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# BIOLOGY OF THE GENUS *HEMILEUCA* (LEPIDOPTERA: SATURNIIDAE) IN MICHIGAN

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## ABSTRACT

The habitats and host plants of buckmoths (*Hemileuca*: Saturniidae: Hemileucinae) in Michigan are described and compared to those of the three species known from eastern North America, *H. maia*, *H. nevadensis*, and *H. lucina*. Michigan populations show variation in host plant and habitat use spanning the entire range of all three species. The presence of transitional phenotypes and the host plant and habitat data suggest that Michigan populations are a single, variable species. These things combined with the intermediate geographical location of Michigan's populations call into question the taxonomic distinctness of the three eastern buckmoth species.

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The genus *Hemileuca*, with 30 currently recognized species in North America and Mexico, is most diverse in Mexico and the southwestern United States (Seitz 1929, Ferguson 1971, Tuskes 1978, Peigler 1985, Peigler and Stone 1989, Lemaire 1993). Females lay large batches of eggs on host plants and early instar larvae feed in aggregations. Host plant choice varies widely with species, including many plant families and genera (Stone 1991). Populations occur in habitats ranging from dry prairies and upland oak woods to wet meadows and soggy fens (Ferguson 1971, pers. obs.).

All populations occurring in Michigan, as well as the rest of eastern North America, are day-fliers and members of the *maia* group. As traditionally understood, this group consists of three species: (1) *Hemileuca maia* (Drury), occurring over much of the eastern United States from Illinois south to Louisiana and Florida and east to Massachusetts, (2) *H. lucina* Hy. Edw., in the northeast from Maine to Massachusetts [Ferguson (1971) indicated possibly northern Michigan also], and (3) *H. nevadensis* Stretch, throughout western North America and Canada, east in the north to Minnesota and Wisconsin. *Hemileuca maia* has generally been recorded as an oak feeder, *lucina* as a meadowsweet feeder and *nevadensis* as a willow feeder (Ferguson 1971).

Michigan populations of *Hemileuca* are of interest for several reasons. In addition to being located geographically between known populations of *nevadensis* and *maia*, buckmoth populations in Michigan appear to show a variety of phenotypes ranging from types similar to Minnesota and Wisconsin *nevadensis* to others virtually indistinguishable from typical *maia* (pers. obs.). The existence of extensive populations in the Upper Peninsula that very closely resemble *lucina* adds an additional complication. The host plants of Michigan populations of *Hemileuca* have not been well documented, but historical

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records from nearby Illinois and Wisconsin suggest an association with willow wetlands (Riley 1873, Worthington 1878, Ely 1954), and records from southern Ohio indicate an upland, oak woodland habitat (Metzler 1980., pers. obs.).

Our objectives in this study were to (1) determine the occurrence and distribution of *Hemileuca* populations in Michigan, (2) document the habitat and host plant associations of the Michigan populations, and (3) compare these associations with those of the described species.

## METHODS

A check of museum records at The University of Michigan and Michigan State University revealed a paucity of known localities for *Hemileuca* in Michigan. In order to better document the range and variation of *Hemileuca* in Michigan, we traveled over much of the state to locate populations. Our fieldwork was concentrated in the spring and fall each year from 1987 to 1990. During the spring, populations were easily located by driving through appropriate habitats and spotting the large, black masses of larvae feeding after hatching from the egg rings. During fall, populations were located by observing adults flying during the day in potential habitats. This endeavor was supplemented by having caged females emitting pheromone to attract males. These females were either reared from larvae collected as early instars, or captured before mating in known populations. Females could be used for several days if not allowed to mate and kept refrigerated in a humid environment between uses.

For several populations, scattered over the range of buckmoths in Michigan, we recorded information about habitats and host plants. These were located in Schoolcraft Co. in the Upper Peninsula, Roscommon Co. in the upper-middle of the Lower Peninsula, and Washtenaw and Monroe Cos. in the southeastern part of the Lower Peninsula. In addition we compared these populations to ones in Vinton Co., Ohio and outside of Ottawa, Ontario as well as to published accounts of the habitats and host plants for the three described species. Voucher specimens for these populations have been deposited in the collections at the University of Michigan (UMMZ) and the Canadian National Collection (CNC) with additional specimens retained in the authors' collections.

