Journal of the Lepidopterists' Society
47(1), 1993, 22–31

TERRITORIALITY ALONG FLYWAYS AS MATE-LOCATING BEHAVIOR IN MALE *LIMENITIS ARTHEMIS* (NYMPHALIDAE)

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ABSTRACT. A central New York population of *Limenitis arthemis* (Drury) was studied during June and July 1983. Males emerged a week before females with an overall male-biased sex ratio of 1.43:1.00. Of the 30 marked males, 7 (23%) were recaptured within the study area with an average longevity of 10.3 days. No marked female was recaptured. During midday mate-locating behavior, males perched an average of 82.5%, flew for 14.0%, and encountered other individuals for 3.5% of the time. Conspecific males were encountered at a rate of 8.3/h. Conspecific encounters averaged significantly longer than heterospecific encounters (12.8 vs. 5.8 sec). Marked males favored certain areas for perching but changed areas fairly frequently resulting in dynamic territories. Nearly half the perches were on sumac, and 68% were 1–3 m above the ground. Favored territories provided good vantage of female flyways.

Additional key words: activity budget, mark-recapture, protandry.

Territoriality in butterflies is a male tactic to locate receptive females (Powell 1968, Baker 1972, Davies 1978, Lederhouse 1982a, Wickman 1985a,b). Commonly, males defend landscape features such as hilltops and ridges that have high female visitation rates despite their lack of concentrated larval or adult resources (Shields 1968, Lederhouse 1982a, Alcock 1983, 1985, Alcock & O'Neill 1986, Alcock & Gwynne 1988, Rutowski et al. 1989). In addition, areas along butterfly flyways are defended (Baker 1972, Douwes 1975, Bitzer & Shaw 1983). Males of several species defend favorable microhabitats where females may raise their body temperature to facilitate activity (Davies 1978, Knapton 1985). Defense of feeding or oviposition resources appears to be uncommon in butterflies (Baker 1972, Rutowski & Gilchrist 1988, Lederhouse et al. 1992), except where they overlap with emergence sites (Dennis 1982).

Two subspecies of *Limenitis arthemis* (Drury) occur in eastern North America. *Limenitis arthemis astyanax* (Fabr.) is a Batesian mimic of the aposematic, distasteful pipevine swallowtail, *Battus philenor* (L.) (Papilionidae) (Platt et al. 1971, Codella & Lederhouse 1990). North of the geographic range of *B. philenor, Limenitis arthemis arthemis* has medial white wing bands. Wing banding is believed to offer protection from predators through disruptive coloration although this has not been demonstrated experimentally (Silberglied et al. 1980). Nearly complete genetic mixing of the two subspecies occurs (Platt & Brower 1968, Platt 1983) except where geographic barriers to gene flow are

present (Waldbauer et al. 1988). In a band between 40° and 45°N latitude, females breed at random with males without regard to degree of male wing banding (Platt 1983).

Males of *Limenitis* species are notoriously aggressive (Pyle 1981, Lederer 1960). Male *Limenitis weidemeyerii* Edwards perch and engage passersby in territorial defense (Rosenberg 1989, Rosenberg & Enquist 1991). Male *L. arthemis* perch in the sun on trees and tall bushes and periodically patrol (Clark 1932, Ebner 1970). Although fidelity of male *L. a. arthemis* (Ebner 1970) and male *L. a. astyanax* (Harris 1972) to particular perches has been noted, Opler and Krizek (1984) stated that male *L. a. astyanax* do not seem faithful to particular sites. This study looked at male mate-locating behavior and population structure of *Limenitis arthemis* in a region of subspecies overlap. In particular, I investigated male longevity, location, aggressiveness, and activity patterns in relation to vegetation structure and local topography.

MATERIALS AND METHODS

The mate-locating behavior of *Limenitis arthemis* was studied near Brooktondale, Tompkins County, New York, during June and July 1983. The study site consisted of a gravel road with hedgerows on each side (Fig. 1). The general area was a mosaic of tilled fields and wooded areas.

