

BEHAVIOR OF THE TERRITORIAL SPECIES
LIMENITIS WEIDEMEYERII (NYMPHALIDAE) WITHIN
TEMPORARY FEEDING AREAS

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ABSTRACT. Behavior of a population of *Limenitis weidemeyerii* Edwards (Nymphalidae) was studied in central Colorado using mark-recapture and observations. In 1984, individuals of both sexes fed on sap excreted from a willow via holes made by sapsuckers. The following season, *L. weidemeyerii* of both sexes fed on honeydew excreted by aphids. In addition, in both years, individuals fed at artificial high-quality food sources experimentally placed within the habitat. Territorial behaviors (patrols, chases, and investigations) were not observed within the temporary feeding areas, possibly because high intruder pressures affected the defendability of these sites. It is suggested that some studies citing a lack of territoriality in lepidopterans may have been conducted within temporary feeding areas.

Additional key words: admiral butterfly, territoriality, sap feeding.

Resource defense territoriality involves defense of resources that are patchy, predictable, and economically defendable (Davies 1978a). In lepidopteran territoriality, males generally defend locations where females reliably can be found: oviposition sites (Baker 1972), landmark sites (Shields 1967, Davies 1978b, Lederhouse 1982), or routes used by females for feeding or oviposition (Fitzpatrick & Wellington 1983, Baker 1972). While food resources are commonly defended in other taxonomic groups (Wittenberger 1981), reports of butterflies defending areas around adult feeding sites are rare. This may stem from the economic defendability of adult lepidopteran feeding sites. Because nectar resources used by butterflies often are widely scattered (Rutowski 1984; but see Murphy 1983, Murphy et al. 1984), it might prove difficult for a butterfly to maintain exclusive use of a patch of flowers, even though other insects (especially bees) do defend floral resources. Male mason bees (*Hoplitis anthocopoides* (Schenck): Megachilidae) for instance, have been found defending patches of flowers (Eickwort & Ginsberg 1980). In addition to floral resources, Lepidoptera often use temporary food sources such as sap holes, puddles, animal excreta, and carrion (Wilson & Hort 1926, Norris 1936, Downes 1973, Adler & Pearson 1982) which might prove to be more economically defendable.

I describe here the behavior of individuals of a territorial species, *Limenitis weidemeyerii* Edwards (Nymphalidae) during two flight seasons when the population had access to an unpredictable, patchy food supply in addition to its normally undefended floral foraging sites. During one season (1984), individuals of both sexes were found feeding

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at holes on a willow made by yellow-bellied sapsuckers (*Sphyrapicus varius* L.: Picidae). The following year this site was not used, presumably because sap no longer flowed freely. Individuals of both sexes were found feeding at another temporary food supply: honeydew on willow leaves in a stand where there were abundant aphids (*Chaitophorus viminalis* Koch: Aphididae). Neither location was used by this species during the previous three years as territorial, feeding, or oviposition sites. Artificial food sources also were placed in similar sites at random locations and times, and presence or absence of territorial behavior was recorded.

METHODS

A population of *Limenitis weidemeyerii* was studied during July and August 1984 and 1985 along Cement Creek in Gunnison Co., Colorado, as part of a larger study of social and genetic organization of populations of this species (Rosenberg 1987). All individuals seen were marked and color-coded using the 1-2-4-7 system of Ehrlich and Davidson (1960), so individuals could be easily identified on the wing. Territorial behavior of this species is reported in greater detail elsewhere (Rosenberg 1987). Briefly, territorial behavior consists of a perched male flying out to investigate any passing object, resulting in either a spiral flight (individuals fly around one another), or a chase (flight directly towards an intruder leading away from the perch site). Territorial behavior also includes patrols: smooth flights from and back to the perch without obvious stimulus. Feeding behavior also was recorded.

During the 1984 flight season individuals of both sexes were found aggregating at a series of holes made by yellow-bellied sapsuckers on a 1.5 m tall willow bush (*Salix* sp., hereafter called sapwillow) located approximately 23 m from the nearest territorial site. Behavior of individuals at this location was recorded at various times through the day (0900–1800 h), over the season (12 July–27 August), and observations also were concentrated for a full day only on activities at this site. Weather conditions (sun, cloud, rain), time of day, sex, identity and behavior as described above were recorded. Ages were estimated by wing-wear in increments of 0.5 from scores of 1 (newly emerged) to 4 (many scales missing), following the conventions of Watt et al. (1977). For unmarked individuals sighted, weather, time of day, and behaviors were recorded; ages were unknown, and sex of only a sample of individuals could be ascertained by noting approximate wing lengths. As with most nymphalids (Howe 1975), females of this species are larger than males.

During the 1985 flight season the sapwillow was no longer used by the butterflies. Instead, they frequented a willow stand of 10 m² area ca. 100 m away (and 90 m from the nearest territorial site) where

approximately 60% of leaves contained aphids on their undersides. Behavior and identity of individuals visiting this site, weather conditions, time of day, sex, and ages of a sample of individuals were recorded during the 1985 season (25 July–27 August). Observers could approach within 0.25 m of individual butterflies at both sites.

Four times each season artificial food sources were placed for a minimum of two days in arbitrary locations in the habitat, and identity, sex and age of individuals feeding there were recorded. Artificial sources contained fermented fruit, beer or wine, and were placed in cages styled after Platt (1969).