At each locality we made notes on habitat, including topography, moisture conditions, and dominant plant species. Where possible we recorded data on both primary (oviposition) and secondary (used by larvae, but not used for oviposition) host plants. Primary hosts were identified either by finding egg rings during the winter, or more commonly by spotting masses of feeding larvae in the spring and then locating the egg ring from which they emerged (generally only a few feet away). Secondary hosts were documented when late instar larvae were found feeding on them (with no oviposition record) or when a larval mass was located on a plant species other than that on which the adjacent egg mass was located (given that the egg mass was on a known larval host, as occasionally egg masses are laid on dead stems or stems of non-hosts near the actual host). We also recorded behavioral observations on female emergence and mating.

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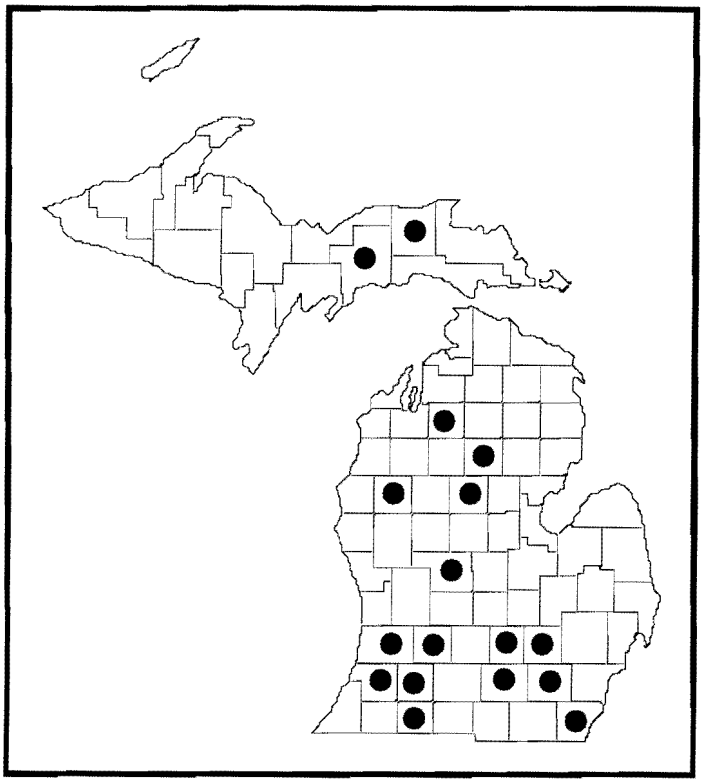

Figure 1. Known distribution of *Hemileuca* in Michigan.

## RESULTS

To our knowledge, at the start of the study, buckmoths were known from only 6 counties in the Lower Peninsula (Moore 1955) and one record from the Upper Peninsula (Voss 1969, Ferguson 1971). During our work we added 10 new county records and documented the extensive distribution of buckmoths across the state, including both peninsulas. Figure 1 shows the present known distribution of *Hemileuca* in Michigan by county. The western section of the Upper Peninsula was not explored. The paucity of records in the upper part of the Lower Peninsula cannot be ascribed to lack of surveying; we made many efforts to locate populations in several counties of this area during the spring and fall. This area seems to have extensive areas of appropriate habitat without buckmoth populations. Buckmoths probably occur in every county in the middle and southern parts of the Lower Peninsula.

The range of variation in the habitats and host plants used by *Hemileuca* in Michigan is much more extensive than previous accounts of these buckmoths would indicate. This host diversity is illustrated by describing the habitats and host plants of the four main study populations (Washtenaw, Monroe, Roscommon, and Schoolcraft Cos.) in addition to the Ohio (Vinton

Table 1. Primary host plants of *Hemileuca* populations in this study.

| Site | Known Primary Hosts |
|---|---|
| Washtenaw Co. 1 | *Salix petiolaris, S. discolor, S. bebbiana, Spiraea alba* |
| Washtenaw Co. 2 | *Salix exigua* |
| Monroe Co. | *Populus deltoides, P. tremuloides, Salix discolor, S. exigua, Salix* undet. |
| Roscommon Co. | *Salix petiolaris, Salix undet., Spiraea alba* |
| Schoolcraft Co. | *Betula pumila, Salix petiolaris, S. pedicellaris, S. serrissima, S. candida* |
| Vinton Co., OH | *Quercus* (black oak group) |
| Ottawa, Ont. | *Menyanthes trifoliata* |

Co.) and Ottawa (Ontario, Canada) populations. Data on the host plants of our study populations is summarized in table 1.