Butterflies were captured with a net, marked individually, and released immediately at the site of capture. Redundant marks were placed on both the right and left sides of the dorsal and ventral wing surfaces using red or green felt-tipped pens following a modification of Lederhouse (1978). The identity of a butterfly could be determined at a distance of 3 m or less through observation of a perched or feeding individual. The term "recapture" is used to denote the identification of a marked butterfly either by capture or observation on any day following the date marked.

The presence of *Limenitis arthemis* in the study area was monitored for a minimum of an hour on most sunny days of the study from 1030 to 1630 EDT. New individuals were captured and marked, and marked individuals were identified. The behavior of marked focal individuals was monitored continuously for 15 minute periods. The duration of each activity was recorded to the nearest second and the location noted. All *Limenitis arthemis* activity was recorded for consecutive 15 minute periods in each of three subunits favored by males. The order in which these subunits were observed was determined by random draw. Behavioral observations were conducted during the periods of greatest *Limenitis arthemis* activity (1100 to 1500 EDT).

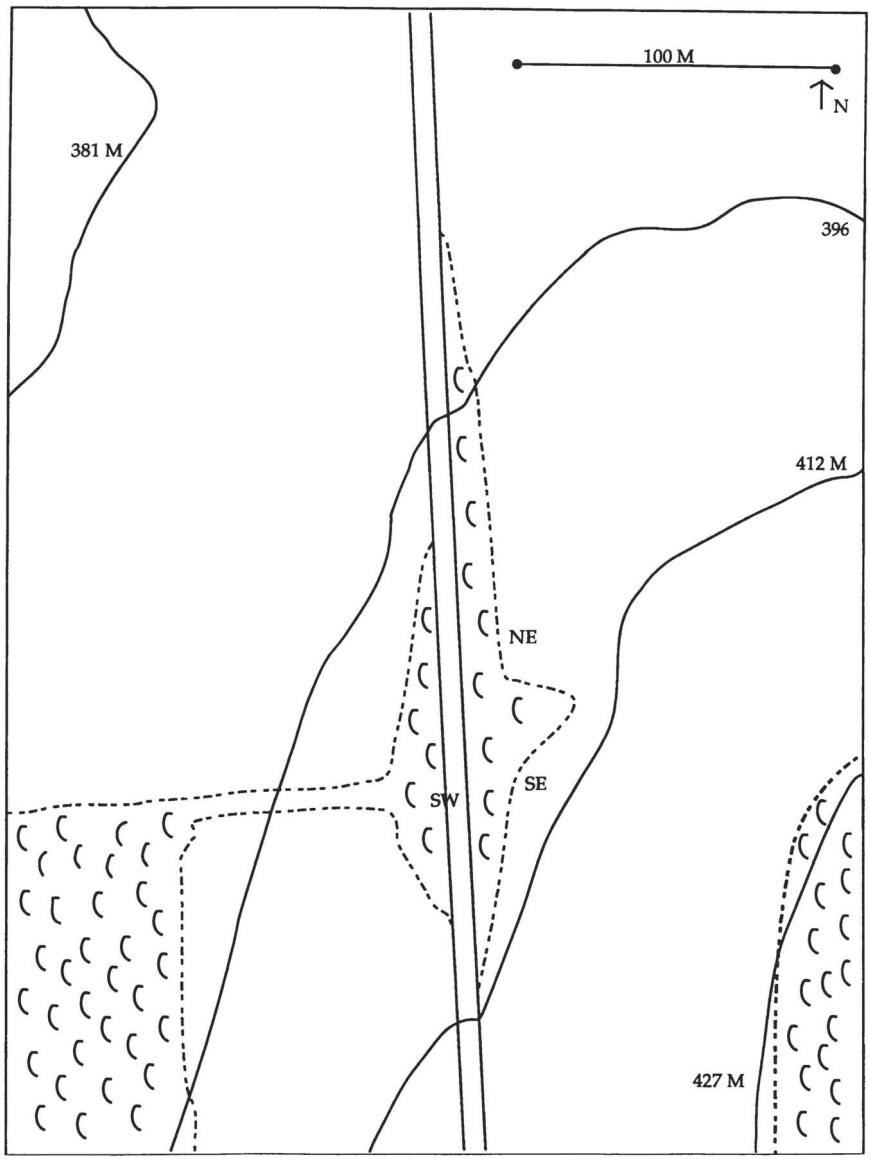

FIG. 1. Map of the Brooktondale, New York, study area.

