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TERRITORIAL BEHAVIOR AND DOMINANCE IN SOME HELICONIINE BUTTERFLIES (NYMPHALIDAE)

WOODRUFF W. BENSON, CÉLIO F. B. HADDAD[1]
AND MÁRCIO ZIKÁN
Departamento de Zoologia, IB, Universidade Estadual de Campinas,
C. P. 6109, 13081 Campinas, São Paulo, Brazil

ABSTRACT. By marking and systematically observing activities of focal individuals of *Heliconius sara*, *H. leucadia*, and *Eueides tales* at six trailside sites at Serra dos Carajás, Pará, Brazil, we found that resident male butterflies returned daily during 1–3-h periods to patrol and defend fixed 10–15-m-long sunny corridors against conspecific males. Defenders expelled intruders about once every 5–20 min, and unoccupied territories were taken over by vagrant males in about the same time interval. Marked primary residents of the two *Heliconius* species won all 149 combats observed with encroachers, and could evict newcomers settling on territories left temporarily vacant. Resident *E. tales* were more than 95% victorious. Besides fleeing vigorously from residents, trespassing *H. sara* and *H. leucadia* frequently departed slowly from territories when accompanied by the resident from below and behind. Resident *H. sara* flew erratic blocking patterns underneath slowly departing invaders, although a trespasser sometimes avoided immediate expulsion by diving to soil level and flying in circles too close to the ground for the accompanying resident to get under it. These ground-circling flights of *H. sara* appear to be contests to decide territory ownership whereas the peculiar slow exits of desisting *H. sara* and *leucadia* apparently function as appeasement behavior that bridles territorial aggression. *Eueides tales* sometimes followed one another through several steep glides (interpreted as ritualized chases) during territorial encounters. Territories seem to be rendezvous sites attractive to receptive females, although *E. aliphera* may defend emergence sites.

Additional key words: appeasement behavior, *Eueides tales*, *Heliconius leucadia*, *H. sara*, mate location.

Territorial behavior gains its advantage by permitting the preferential use of resources in restricted areas (Brown & Orians 1970). Territorial defense has been reported repeatedly in temperate-zone butterflies (Powell 1968, Baker 1972, Wellington 1974, Douwes 1975, Davies 1978, Bitzer & Shaw 1980, 1983, Lederhouse 1982, Dennis 1982, Alcock 1983, 1985, Knapton 1985, Wickman 1985a, Dennis & Williams 1987), where, so far as known, males defend probable mate encounter sites against other males (Baker 1983).

Defended encounter sites are frequently defined by landmarks, such as hilltops (Shields 1968, Alcock & O'Neill 1986) and other landscape features that reliably bring the sexes together (Parker 1978). Thus, butterfly territories may occur along flyways (Baker 1972, Bitzer & Shaw 1983) or occupy sheltered sites offering favorable conditions until matings occur (Knapton 1985, Wickman 1986). Oviposition sites frequented by gravid females (Baker 1972) and female emergence sites

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[1] Present address: Departamento de Zoologia, IB, Universidade Estadual Paulista, 13500 Rio Claro, São Paulo, Brazil.

(Dennis 1982) may also be defended. Territorial males often return to defend the same place over a period of days or weeks (L. E. Gilbert *in* Maynard-Smith & Parker 1976, Lederhouse 1982, Alcock 1983, Knapton 1985, Wickman 1985a).

Territorial interactions in butterflies may be characterized by their greater duration (Wickman & Wiklund 1983, Wickman 1985a) and by the peculiar combat behavior of residents (Fitzpatrick & Wellington 1983, Wickman & Wiklund 1983). Territorially related dominance hierarchies and appeasement behavior, although present in other nonsocial insects (Ewing 1972, Raw 1976), are apparently unreported for Lepidoptera.

Recently Baker (1983) suggested that tropical *Heliconius* butterflies are territorial. Indeed, Seitz (1913) reported seeing male heliconiines "... showing some characteristic defect, daily during four weeks flying at about the same place ... up and down in that characteristic fashion ... called 'promenading,'" and added, "this habit of flying for hours or half days at a time up and down for a certain distance, turning sharply around at a certain point and returning the same way ... is nowhere quite so distinct as in the genera *Eueides* and *Heliconius*." On the other hand, Crane (1957) found no evidence for territorial behavior or social hierarchies during insectary studies of six species of Trinidad heliconiines. Murawski (1987), however, observed territory-like stationary defense of flowers by *Heliconius* when floral resources were scarce.

The "large scale promenading" reported for several *Heliconius* (Brown & Mielke 1972, Brown 1972, Cook et al. 1976, Mallet & Jackson 1980) refers to the repeated use of flyways within daily activity ranges, and does not correspond to the behavior reported by Seitz (1913).

We report here observations on male *Heliconius sara thamar* (Hübner), *H. leucadia pseudorhea* Staudinger, *Eueides tales pythagoras* Kirby and *E. aliphera* (Godart) patrolling and expelling conspecifics from territories. Results show that defense is often achieved through specialized ejection behavior, and that invaders rapidly occupy vacant territories. Notes are given for other heliconiines indicating that similar behavior may occur widely in these insects.

