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Territoriality by the dawn's early light: the Neotropical owl butterfly *Caligo idomenaeus* (Nymphalidae: Brassolinae)

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Abstract. Males of the Neotropical owl butterfly *Caligo idomenaeus* defend unusual dawn territories along dirt roads in the Linhares Forest Reserve, Espírito Santo, Brazil. The territories are notable for their wide spacing and the brief period in which owners are present. During mid-winter insects arrived on the territories shortly after 0550 h, as the last bright stars disappeared from the sky, and remained approximately 15 min before flying back into the forest. Dawn perching seemed unaffected by substrate temperatures as low as 12.5° C. Perches were about 100 m apart and resident butterflies returned to and seemingly repelled invaders from their territories on consecutive mornings. Territories contained no material resources. The brief dawn occupancy may be related to the activity period of receptive females and to predator risk in these large, palatable insects.

Key Words. Brassolinae, Brazil, *Caligo*, Crepuscular, Mating Behavior, Territoriality

Introduction

Male defense of encounter sites is a common mate-locating tactic in butterflies (Baker 1983, Rutowski 1991). Mating territories have been recorded for many taxa and geographic regions, but are especially well documented for temperate zone species, especially papilionids (Lederhouse, 1982), lycaenids (Douwes 1975, Alcock 1983a, Alcock & O'Neill 1986) and the nymphalid subfamilies Nymphalinae (Baker 1972, Bitzer & Shaw, 1980, 1983, Alcock 1983b, Alcock & Gwynne 1988, Rosenberg & Enquist 1991) and Satyrinae (Davies 1978, Knapton 1985, Wickman 1985). The few tropical studies to date have reported territorial behavior in typical tropical taxa (Riodininae, Alcock 1988; Heliconiinae, Benson et al. 1989) as well as in taxa already studied in temperate areas (Papilionidae, Pinheiro 1990; Nymphalinae, Rutowski 1991b, 1992, Lederhouse et al. 1992).

Independent of region, territorial behavior, like flight activity in general (Srygley & Chai 1990), is characteristic of sunny habitats with mild thermal environments (Alcock 1983b, Wickman 1985a, Alcock & O'Neill 1986). This rule is not universal, and several species of *Vanessa* defend near sundown (Alcock & Gwynne 1988, Brown & Alcock 1991). The exclusively Neotropi-

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cal Brassolinae may provide other exceptions. In Panama, *Caligo memnon* Felder engages in territorial-like mating behavior at dusk, and *Opsiphanes cassina* Felder (Brassolinae) behaves similarly (Srygley 1994). In the state of Espírito Santo in southeastern Brazil *Caligo illioneus* Cramer and *Catoblepia amphirrhoe* Hübner perch along roadsides at dusk (W.W. Benson, pers. obs.), whereas *Caligo idomenaeus rhoetus* Staudinger does this shortly before dawn, even during cool winter weather. In the winter of 1992 we studied *C. idomenaeus* with the intent of clarifying the significance of dawn perching behavior in this insect and gain insights into the possible influence of light and temperature.

Methods

The study was carried out from 27.VII to 6.VIII.1992 (no observations were made on 4.VIII) along an east-west stretch of 4 m wide dirt road passing through mature subtropical moist forest in the Linhares Forest Reserve (Reserva Florestal de Linhares) at Linhares, Espírito Santo, Brazil (19° 10′ S, 40° 00′ W). Mean winter temperatures at the reserve are near 20° C, with extremes for the months of July and August (mid-winter) approximately 10º and 30° C (Companhia Vale do Rio Doce, unpub. data).

The study area was selected based on the confirmed presence of *Caligo idomenaeus*. A 450 m long area was marked off in 50 m segments to aid mapping of butterfly perches and behavioral events. We conducted observations daily from about 0545 to 0620 h (early dawn to shortly after sunrise). The owl butterflies were very difficult to see in the dim light at the beginning of their activity period, especially where trees arched over the road, and we were only able to follow insects at this time by spacing ourselves along the road and calling to each other as butterflies passed. When possible, butterflies were netted and marked by cutting distinguishing notches along wing margins. The owl butterflies are large and robust and apparently not impaired by this procedure. Some uncaptured individuals could be individually recognized by distinctive wing damage. Road-surface temperature was measured daily at the beginning of butterfly activity using a mercury thermometer. On one morning during the *Caligo idomenaeus* activity period we measured incident light at road level near the perch site at the widest and least obstructed part of the road using a digital luximeter with 1 lux sensitivity (Extech Instruments). Civil twilight period and sunrise were obtained from the computer program Earthsun 4.5 (© W. Scott Thoman, Dryden, NY, 1995).