RESULTS

During the study, 30 males and 21 females were marked. Males first appeared about a week before females; 47% of the males were captured before the first female (Fig. 2). This protandry was significant (Kol-

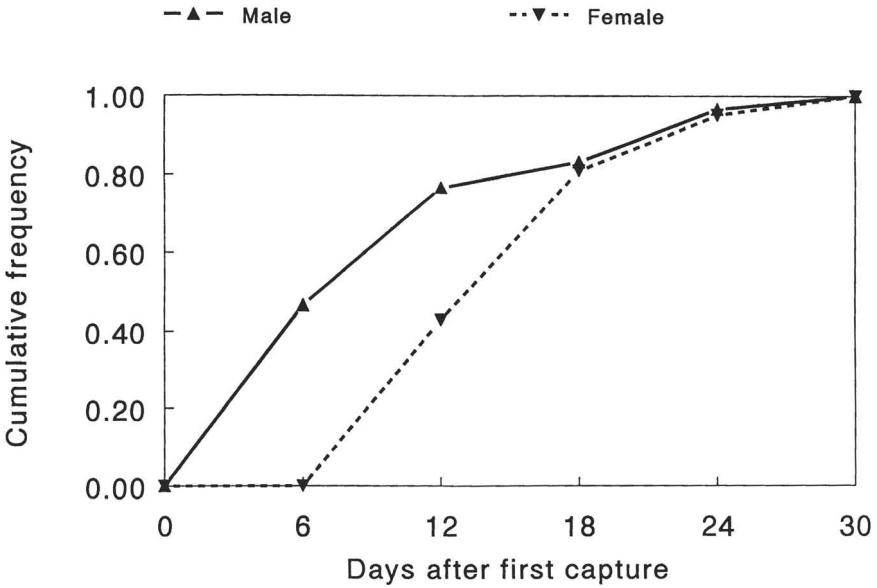

FIG. 2. Cumulative frequencies of male and female captures at the Brooktondale, New York, study area per six day intervals. Day 1 of the generation was 21 June.

mogorov-Smirnov two sample test, $P < 0.01$). Just over 23% of the 30 marked males were recaptured within the study area at least once. Of 7 males recaptured at least once, 71% were recaptured more than once. These 7 males were seen on an average of 4.0 (SE = 0.7) different days. Among multiply recaptured males, the average duration between first and last capture was 10.3 days (SE = 2.0), with three males observed over 17, 16, and 13 day periods. No marked female was recaptured. The overall sex ratio was male-biased (1.43:1.00). Using the method of Manly and Parr (1968) and Manly (1969), the male population was estimated to be 9.3 (SD = 2.0) males for day 7 and 9.0 (SD = 3.0) for day 12 of the study. Only 7% of males and 5% of females had the unbanded *astyanax*-like wing pattern.

Mate-locating behavior by males occurred primarily between 1100 and 1600 EDT. Activity budgets were calculated for a composite male based on 195 min during a total of 11 observation periods of 6 different marked males. Observations were made on sunny days between 1230 and 1500 EDT. The composite male perched 82.5% (SE = 3.8), flew 14.0% (SE = 3.2), and encountered other individuals 3.5% (SE = 0.9) of the time. Encounters with other species occurred at a rate of 1.9 per h; conspecific males were encountered at a rate of 8.3 per h. Heterospecific encounters were usually brief chases, averaging 5.8 sec (SE =

0.7, n = 6). Conspecific encounters were either longer chases or spiral flights and averaged 12.8 sec (SE = 1.0, n = 29). The difference in duration of conspecific and heterospecific encounters was significant (t-test, $P < 0.01$). Encounters between banded males (13.2 sec, SE = 1.8, n = 10) did not differ from those between banded and unbanded males (12.5 sec, SE = 1.2, n = 19).

Most encounters resulted from a perching male engaging another male that flew in the vicinity. The resident male returned from conspecific encounters to the same perch or one within 5 m in 93% of 27 cases. The challenging male returned within a minute after the end of an encounter in 32% of 25 cases. This usually resulted in repeated encounters until only the resident returned. At the study site, territories were linear arrays of perches along the hedgerows. The distance between the two most separate perches for the 11 focal male samples averaged 4.2 m (SE = 0.6). Focal males achieved exclusive use of their defended area for 95.1% of the observed period (n = 195 min).