## Washtenaw County

Two populations in northwest Washtenaw County were extensively studied during our work. Site 1 is a fen dominated around the periphery by grasses and sedges, grading into a tamarack bog in the center. It is located on Roe Rd. in Section 19 of Lyndon Twp. Buckmoths fly over this entire area, but concentrate oviposition at the edge of the wooded area where willows (*Salix* spp.; Salicaceae), meadowsweet (*Spiraea alba*; Rosaceae) and bog birch (*Betula pumila*; Betulaceae) are the dominant woody vegetation.

Flight records at this locality are from 24 September to 29 October, with the peak flight during the second week of October. Long term monitoring of this population by Wagner indicates that population levels fluctuate considerably from year to year.

The documented oviposition hosts at this site are almost exclusively willows (*Salix petiolaris, S. discolor,* and *S. bebbiana*) with only a single egg ring found on *Spiraea alba* over a period of 3 years. Two plant species present, but not used as host plants at this site, *Betula pumila* (bog birch) and *Menyanthes trifoliata* (bog buckbean; Gentianaceae), are used as primary hosts in other populations.

Site 2 in Washtenaw County occurs on the rights of way on both sides of the Freer Rd. overpass on Interstate 94, and the area adjacent to a nearby farm pond. Most of this area is willow wetland, some spots being dry and others having standing water nearly year-round. The dominant plants are sedges (*Carex* and *Scirpus* spp.) and cattails (*Typha* spp.) in the wettest sections and willows as the habitat grades into drier areas.

The flight period is virtually identical to the site 1 population, with records of adults from 5 to 16 October. In 1988 we found more than 20 egg rings during a one-day, winter search of the habitat. We returned the next spring to check on these flagged egg masses and found additional ones had gone undetected until the emergence of the larvae. Populations at this site also seem to fluctuate, although we have records only from the years of our study.

The only documented oviposition host at site 2 is also a willow (*Salix exigua*). An additional possibility is *Spiraea*, but only a small number of plants are present in the habitat.

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### Monroe County

In the Petersburg State Game Area, a population of buckmoths occurs on a much drier site than those in Washtenaw County. The different moisture conditions here may be partly a result of the channeling of the water courses, and there may have been more extensive wetlands in the past. However, now the habitat is dominated by small quaking aspens (*Populus tremuloides*) and cottonwood (*P. deltoides*)(Salicaceae), upland willows and other shrubs interspersed with grassy areas and cultivated fields.

Flight times at this site are similar to those of the Washtenaw County localities. The earliest recorded adult flight date is 20 September and the latest 24 October. We flagged 2 egg rings during the winter of 1988 and located 7 additional larval masses the following spring during a quick search. M. C. Nielsen (pers. comm.) and other collectors with experience in the area note that the population size has apparently dropped in recent years, perhaps due to the changing successional age of most of the habitat. Other lepidopteran species that occur on the remnant prairie habitats in the game area have also declined in numbers, and some may now be extirpated (e.g. the butterflies *Lycaeides melissa* and *Incisalia irus*, both Lycaenidae). Management of these areas using carefully prescribed burns might reverse this trend.

We recorded *Populus deltoides*, *P. tremuloides*, *Salix discolor*, *S. exigua*, and an undetermined *Salix* as the primary larval hosts at this site. On occasion each of these may be used as a secondary host because the branches often grow intertwined and at least one larval mass was found feeding on *Populus* and *Salix* simultaneously. Although not abundant in the area, *Spiraea* and possibly *Quercus* are potential host plants.

### Roscommon County

The habitat in Roscommon County, near Houghton Lake (and extending into adjacent Clare County), consists of extensive willow-meadowsweet wetlands with sedges as the dominant graminoids. Here, virtually the entire habitat has standing water or waterlogged soil throughout the year and is fairly uniform in its composition. At the margins of the wetland the habitat grades into aspen woods.

Adults fly at this locality from the beginning of September almost through the end of the month with the main flight during about the second week of the month. The population in Roscommon County is consistently very large and certainly numbers in the thousands each year. On a suitable fall day hundreds of buckmoths can be seen flying over the habitat.