Results

The only large owl butterfly observed at dawn was *Caligo idomenaeus*. We observed 3 of the 4 individually recognizable insects on more than one day. Two individuals marked on perches at dawn were males, and others observed in the study area were inferred to be males by their behavior. Other *Caligo* captured during twilight hours while perched along reserve roadways have always proved to be males of *C. illioneus* and *C. idomenaeus* (W.W. Benson, pers. obs.).

On most mornings we observed 3–5 *Caligo* perching in the area and as

many as 4 non-residents making "fly-throughs." Perching *Caligo* were punctual, with the first individual arriving between 0550 and 0556 h (x = 0552.7 h, s.d. = 2.3 min , n = 7; six observations on marked individual #3) and the last *Caligo* departing around the time of sunrise between 0609 and 0612 h (x = 0610.1 h, s.d. = 0.9 min, n = 8; seven observations on individual #3). Between 27.VII and 2.VIII, when the bulk of the observations were made, civil twilight began between 0547 and 0545 h and the sun rose between 0609 and 0607 h. Brighter stars remained visible until about 0550 h, and the planet Venus could be seen until 0553 h.

Butterflies occasionally arrived in the area and patrolled back and forth as much as 3 min before perching. The time span over which one or more individuals were present in the area on a given morning varied between 13 and 20 min (x = 16.7 min, s.d. = 2.5 min, n = 6). The time of arrival and departure did not seem to be strongly influenced by cloud conditions (clear to cloudy) or temperature (12.5–18.0° C), and even with a soil temperature of 12.5° C, four butterflies were active. On 2.VIII under an almost cloudless sky, the light intensity increased approximately exponentially from about 2 lux at 0551 h when the first *Caligo* arrived to 180 lux when the last one departed at 0610 h.

When arriving in the area, an owl butterfly often patrolled back and forth several (maximum of nine) times along 10–50 m of road before landing. The flight was swift and erratic about 1–2 m above the ground. After arrival, butterflies perched near the center of the patrolled area on the ground in the roadway or on low (< 1 m high) roadside vegetation. Although most arriving (and departing) butterflies that we followed left (or entered) the forest within 25 m of the perch, one was observed to fly approximately 240 m before entering the forest.

Interactions occurred when flying butterflies met or a presumed male was chased when it flew over a perched resident. Interacting owl butterflies flew in tight circles about each other in level or ascending flight approximately 1–2 m (up to 5 m) above the ground while batting their wings together. Most interactions terminated after a few 10s of seconds. In 6 of the 7 observed encounters involving marked resident males, the original male returned to its perch after the intruder had left. In the remaining case observed near the end of the territorial period neither butterfly returned. On two occasions, two *C. idomenaeus* were observed to perch 10–20 m apart, apparently without seeing one another.

During 9 days of observations we identified 5 sites preferred by *Caligo idomenaeus* for perching: 10 m (used on 2 d), 100/120 m (3 d), 160 m (7 d), 220/280 m (3 d), and 380 m (9 d) from the west boundary of the study area. The 3 marked males that returned to the area showed perch fidelity on successive days. On 5 consecutive days (27–31.VII) male #1 landed at the 160 m perch (and once at the 10 m perch as it was leaving the area). Unmarked individual(s) occupied this perch on the 2 days following the disappearance of #1. Male #2, seen in the area 27–28.VII, occupied perches at 100 and 120 m, from which it was expelled by male #1. Male #3 perched in the road at 380

m on seven consecutive days (28.VII–3.VIII) and subsequently on 5– 6.VIII. Males #1 and #3 usually rested in the road near fallen, dead *Cecropia* leaves. Otherwise, there was no indication that the butterflies selected perching sites with respect to specific habitat features.

Discussion

Patrolling behavior, interactions between individuals and spacing in male *Caligo idomenaeus* are almost certainly related to territorial defense. Individuals returned daily to specific perches spaced about 100 m apart. These residents seemed to patrol road segments around their perches and interact by expelling intruders. Although we saw neither courtship nor mating, defense of mating territories is common in butterflies (see Introduction), and other *Caligo* mate during crepuscular encounters (Srygley 1994). Although only 3 individually recognizible butterflies were monitored, we believe that our observations on these are representative of the study population. On the other hand, our unsuccessful attempts to capture unmarked individuals may have frightened some butterflies from the area and diminished perch occupation.

