Journal of the Lepidopterists' Society
61(2), 2007, 67–71

DAILY HABITAT SHIFTS BY THE NEOTROPICAL BUTTERFLY *MANATARIA MACULATA* (NYMPHALIDAE: SATYRINAE) IS DRIVEN BY PREDATION

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ABSTRACT: The nymphalid butterfly *Manataria maculata* in the Monteverde cloud forest in Costa Rica moves daily between communal day roosts on the ground and individual night roosts in the trees. We studied these movements through an experimental setup where we exposed dead butterflies on the ground and in trees to natural predation for 24 h periods. *M. maculata* glued to the ground were never taken by predators during the day but often by rodents (*Peromyscus* sp.) at night. Butterflies glued to branches and leaves of trees were taken day and night, but most often by birds during the day. We conclude that the daily habitat shifts of *M. maculata* may be driven by differential predation pressure, so that the ground is unsafe by night (rodents) and the trees by day (birds).

Key words: Costa Rica, Monteverde, migration, tropical rain forest

Manataria maculata (Hopffer), a large brown forest nymph (forewing length 40–45 mm; Nymphalidae: Satyrinae) of the neotropics, is known for its peculiar behavior, including a predominantly crepuscular activity period and strange movement patterns (DeVries 1987, Stevenson & Haber 1996, 2000). It is also unusual because it is the only known true butterfly (Superfamily Papilionoidea) with functional ultrasonic hearing, strongly suggesting that flying individuals are subject to predation pressure from echolocating bats at night (Rydell *et al*. 2003).

In Costa Rica *M. maculata* reproduces in deciduous forests on the Pacific lowland during the April–May wet season, when the larvae feed on bamboo. In July–August the recently emerged and virgin butterflies migrate eastwards upslope to the cloud forest at Monteverde and other evergreen forests east of the continental divide, a distance of 100 km or more. The butterflies stay in this area and remain in reproductive diapause for 9–10 months until the following wet season, when they return west to the lowlands to mate and breed. Hence the adults live for almost a year before they reproduce. Adult butterflies feed on rotting fruit and tree sap during the day, just like most other satyrines, but during the reproductive diapause in the highlands feeding occurs only sporadically and is seldom observed (Murillo and Nishida 2003, Stevenson and Haber 1996, 2000).

In Monteverde *M. maculata* are inactive most of the time. The main exceptions are at dusk and dawn when the butterflies move between communal day roosts on the ground and individual night roosts in the tree canopies (Stevenson and Haber 1996, 2000). Day roosts are typically located in protected and shady places on or near the ground such as behind roots and in crevices and hollows in trees, places to which the coloration of the butterflies is well matched. At dusk the butterflies usually leave the day roosts as cohesive groups, which may contain from a few to *ca.* 30 individuals, occasionally 50. The butterflies then disperse among the canopies of surrounding trees and form individual night roosts on leaves and branches. They return to the communal day roost on or near the ground at dawn, usually one by one (Rydell *et al*. 2003).

In general daily movements between day- and night roosts are unusual among butterflies, but at least in Monteverde the movements are regular and apparently consistent among all individuals of *M. maculata* (Stevenson and Haber 2000). It seems hard to explain these habitat shifts by anything related to mating or feeding, because the butterflies are reproductively inactive and feed only occasionally during this period. Instead, we hypothesized that the movement is a response to differential predation pressure at different times of the day, so that the day roosts become unsafe during the night and vice versa. This implies, of course, that diurnal and nocturnal predators on roosting butterflies hunt in different places and that there is no place that is safe both day and night.

We tested the differential predation hypothesis in a field experiment. We displayed dead *M. maculata* in groups on the ground, thus simulating a communal day

roost, for 24 hours, and recorded predation frequencies during the day and night. We followed the same procedure for night roosts, where dead butterflies were glued individually to branches and leaves of trees. According to our hypothesis, we predicted that butterflies in day roosts (on the ground) should be predated predominantly at night and butterflies at night roosts (among the foliage) should be predated predominantly during the day. Possible predators could be, for example, small mammals and insectivorous birds, respectively, but also spiders, ants and other invertebrates.

MATERIALS AND METHODS

The study was made at Estación Biologica de Monteverde in Costa Rica, 15–20 November 2001 and 19–25 September 2005. The study area mostly consists of mature cloud forest and is located at 1550–1600 m above sea level.