Both willows (*Salix petiolaris* and an undetermined *Salix*) and meadowsweet (*Spiraea alba*) are used as primary hosts in the habitat, and both are abundant at the site. During one census on 21 May 1988 we counted early instar larval masses in a small area of the habitat and recorded 25 on willow and 3 on meadowsweet. In the main habitat these appear to be the only host genera, but *Populus* bordering the wetland may be used also. Buckmoths were frequently seen entering and leaving the wooded area, although no egg rings or larval masses were located on aspen.

### Schoolcraft County

Although one record of two adult specimens from Manistique exists (Ferguson 1971), the populations in the Upper Peninsula were not relocated until 1987–88. At this time specimens were presented to Wagner for identifi-

cation by colleagues who had been birding early in the fall. He visited the locality shortly thereafter and found extensive buckmoth populations. The previous summer, a larva had been given to Scholtens by Dr. Barbara Madsen, who related that this species was abundant at her Upper Peninsula field site, and seemed to be eating mainly bog birch (*Betula pumila*). The larva completed development on paper birch (*Betula papyrifera*), pupated, overwintered, and emerged the following summer, simultaneous with Wagner's investigation of the Upper Peninsula buckmoth populations.

The populations in Schoolcraft and Luce Counties in the Upper Peninsula are probably the most extensive in the state, due in large part to the great expanse of available habitat (thousands of acres), much of it inaccessible. Madsen's field site, for example, is reached by a long hike through wetlands. Much of our work was done at or near Seney National Wildlife Refuge where populations are readily accessible.

The habitat comprises willow-bog birch-alder wetlands broken by sandy ridges, which are forested primarily with pines. The dominant graminoids are sedges, with grasses on the drier areas. These wetlands are permanently soggy, generally with standing water. Wetlands similar to this are found throughout much of the central part of the Upper Peninsula.

At these sites buckmoths fly from mid-August through mid-September, with peak flight during about the first week of September. The population sizes at these sites are comparable to or larger than those at the Roscommon County site, and flights of hundreds of individuals can be observed on even minimally warm (16°-18°C), sunny days.

Both willows and bog birch are used extensively as primary hosts in these habitats. On 9 June 1988 Wagner recorded host plants for larval masses located in one section of Seney National Wildlife Refuge. This count indicated that the two host genera are almost equally used by *Hemileuca* at this site, with 10 masses found on *Betula pumila*, 4 on *Salix petiolaris*, 1 on *S. pedicellaris*, 1 on *S. serrissima*, and 2 on an undetermined *Salix*. Subsequently we located a larval mass on *S. candida*. During this visit, Wagner specifically noted that no larvae were found on *Alnus rugosa* (Betulaceae) (abundant in the habitat), *Spiraea alba* (frequent), *Spiraea tomentosa* (occasional), *Rubus* sp. (Rosaceae) (occasional), or *Potentilla fruticosa* (Rosaceae) (occasional). By 17 June 1988, larvae had dispersed and few were in groups of more than two. They remained most abundant on *Betula* and *Salix*, but a few were found on *Spiraea*, *Vaccinium* (Ericaceae) (on sandy upland), or even grasses. Feeding on these plants was not specifically noted, and larvae may simply have been wandering to locate a pupation site. At appropriate sites in these habitats, either *Spiraea* or *Menyanthes* might be possible alternative hosts.

### *H. maia* population from Vinton Co., Ohio

The habitat at this site is an upland, primarily oak woodland. The understory consists of typical deciduous woodland shrubs, notably lacking in willow and spiraea.

Adults fly at this locality from mid-October through early November. We examined the population on 27 October 1989. In this year the population was very large. During one afternoon, we easily saw several hundred adult buckmoths, and we stopped our search before the afternoon flight ended. Local Ohio collectors report significant fluctuation in the population size from year to year, similar to that seen in some southern Michigan populations (Metzler pers. comm.).

Because we were present only during the adult flight season, we did not

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directly observe egg rings or larval masses on host plants. The presumed hosts are oaks in the black oak group, and *Quercus* (Fagaceae) is apparently the only known host genus present in numbers at the site.

We have not located any Michigan populations of *Hemileuca* on sites similar to that in Vinton Co., OH. However, Nielsen reared adults collected from larvae found on black oak in the Barry State Game Area (Barry Co.) in 1969. We revisited this site, which is dominated by oaks on sandy, upland soil, but did not relocate an oak-feeding population.