Territorial *Caligo idomenaeus* patrol corridors up to 50 m long around their perches. In contrast, territorial *Heliconius* patrol corridors about 15 m long (Benson et al. 1989), and similar territory sizes seem to exist in tropical *Heraclides* and *Battus* (Pinheiro 1990). *C. idomenaeus* is large for a butterfly (wing length 80 mm), and for this reason territory size may be less constrained than in smaller species. The wide spacing between perches may be advantageous in reducing mate competition between neighbors. Although *C. idomenaeus* occurs spottily along roadsides in the Linhares Forest Reserve, males do not seem to lek around conspicuous landmarks as has sometimes been reported for other butterflies (DeVries 1980, Lederhouse 1982, Alcock 1983a, Knapton 1985, Alcock & Gwynne 1987) and population distribution may be more related to habitat favorability than classical lek formation.

Low temperature can prevent butterfly flight, and the ability of *C. idomenaeus* to maintain full activity before sunrise with substrate temperatures below 13° C is probably aided by its large size and *Caligo*'s ability to increase body temperature by shivering (Srygley, 1994). Our study site is subtropical with cool winters, and it is interesting to note that *C. idomenaeus* was active at temperatures ($\bar{x} = 16.2°$ C, s.d. = 1.9° C, n = 8) uniformly lower than Srygley's (1994) estimate of 19–20° C for the lower critical temperature for flight in Panamanian *C. eurilochus*.

Two possibly unique characteristics of territoriality in *Caligo idomenaeus* and other brassolids (see Introduction; Srygley 1994) are its occurrence during twilight hours and the extreme brevity of the territorial bouts. Because owl butterflies are palatable (Chai 1986) and presumably especially profitable prey items due to their large body mass and high visibility when in movement, birds may select strongly against late-flying *C. idomenaeus* and thereby constrain activity to situations where their visiblity to predators is

hampered. Restricted activity of receptive females could have the same cause, and same effect on mating conventions.

Published studies suggest that tropical forest butterflies usually spend less time in territorial defense than butterflies of other environments. Excluding desert butterflies such as *Chlosyne californica* (Wright) (Alcock 1983b) and *Strymon melinus* Hübner (Alcock & O'Neill 1986) whose activity is apparently limited by high midday temperatures, and species of the cosmopolitan genus *Vanessa* that defend territories just before sundown (Bitzer & Shaw 1980, 1983, Alcock & Gwynne 1988; Brown & Alcock 1991), 64% of the 14 temperate-zone butterflies for which data are available typically defend territories 3–6 h daily (Powell 1968, Baker 1972, Douwes 1975, Davies 1978, Wickman & Wicklund 1983, Alcock 1983a, Bitzer & Shaw 1983, Rutowski & Gilchrist 1988) and an additional 29% defend 6 h or more (see Lederhouse 1982, Wickman 1985b, Knapton 1985, Rosenberg & Enquist 1991). Similarly long shifts of territorial defense have been reported for *Hypolimnas* and *Junonia* in tropical savanna (Rutowski 1991b, l992). Excluding the desert species and *Vanessa* mentioned above, *Polygonia comma* Harris is to our knowledge the only temperate butterfly reported to be territorially active for 3 or fewer hours a day (Bitzer & Shaw 1983).

The seven tropical forest butterflies for which data have been published defend territories over relatively shorter time spans, five for 3 h or less daily and the two remaining for up to 6 h. Besides the 0.25 h period reported here for *C. idomenaeus*, the heliconiines *Heliconius sara* (Fabr.), *H. leucadia* (Bates) and *Eueides tales* (Cramer) defend for 1 to 2.5 h daily in Brazil, and *E. aliphera* (Godart) is territorial for about 5 h daily in Costa Rica (Benson et al. 1989). Alcock (1988) reports that the Costa Rican forest hesperiids *Celaenorrhinus approximatus* William & Bell and *Astraptes galesus cassius* Evans defend for about 2 and 3 h respectively, whereas males of the riodine *Mesosemia a. asa* Hewitson spend about 4 h per day on territories. Although each species is no doubt adapted to a unique set of ecological conditions, we believe the general phenomenon of shorter defense shifts in tropical forest butteflies may be related to fine-tuning in mate search resulting from the greater temporal structuring of this environment. However, because of the small number and limited taxonomic distribution of species studied to date, and the general lack of information on temporal variation in the costs and benefits of territorial defense, our purpose here is more to draw attention to the phenomenon than to provide explanations.

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