Males did not selectively perch on larval hosts. Only 7.7% of 142 perches were on the potential host, black cherry, *Prunus serotina* Ehrh. (Rosaceae). Perches were often on nonhosts staghorn sumac (*Rhus typhina* L.; Anacardiaceae) (48.6%) and white ash (*Fraxinus americana* L.; Oleaceae) (31.0%). The remaining perches were on foliage of nonhost trees such as maple and elm, but even raspberry bushes, grape vines, corn, and goldenrod were used. Likelihood of males to perch on sumac during its period of blooming (July 1 to July 10) was not greater than before or after its blooming period (55.0%, n = 40, $\chi^2 = 0.9$, $P > 0.3$). Perches were 1–7 m from the ground (Fig. 3) with a mean of 2.9 m (SE = 0.2, n = 142). The most frequent classes were 2 m (33.8%) and 1 m (21.8%).

Certain locations within the entire study area (Fig. 1) were favored by perching males (Table 1). The southeast (SE) sampling subunit was defended during all but one of the observation periods, and twice as many males were observed in that subunit than in the next most used subunit. Males showed varying site fidelity (Table 1). For 7 males observed on multiple days, a male restricted to a subunit on one day was located in the same subunit on the next day in 62% of 21 possible cases. However, males voluntarily abandoned their territories for short periods. During the observation periods, 27% of 11 focal males were lost when they flew away from the area they had been defending, but were seen in the same areas later the same day.

More females were observed in the SW subunit, which had low male activity. During the study, two unsuccessful courtships were observed. On 27 June at 1318 EDT in the SE unit, a courted fresh female landed on a branch tip with her wings dorsally appressed. The male flew near

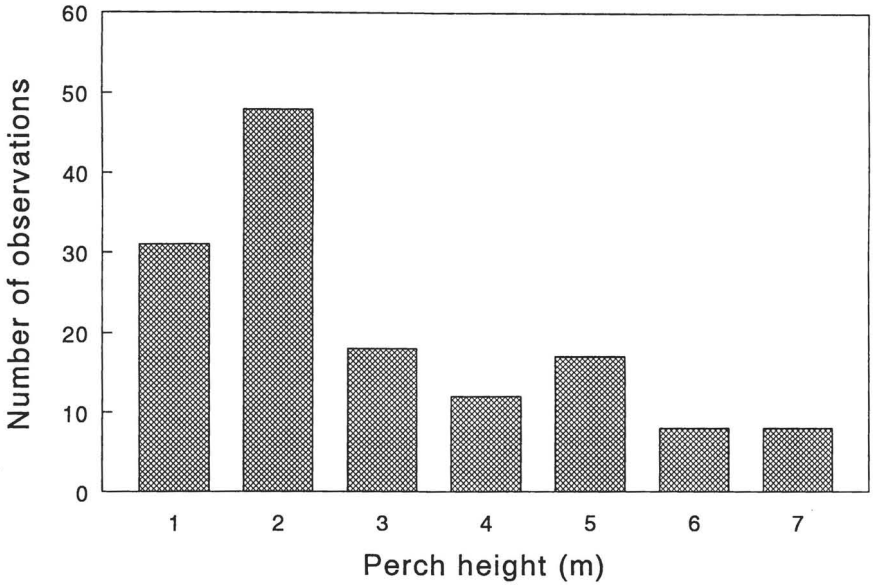

FIG. 3. Distribution of male perches by height in meters. Total sample size is 142 perches.

the female for 10 sec, landed on the same branch, and tried to copulate. The female flew about 1 m and landed on the underside of a leaf with wings dorsally appressed. The male followed the female, landed, and again tried to copulate, but flew off when he was not successful. At 1353 h on 8 July in the NE subunit, another courted fresh female perched on the underside of a leaf, and the male was unsuccessful in his attempts to copulate.