### *Hemileuca* population near Ottawa, Ontario

With the help of Dr. J. Donald Lafontaine at the Canadian National Collection, Scholtens was able to examine two sites near Ottawa during the fall of 1990. Both of these localities are wet fens characterized by graminoids with very little shrubby growth. Sedges dominate much of the habitat, most of the mat consisting of *Carex lasiocarpa* with *Scirpus* also common. At the larger of the two sites, Richmond Fen, the grass *Phragmites* is a significant component. *Thuja* and *Larix* are both present as small trees on the mat. The main shrubs of the habitat are *Betula pumila* (found near the margins) and *Myrica gale* (in hummocks throughout), with only a small amount of *Salix candida* and 1 undetermined *Salix*.

The flight period at these sites is from about mid-September through early October. According to Lafontaine, populations at these sites, especially the second, can be very large. We visited on 3 and 4 October 1990, near the end of the flight period.

The host plant at these localities is bog buckbean, *Menyanthes trifoliata*. Females are apparently unable to locate foliage of the host itself when ovipositing because it has already senesced. This was the case during the trip of 1990. Instead, females search for sturdy stems of grass or sedge, often *Carex*, and place egg rings on these. Upon hatching in the spring, larvae then locate newly flushed plants of buckbean (Lafontaine, pers. comm.). A similar population is known from New York (R. Dirig and J. Cryan, pers. comm.), and M. Nielsen and L. Ferge (pers. comm.) found larvae in a Wisconsin population feeding on buckbean and willow, with the egg ring on a nearby sedge stem. At Richmond Fen, the willows and bog birches present at the periphery of the habitat may be used as primary or secondary hosts on occasion, but neither has been recorded at this locality as a host (Lafontaine, pers. comm.).

### Behavioral Observations

During the course of our fieldwork we observed emergence and mating behaviors of buckmoths at the main study sites, primarily in Schoolcraft and Roscommon Counties where populations are largest.

On most days during the flight season, night and early morning temperatures are cool or cold, and buckmoths do not become active until late morning. Activity is first indicated by males flying over the habitat in the typical straight-line flight. Females are often found emerging and expanding their wings at the margins of the wet areas of the habitat, just onto higher ground. Mating follows emergence very closely, often occurring before the female's wings are completely expanded. Emerging females are easily located by watching males follow pheromone trails and tracing their path to the female. Flights by females are observed later in the day, usually in mid-to late afternoon.

We often attracted male buckmoths using unmated females that were reared or captured before mating. We found that Roscommon County females would easily attract both Schoolcraft and Washtenaw County males. Females from other sites were not available at appropriate times to test the reciprocal attraction in each case. Washtenaw County females were taken to Vinton Co., OH, but apparently did not attract males from this population; none were seen approaching and hovering around the cage as they did at other sites.

Although buckmoths are quite apparent during their flight season, we observed only one act of predation (and saw no other attempts), when a dragonfly (*Aeshna* sp.: Aeshnidae) took a male buckmoth on the wing at the Schoolcraft Co. site.

## DISCUSSION

The distribution of buckmoths in Michigan is much more widespread than previously believed (Fig. 1). Populations are most common in the southern part of the Lower Peninsula, but the largest populations occur in the central part of the Lower Peninsula and the Upper Peninsula. In Michigan, populations apparently can occur wherever there are sufficient wetlands of an appropriate type. One exception to this is the unexplained paucity of records from the upper Lower Peninsula. We suspect that few records existed for buckmoths before our study primarily because of the late flight season of these moths. Most lepidopterists have hung up their nets by the time *Hemileuca* is on the wing. Even though the larval masses are very conspicuous, only a few lepidopterists spend time rearing larvae, and the buckmoth larvae may often be passed over as those of the similar appearing Mourning Cloak (*Nymphalis antiopa*; Nymphalidae) (Ferguson 1971, pers. obs.).

*Hemileuca* populations in Michigan span nearly the entire range of host plants and habitats previously attributed to the three described species of the *maia* group. For these three species, host plant and habitat specialization has been regarded as a significant factor isolating the species (Ferguson 1971). *Spiraea*, the reported host plant of *H. lucina*, is used in the Roscommon population side by side with *Salix*, the main host plant of the western *H. nevadensis*. In addition, *Populus* and *Betula*, a newly reported host, are also commonly used by at least some populations. Of the host plants of the three described species, *Quercus*, that of *H. maia*, was the only one not documented during the course of our study. This is despite the fact that the populations in Michigan have traditionally been labelled *H. maia*. Even for oak, a record exists documenting its use in Michigan. The recently discovered populations in New York and Ontario that feed on *Menyanthes* add additional complications, and the discovery of Wisconsin larvae on this same host suggests that this association may also be more widespread.