RESULTS

In the 1984 season there were 70 sightings of *L. weidemeyerii* feeding at the sapwillow: 20 marked males, 4 marked females, and 21 unmarked individuals. The marked butterflies fed there 49 different times on 13 separate days, many of these individuals (42%) feeding there repeatedly on different days. It is possible that unmarked butterflies also were resighted on different days. Individuals of various ages were found at this site feeding at all times of the day and in all weather conditions. The majority of the marked butterflies (84%) were not newly emerged; the average age-class was approximately 2. In more than 30 h of observation, only feeding was observed at the sapwillow; no territorial behaviors (patrols, chases, investigations) were observed. Other taxa also fed there, including unidentified species of Diptera and Hymenoptera, and other Lepidoptera such as *Vanessa atalanta* L., *Nymphalis antiopa* L., and birds such as yellow-bellied sapsucker, and broad-tailed hummingbird.

In the 1985 season there were 62 sightings of *L. weidemeyerii* of both sexes feeding at the willow stand containing aphids: 1 marked female, 16 marked males, and 34 unmarked individuals (at least 4 of the last were females). Marked butterflies were sighted there 28 times; 8 of the marked males fed there on multiple days. Some of the unmarked butterflies also may have fed there on different days. The only marked female sighted had previously mated (as evidenced by a sperm plug). No newly emerged individuals were found there. On average, the marked individuals were of age-class 3 (out of a maximum wing-wear score of 4). Weather conditions were noted for 23 observations: only 4 sightings occurred during a cloudy period, the other 19 when there was sunshine. Feeding was observed at all times of day. Individuals within the site spent most of their time probing with their proboscides on sticky spots on leaf surfaces. The butterflies apparently were feeding on the honeydew flicked onto the top surfaces by the aphids on leaves above (as in Wilson 1971). In the laboratory after feeding, I observed *L.*

weidemeyerii regurgitate and probe repeatedly at the regurgitant. Because in the field this species was observed to probe repeatedly on the leaves, it is reasonable to assume they were imbibing fresh (or possibly dissolved) honeydew. In more than 10 h of intensive observation, patrol flights never were seen in this area. Interactions between individuals were extremely brief and slow moving, and rather than involving chases away from the site, always resulted in the individuals landing on leaves there and feeding. Other taxa also were observed feeding on the honeydew including Diptera (Sarcophagidae, Muscidae) and Hymenoptera (*Dolichovespula arenaria* (Fabricius): Vespidae, and *Dialictus* sp.: Halictidae).

Five individuals were found at artificial food sources placed in the field: four males and one female. These individuals on average were scored as age 2 (out of a total wing-wear score of 4). In more than 6 h of observation, no territorial behavior was observed at or near these sources.

DISCUSSION

Patchy and predictable resources in nature often are defended via territoriality (Davies 1978a). Unpredictable sources, even if high quality often are not defended. Male territorial behavior (perching, patrolling, investigating, chasing) was not observed at three temporary feeding sites of a population of *Limenitis weidemeyerii* in central Colorado. These feeding sites, at sapsucker sap holes, leaves with aphid honeydew, and artificial sources, were high-quality sources rich in sugars and free amino acids. Four other willow stands with evidence of previous sapsucker damage were found within the boundaries of this population, suggesting that although this food source is unpredictable in time and space, it had been encountered by this population of *L. weidemeyerii* previously. *Limenitis* butterflies have been reported feeding at sap holes (Flemwell 1914, Wilson & Hort 1926) and Platt (1969) successfully traps *Limenitis* using baits. To date there have been only a few reports of adult butterflies other than lycaenids feeding on aphid honeydew (Kershaw 1907, Bingham 1907, Johnson & Stafford 1986).

Limenitis weidemeyerii males defend sites where they have good vantage points of approaching conspecifics, generally either at locations of emerging females or along flyways with an open central area bounded on other sides by vegetation (Rosenberg 1987). Although feeding locations described here proved to be good rendezvous sites for a single season, they were within wide open areas, and there is no guarantee of their utility in the following generation. Males appear to mate with females emerging within their territorial sites (Rosenberg 1987); thus, ovipositing within a previously unused territorial site might lead to

offspring being unmated longer. Also, larvae in these sites might be harmed because sap can attract adults of predatory and parasitic groups (Stary 1970), and also can breed bacteria. Finally, females visiting these sites were older ones, hence probably not receptive anyway (Rosenberg 1987), so defense of these locations may have been a waste of a territorial male's time and energy.

Butterflies were observed feeding at these sites under all weather conditions. Finding males feeding there on sunny days is particularly interesting because in most butterfly species territorial defense occurs on sunny days (Baker 1972, Davies 1978b, Lederhouse 1982, Wickman & Wiklund 1983, Rosenberg 1987). It is probable that individuals come to the temporary sites to quickly stoke up with a high energy food source to support other activities such as territorial defense, mating, and oviposition.

Alternatively, these high energy sources may not be defended territorially because it would be uneconomical on account of high intruder pressures. A breakdown of territorial behavior at feeding sites also has been noted for other butterfly species (Baker 1972, Fukuda 1974), as well as for birds (Gill & Wolf 1975).

Before the recent acceptance of lepidopteran territoriality, there were a number of reports on a "lack of territoriality" in butterflies (Ross 1963, Suzuki 1976, Scott 1974). One such report, on two species of *Hamadryas*, seems to have been undertaken at a temporary feeding area; Ross (1963) described tree sapholes within the study site. The "lack of territoriality" hence may only refer to this feeding location. More detailed study of these species away from a potential high-quality temporary feeding area may indicate these to be territorial species. If so, it is unfortunate that Ross's study has been so widely cited as negative evidence for lepidopteran territoriality. Further studies of the behavior of individuals with and without unpredictable high quality food sources can help us to better understand territoriality in Lepidoptera.

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