The experiments were made at three sites within 1 km of Estación Biologica; site A, used in 2001, and sites B and C, used in 2005. On each site 5–8 dead butterflies were glued to the ground in a cohesive group, forming a day roost in a shady spot beneath a tree root or in a small rock crevice. Another 5–9 butterflies were spaced out >0.5 m above the ground among branches and leaves of surrounding trees, forming a night roost. All roosts were in places where *M. maculata* had been seen roosting naturally. The roosts were examined for removed or destroyed butterflies before dusk (about 1700 h) and after dawn (about 0700 h). Occasional observations were made in between. Removed or destroyed butterflies were replaced at dusk and dawn whenever fresh specimens were available. The same procedure was repeated for 3–5 consecutive days at each site. Butterflies for the experiments were collected as needed from day roosts in the vicinity of the station. Before the experiments they were killed by quickly squeezing the thorax.

In both years we set a live mousetrap overnight (one or two days per roost) within part of the day roosts in order to catch and identify the presumed predator. The trap was baited with dead *M. maculata*. Caught rodents were released at the site of capture after identification.

RESULTS

During both study periods the trade winds blew strongly from the east and brought frequent and sometimes heavy rain and mist. In 2005 rains were particularly heavy and persistent and often accompanied by strong winds. In fact it rained most of the time during the 2005 experiment and for the last two days it rained continuously. It was our impression that the activity of birds and insects was much lower during the 2005 experimental period compared to 2001, when the weather was more normal and much drier.

Our data from day roosts on the ground were clear and supported our hypothesis. We observed no predation by day but substantial predation at night. The butterflies (5–8 individuals) disappeared over night in

Table 1. Predation at communal day roosts where groups (5–8 individuals) of dead butterflies were glued to the ground in crevices and behind tree roots and left for one day (24 h). Predation was scored if the butterflies were obviously affected or had disappeared at the end of the observation period.

Site	Day no.	Daytime		Nighttime		Sign. (χ^2)
		% predated	N	% predated	N	
Site A 2001	1	0	8	100	8	p<0.001
	2	0	7	100	7	p<0.001
	3	0	5	100	6	p<0.01
Site B 2005	1	0	5	0	5	ns
	2	0	5	0	5	ns
	3	0	5	100	7	p<0.001
	4	0	5	100	5	p<0.01
	5	0	5	100	6	p<0.01
Site C 2005	1	0	5	0	5	ns
	2	0	6	0	5	ns
	3	0	5	100	7	p<0.001
	4	0	7	100	7	p<0.001
	5	–	–	100	7	–
Predation (% of days)		0	N=12	69.2	N=13	

Table 2. Predation at individual night roosts, where dead butterflies were glued to branches and leaves of trees and left for one day (24 h). Predation was scored if butterflies were obviously affected or had disappeared at the end of the observation period.

	Day no.	Daytime		Nighttime		Sign. (χ^2)
		% predated	N	% predated	N	
Site A 2001	1	88	8	0	5	p<0.01
	2	60	5	20	5	ns
	3	40	5	0	7	ns
	4	80	5	–	–	
Site B 2005	1	0	6	0	5	ns
	2	33	6	0	6	ns
	3	0	7	0	7	ns
	4	33	6	43	7	ns
	5	60	5	60	5	ns
Site C 2005	1	33	6	0	6	ns
	2	0	9	0	8	ns
	3	25	8	38	8	ns
	4	57	7	71	7	ns
	5	–	–	12	8	-
Predation (% of days)		83.3	N=12	50.0	N=12	

eight out of twelve cases, so predation either affected all or none of the individual butterflies in a roost. The result was consistent across the two years and three sites (Table 1). We typically found *M. maculata* wings piled up in a spot near the roost, suggesting that the same predator had eaten them all (Table 3). We caught one *Peromyscus* sp. (*P. mexicanus* or *P. nudipes* – the two are hard to distinguish) in the trap set at the roost both at site A (2001) and site B (2005).

Predation at night roosts in the trees was qualitatively and quantitatively different from that at the day roosts, partly because the butterflies were spread out. The results were less clear with respect to our hypothesis. At night roosts predation only affected some individuals at a time, occurring both by day and by night, but it was slightly more frequent and affected more individuals on average during the day (Table 2). This difference was consistent and significant at site A (2001) but not at sites B and C (2005). The only predators actually observed eating butterflies in a night roost were a wasp and a wolf spider. However, most attacked butterflies showed beak marks on the remaining wings, suggesting that insectivorous birds were in fact the most frequent predators (Table 3).

Discussion

Communal roosts on the ground appeared relatively safe during the day, as expected, but very unsafe during the night, when they were heavily exploited by *Peromyscus*. Hence, nocturnal predation by rodents seems to explain why *M. maculata* leaves the ground at dusk.

