and *Argiope aurantia* Lucas, preyed upon adult buck moths (Fig. 5). Webs from both spider species were common in the fens and stretched across the shrubby peripheries. Several silk-wrapped BBM bodies were found below the web of one *A. aurantia*, and the spider was eating another.

On 23 September 1995 a Solitary Vireo, *Vireo solitarius* (Wilson) (Vireonidae), took a male BBM in flight, landed in a nearby *Larix laricina*, and ate the body of the moth after discarding the wings. Many in-

sectivorous birds, migrating south in the fall and abundant in the fens, are potential predators of BBMs. Eastern Phoebes, *Sayornis phoebe* (Latham) (Tyrannidae), and other birds were observed feeding in the fens on other insects, and are possible predators of BBMs. Also, dragonflies (Aeshnidae) are potential aerial predators of buck moths, as reported by Scholtens and Wagner (1994).

DISCUSSION

The BBM has adapted to life in wetland habitats. Their reluctance to fall to the ground when disturbed, unlike other populations of *Hemileuca* (Tuskes et al. 1996), appears to be a unique behavior and may prevent them from falling into standing water.

The apparent annual clustering of egg rings strongly suggests that an ovipositional cue is present. Since the herbacious hostplant *M. trifoliata* dies back in late summer, the moths must oviposit on other plants. As the BBMs oviposited so frequently on the dried, broken stems of *A. virginica* at one bog-like site, I believe the ovipositional cues are structural (correct diameter and height) and perhaps chemical. An oviposition-stimulating, egg-isolated or larval silk-isolated semiochemical might account for the clustered distribution of egg rings year after year. Such a chemical cue might also explain the seamless joining of two egg rings laid in different seasons on the same stem (Fig. 4).

The possibility of oviposition on slender, upper stems of plants over a meter high is unlikely due to the low flight behavior of the female moths; I doubt that a heavily-laden female would fly up into a small tree or shrub when faced with abundant stems of suitable diameter at lower levels. The question thus arises: Why are the egg rings deposited so low in fen habitats, where flooding is a potential threat? Perhaps the low egg ring height may be advantageous for overwintering success. Rabbits and deer would browse on stems above the level of snow. Mice might feed on the egg rings that are not buried in snow, as has been reported in some New Jersey populations of *Hemileuca* (D. Schweitzer, pers. comm.). Also, temperatures under a blanket of snow fluctuate less than air temperatures, thus egg rings would be at less risk of over-freezing or premature warming. Larvae can tolerate some inundation; Legge et al. (1996) observed that larvae swim or walk on the surface tension of water for short periods of time.

Experimental transect sampling of egg rings and larvae did not provide consistent or reliable results for a censusing technique. The censusing method which I developed for this study provides a population estimate that can be compared with future census results for conservation and monitoring purposes. Based on my field observations, one cannot assume at any time that only males are flying, and that an equal number

of females are hidden in the vegetation (or vice versa). Therefore, doubling the census results would not provide an estimate of the overall population, as otherwise might be expected.

Adult BBMs focus their behavior on reproduction, not dispersal. However, I believe it is possible that an adult moth could disperse to a nearby site via strong updrafts or powered flight if the surrounding vegetation did not impede them. The present distribution of the BBM may thus be the remnants of a buck moth expansion from western North America following the last glacial retreat in the Northeast. As the forests reclaimed the wetland habitats, the BBM may have been confined to the remaining fens and bogs.

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