Both males and females fed avidly at the flowers of staghorn sumac. Starting at 1428 h on 1 July, two marked males fed together without aggressive encounters although they were so close that there was some physical contact at the flowers. One female laid an egg on black cherry at 1249 h on 1 July, another laid an egg on apple, *Pyrus malus* L. at

TABLE 1. Male behavior and location of individuals in regard to subunits of the study area. The first two parameters are for 12 0.25-h periods in each area. The last three parameters are for the entire study. Fidelity is the percent of resightings within the same unit. Total females include captures and observations.

	SE	NE	SW
% samples area defended	92	67	50
Total observed males	20	10	7
Initial male captures	11	2	13
% male fidelity to area	82	0	44
Total females	8	1	13

1248 h on 2 July, and another laid two eggs on choke cherry, *Prunus virginiana* L. starting at 1354 h on 5 July. An additional seven eggs and small larvae were found on choke cherry, mostly in the SW subunit.

DISCUSSION

Males of *Limenitis arthemis* defended territories as mate-locating behavior in central New York. Males were localized during midday and early afternoon. Site fidelity from day to day was generally high. Male chases of other males served to secure nearly exclusive use of these sites for the resident male. As in other territorial butterflies (Davies 1978, Rutowski & Gilchrist 1988, Rosenberg & Enquist 1991), the resident generally won these encounters. Conspecific encounters lasted over twice as long as those with other butterflies. The duration of conspecific encounters was quite similar to that for *L. weidemeyerii* (Rosenberg & Enquist 1991), and seems more than adequate to determine the species and sex of the intruder (Scott 1974). Territory turnover was somewhat higher than seen in territorial males of some species (Lederhouse 1982a) but similar to that seen in others (Lederer 1960, Alcock & O'Neill 1986, Rutowski et al. 1989, Lederhouse et al. 1992). Apparently, voluntary abandonment of defended areas was relatively frequent.

The area most regularly defended did not correspond to where most females were observed. The area with the greatest number of females had more trees including more host plants. Five females were observed in oviposition flight in that area. Areas defended by males in this study were independent of larval hosts as in *Limenitis camella* and *L. populi* (Lederer 1960) or adjacent to hosts as in *L. camella, L. populi,* and *L. weidemeyerii* (Lederer 1960, Rosenberg 1989, Rosenberg & Enquist 1991). Also, males did not change where they defended during the blooming period of sumac. This suggests that areas most regularly defended are flyways, but not necessarily concentrations of hosts or nectar plants. This is further supported by the preponderance of male perches on nonhosts. Although copulations were not observed during this study, two mating refusal interactions were seen in the early afternoon. Shull (1987) found mating pairs of *L. a. astyanax* at a similar time.

The probability that a marked male would be recaptured was lower than that reported for many territorial species but greater than that reported for patrolling species (Lederhouse 1982b). However, for those males that were recaptured once, the probability of further recaptures was similar to that for other territorial species, as was the number of times those males were seen in the study area. The average residency of territorial males in this study is quite similar to that for the black

swallowtail, *Papilio polyxenes* Fabr. (Papilionidae) from the same area (Lederhouse 1983). The two *astyanax*-like males of *L. a. astyanax* seen in the study area were observed over 16 and 13 day periods, two of the three longest. Central New York is north of the usual range of *Battus philenor* although late season strays are regularly seen there (Shapiro 1974). It is worth further study to determine whether the longevity of these two males was merely coincidental or related to their phenotype.

Although most individuals in this study were banded, their behavior encompassed published accounts for both *L. a. astyanax* and *L. a. arthemis*. Banded and unbanded males clearly recognized each other as competitors for the same territories. Encounter durations between unbanded and banded males did not differ from those between banded males, but both were significantly longer than encounters with other species. This is consistent with the apparent panmixia that occurs where the two subspecies come into contact (Platt & Brower 1968, Platt 1983). Although all females that were observed ovipositing were banded, they laid on hosts usually considered to be hosts of *L. a. astyanax* (Pyle 1981).

ACKNOWLEDGMENTS

I thank M. Ayres, J. Scott, and an anonymous reviewer for helpful criticism of the manuscript. F. Sperling and K. Mikkola translated the Lederer reference. Completion of this project was supported by National Science Foundation Award BSR 91-07139.

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Received for publication 20 March 1992; revised and accepted 21 September 1992.