STUDY SITES AND METHODS

Systematic observations were undertaken during the austral dry season (July) of 1986 and 1987 in the Serra dos Carajás near Serra Norte, Pará, Brazil (6°03'S, 50°07'W), at sites occupied by promenading (*sensu* Seitz 1913) heliconiine butterflies. *Heliconius sara* (Fabr.), *H. leucadia* Bates and *Eueides tales* (Cramer) were observed along trails near Caldeirão (5°53'S, 50°27'W), an abandoned mineralogical camp at 210 m elev. by State Road PA-275 where it crosses the Rio Itacaiúnas. A second site, with only *H. sara*, was at 650 m on an abandoned spur of PA-275, 2 km N of the iron ore outcrop called "N-1" (5°59′S, 50°16′W). In 1987, males of *H. sara* held territories at three points 100–200 m apart at Caldeirão, here referred to as Areas 1, 2, and 3, and 3 others—4, 5, and 6—arranged linearly 75–100 m apart at the N-1 site. Only Caldeirão was worked in 1986 where *H. sara* territories were observed at Areas 1 and 2. *Heliconius leucadia* was observed only in 1987 defending territories at Areas 1 and 3. *Eueides tales* defended in both years at Area 1. Observations on territorial *H. sara* totaled 1194 min, on *H. leucadia* 664 min, and on *E. tales* 627 min. Notes on territorial *Eueides aliphera* were mostly taken in Costa Rica.

The climate at Carajás is moist tropical with mean annual rainfall 2100 mm (CV = 23%) and mean temperature between 24° and 26°C, depending on altitude. Temperatures and relative humidities during observation periods at Caldeirão were typically near 24°C and 90–95% at 0930 h and 30°C and 75% at 1130 h. Most days were cloudless or with scattered clouds only appearing at the ends of observation periods.

Net-captured butterflies were marked using colored porous-point pens or by cutting notches from wing margins. Individually recognizable animals were merely netted to establish positive species identification. Sex, wing length, and wing damage and wear indicative of age were noted. Behavioral observations were made from trailsides with the aid of a stopwatch and binoculars. In territorial interactions, sex of unmarked nonresident butterflies was inferred from their behavior using Crane (1957) and observations on marked intruders of known sex. Male *Eueides tales* were distinguished from females by their narrower wings. During 1987 observation periods, specific activity of focal individuals (Altmann 1974) was monitored continuously or noted every 15 sec for time budgets. For measured variables we give arithmetic means and use standard deviations (SD) to describe data variation.

RESULTS

Territoriality in *Heliconius sara*, *H. leucadia*, and *Eueides tales* is broadly similar. Defending males divided their time between perching and promenading over 10–15-m-long territories situated in sunlit vegetation corridors. Territory cores were normally delimited by conspicuous features such as overhanging limbs or jutting bushes, and were adjoined by less frequently visited peripheral areas of 5–30 m at one or both ends. Males did not feed when engaged in territorial activity nor were host-plants or other resources consistently present on territories. *Heliconius leucadia* and *H. sara* flew irregular paths 1–2 m wide, usually staying within 1–2 m of neighboring vegetation whereas *E. tales* tended to occupy the center of the approximately 5-m-wide trail clearing. A complete circuit of a core area took approximately 10–15 sec when butterflies did not tarry in localized circling. In all three species, conspecific males were challenged when approaching within 2–3 m of a resident. Pursuing residents normally followed intruders well beyond the patrolled area where they broke off the chases.

Territorial behavior. Discounting courtships and matings, approximately 100 conspecific interactions were observed in each of the three main heliconiine species studied (Table 1). These were almost always lengthy, and continued until one butterfly was either driven from the territory or was able to evade the other.

In *Heliconius sara*, a resident male often followed, rather than chased, a male encroacher, and attempted to get below it. Eighteen of 32 interactions observed in 1986 began with downward flight that tended to bring the two butterflies to ground level (the other 14 were rapid, straightforward chases). In five of these chases, the insects descended almost to the ground, and in two, terminating in relatively open undergrowth, the butterflies flew 5 to 15 cm above the ground, and circled and weaved back and forth over contiguous areas 30–40 cm in diam.

We have observed such ground circling behavior on many additional occasions. Circling may last from a few seconds to a minute or more, after which normally the interloper begins flying upwards with the resident joining to accompany it from below and behind. Low flight apparently prevents the dominant butterfly from getting under and expelling the subordinate. On occasion, and despite apparent attempts to block it, an intruder may slip past a resident and initiate another bout of circling. One series of interactions of this type observed in 1987, involving several individuals, went on for 15 min.