Although there is no obvious link between the known host genera, one possibility is the presence of phenolic glycosides as secondary chemicals. Some species of *Salix*, *Populus*, and *Betula* are known to contain these chemicals (Palo 1984, Rowell-Rahier and Pasteels 1990), but we are presently unaware of their occurrence in *Quercus*, *Spiraea*, and *Menyanthes*. Other insect herbivores are known to specialize on plants containing these chemicals (Rowell-Rahier 1984, Lindroth et al. 1988), and some make use of them for their own protection (Pasteels et al. 1988), an interesting possibility for *Hemileuca* considering its bold, black and white markings. Even if no secondary chemical link can be found among the host plants, the wide diet breadth would not be unexpected when compared to other members of the Saturniidae, which

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are often oligophagous feeders on woody plants (Covell 1984, Stone 1991, Tietz 1972).

The habitats in which buckmoths occur in Michigan are most similar to those described for *nevadensis* or *lucina* (Fergusen 1971, Covell 1984). Both often occur in wetlands, where their host plants can be found in abundance. Drier habitats, such as those used by typical *H. maia*, are not entirely excluded from the known sites (e.g. Monroe Co. or, historically, Barry Co.), but, at least in Michigan, they are not as common.

Michigan's buckmoth populations are a puzzle when trying to apply the nomenclature now attached to the three described species in the *maia* group. These three taxa have been treated as distinct species because of differences in maculation, geographically separated ranges, and divergence in habitat and host plant use (Ferguson 1971). Michigan's populations, historically identified as *H. maia* (and perhaps *H. lucina* in the Upper Peninsula), are now known to span most of the gaps between the three described species. In habitat use they most resemble *nevadensis* and *lucina*, being found primarily in wetlands. The primary hosts used by these populations include those normally associated with *nevadensis* (willow and aspen), *lucina* (meadowsweet), and an historical record includes the typical host of *maia* (oak). In addition they use the newly reported host, bog birch.

The maculation of Michigan buckmoth populations also spans nearly the entire range of known variation in the three species (Scholtens and Wagner in review). Populations in the southern Lower Peninsula are indistinguishable from more southern or eastern populations of *maia*, with relatively narrow white bands on dark black, heavily-scaled wings. Those in the Upper Peninsula show only slight differences from typical northeastern populations of *lucina*, with a somewhat wider white band than typical *maia* and extremely glassy wings due to smaller, less dense scales (Scholtens and Wagner in review). Populations in the central part of the Lower Peninsula are intermediate between these two extremes in both respects. All populations, however, show a significant amount of variation, and within any one population individuals can be found that very closely match phenotypes typical of other populations. Some individuals even have white bands that approach the extreme width of typical *nevadensis*, and Roscommon County individuals strongly resemble specimens identified as *nevadensis* from northwestern Wisconsin and Minnesota (Scholtens and Wagner pers. obs.).

Several possible taxonomic alternatives exist for the Michigan populations. Phenotypically, the three main geographic areas of our study could easily be viewed as different entities, the southernmost fitting nicely into descriptions of *maia* and the northernmost matching *lucina*, but our findings on host plant and habitat use as well as the clinal nature of the variation in maculation (Scholtens and Wagner in review) argue against these populations being separate taxonomic entities. Unlike the traditional belief, the habitats and host plants of buckmoth populations may be combined in various ways, depending on the available hosts.

Michigan populations also lie geographically between at least two of the described species ranges, those of *nevadensis* and *maia*, in an area where transitions between known phenotypes would be expected to occur. Because all buckmoths have very similar genitalia (but see Ferguson 1971, for possible differences in the genitalia of *lucina*), this often reliable character is of little help in determining if these populations are taxonomically distinct.

Ultimately, interbreeding and producing viable offspring would be the most convincing argument against separate species, but at this time data of this sort are unavailable. Previous work with buckmoths indicates that cross attraction and interbreeding is indeed possible and hybrids can be produced (Peigler and Williams 1984). The presumed geographic barrier separating the

phenotypically distinct populations is not present in Michigan. All populations in Michigan appear to be capable of genetic exchange with other, phenotypically different populations. Further work relating these populations to others in North America should resolve the status of what name to apply to Michigan's buckmoths.

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