The 2001 results from the night roosts suggest that diurnal predation by birds could explain why *M. maculata* leave the trees at dawn and return to the ground. The 2005 results are difficult to evaluate, because the predation pressure did not differ significantly between the day and the night. We suspect that the unusually wet weather in 2005 resulted in depressed foraging activity of insectivorous birds in daytime, so that the diurnal predation pressure on the experimental butterflies became lower than normal. Furthermore, we cannot exclude the possibility that some of the specimens that disappeared from the night roosts in 2005 actually were washed away by the rain. Regardless of the details, the ground was clearly safer than the trees in daytime, and the trees appeared safer than the ground at night. Hence, our results are not inconsistent with the hypothesis that the switching between day- and night roosts of *M. maculata* facilitates the avoidance of nocturnal and diurnal predators, respectively.

The diurnal defense of *M. maculata* is not only a matter of location of the communal roosts on the ground and the cryptic coloration of the butterflies, but also of the behavior and cohesiveness of the roosting group. In daylight roosting butterflies are very alert to visual and tactile stimuli. They are easily flushed when

Table 3. Details of the observations presented in Tables 1 and 2. Nocturnal predation at communal day roosts (a) and diurnal (b) and nocturnal (c) predation at individual night roosts. Diurnal predation at communal day roosts was zero and is not included in the table.

a) Nocturnal predation at communal day roosts (butterflies in groups on the ground).

Site	Day no.	Observation
A	1	All 8 disappeared, wings left in pile
	2	All 7 disappeared, wings left in pile
	3	All 6 disappeared, wings left in pile; Peromyscus caught at roost
B	1	No predation
	2	No predation
	3	All 7 disappeared, wings left in pile
	4	All 5 disappeared, wings left in pile
	5	All 6 disappeared, wings left in pile; Peromyscus caught at roost
C	1	No predation
	2	No predation
	3	All 7 disappeared, wings left in pile
	4	All 7 disappeared, wings left in pile
	5	All 7 disappeared, wings left in pile

b) Diurnal predation at individual night roosts (butterflies spaced out in trees)

Site	Day no.	Observation
A	1	7 of 8 bodies removed, wings found with beak marks
	2	3 of 5 bodies removed, wings found with beak marks
	3	2 of 5 bodies removed
	4	4 of 5 bodies removed, wings found with beak marks
B	1	No predation
	2	1 disappeared; 1 seen eaten by wasp; 4 left intact
	3	No predation
	4	1 disappeared; 1 body removed, wings left behind; 4 left intact
	5	3 of 5 bodies removed, wings left behind
C	1	2 of 6 individuals with beak marks
	2	No predation
	3	1 disappeared; 1 body removed, wings with beak marks; 6 left intact
	4	1 disappeared; 3 bodies removed, wings with beak marks: 3 left intact

c) Nocturnal predation at individual night roosts (butterflies spaced out in trees)

Site	Day no.	Observation
A	1	No predation
	2	1 of 5 with body eaten
	3	No predation
B	1	No predation
	2	No predation
	3	No predation
	4	3 of 7 disappeared
	5	2 disappeared; 1 with body eaten; 2 left intact
C	1	No predation
	2	No predation
	3	2 disappeared; 1 with body eaten; 5 left intact
	4	3 disappeared; 2 with body eaten; 2 left intact
	5	1 of 8 disappeared

disturbed and usually leave the roost as a cohesive group. This means that a predator attack on a real day roost of *M. maculata* would probably be less disastrous than our experiment with dead butterflies suggests. The predator would most likely be able to catch one butterfly at most before the others disappear, not all as in our experiment.

The results of this study suggest that *M. maculata* uses different defensive strategies at different parts of the day. Its defensive behavior is also dependent on the kind of stimuli. For example, *M. maculata* resting in daytime do not react at all when exposed to ultrasound, stimuli to which flying individuals at night are very sensitive and react evasively (Rydell *et al* 2003). Thus the predatory defense strategy of *M. maculata* is complex and the defensive behavior is strongly dependent on the prevailing situation.

It has been suggested that wintering monarch butterflies, *Danaus plexippus* (L.) in Mexico minimize predation by rodents by roosting in trees rather than on the ground (Brower *et al*. 1985). Our results give substantial support to this idea. In contrast to *M. maculata*, which is cryptically colored, *D. plexippus* has warning coloration and possesses a strong chemical defense functional against birds (Rothschild 1985). Presumably lacking such protection against birds, *M. maculata* apparently cannot spend the day in the trees but has to pay the energetic cost of daily movements and vigilance in the day roost.

Acknowledgments

We deeply acknowledge the personnel at Estación Biologica, particularly M Hidalgo, for extensive support, Ministerio del Ambiente y Energia Sistema Nacional de Areas de Conservation for permission, M. Morales, M. Tamez and the Masters Couple for assistance and M. B. Fenton for comments on the manuscript.

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Recieved for publication 18 September 2006; revised and accepted 15 January 2007.