Once the resident succeeded in getting under the trespasser, a characteristic ascending ejection generally followed. Initially, when flying through vegetation, if the intruder became separated from the resident by more than 30–40 cm, the latter usually dashed in the interloper's direction until again immediately below and behind. Once free of confining foliage, an intruder tended to fly slowly upwards, almost hovering, with the resident darting erratically back and forth almost directly underneath it. Ejections gave the impression of the invader being driven upwards by the resident, and in one instance the lower butterfly was seen to dart several times at a subordinate that was ascending at an abnormally slow pace. Butterfly pairs habitually rose 15 m or more to pass over vegetation bounding the territory, and could wander as far as 40 m laterally before the resident disengaged. Expulsions sometimes ended with the intruder bolting away with the resident in pursuit. Territory holders returned from such excursions

TABLE 1. Summary of observations on four species of territorial heliconiine butterflies. SD and number of sample days in parentheses; SD of times in min. Caldeirão (Cald) and N-1 are in the Serra dos Carajás, Pará, Brazil.

Species	Site, area no., year	Marked**	Time elapsed in min, no. days obs.	% time in flight*	Hour of:		No. territorial expulsions	No. expulsions/h*
					Arrival	Departure		
Heliconius sara	Cald, 1, 86	No	178, 2	—	1003 (5.7; 2)	1121 (6.4; 2)	26	7.6 (1.4; 2)
	Cald, 2, 86	Yes	92, 2	—	0935 (—; 1)	1107 (17.7; 2)	6	3.9†
	Cald, 3, 87	Yes	294, 3	42.8 (4.8; 3)	0940 (12.2; 3)	1203 (—; 1)	36	7.0 (1.7; 3)
	N-1, 4, 87	No	207, 2	53.1 (9.3; 2)	0927 (21.5; 3)	—	15	4.4 (3.1; 2)
	N-1, 4, 87	Yes	237, 2	42.7 (3.5; 2)	—	—	10	2.6 (0.25; 2)
	N-1, 5, 87	No	154, 2	40.3 (5.0; 2)	—	—	11	4.3†
H. leucadia	Cald, 1, 87	Yes	384, 6	62.5 (12.6; 5)	0943 (12.6; 4)	1057 (18.8; 4)	50	8.8 (4.2; 6)
	Cald, 3, 87	Yes	263, 6	72.3 (5.0; 5)	1000 (14.4; 6)	1047 (29.0; 6)	47	12.8 (2.4; 4)
Eueides tales	Cald, 1, 86	No	321, 3	93.6 (—; 1)	1058 (27.8; 5)	1238 (15.5; 3)	41	7.5 (3.5; 3)
	Cald, 1, 87	Yes	183, 3	95.7 (1.8; 2)	1053 (28.2; 3)	1209 (19.1; 2)	33	12.6 (4.8; 3)
	Cald, 1, 87	No	87, 1	84.4 (—; 1)	1105 (26.3; 3)	1232 (17.4; 3)	23	15.9†
E. aliphera	Costa Rica, 67	No & yes	113, 3	—	0830#	1404 (36.4; 3)	11	5.1†

* Only days with ½ h or more of observation used to estimate means.

** Observations on unmarked butterflies may have included more than 1 individual.

† Expulsion rate calculated as No. territorial expulsions/time elapsed.

Time of earliest observed patrolling; no arrivals observed.

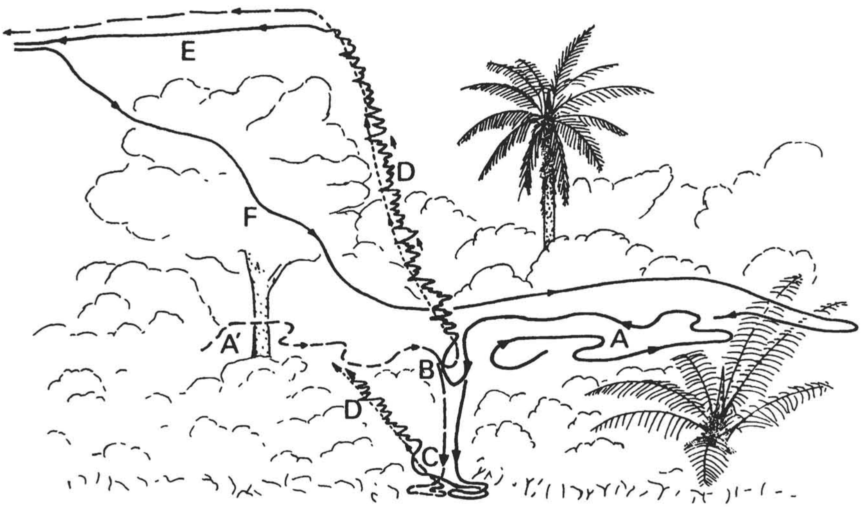

FIG. 1. Typical territorial interaction in *Heliconius sara* at Serra dos Carajás, Pará, Brazil. Resident *H. sara* (solid line) promenades (A) or perches on territory while intruder (broken line, segment length approximately proportional to intruder velocity) patrols along forest margin (A'). One or both butterflies attack, with resident attempting to get below invader (B) and both butterflies sometimes diving to ground where they circle adjacent to one another (C). Intruder starts flying slowly upwards with resident darting back and forth below and behind it (D) until reaching tree-top level where invader may dash away with resident in pursuit (E). Resident returns to territory where it flies briskly over core and peripheral areas as it resumes promenading (F).

generally after a few 10s of seconds, flying briskly over the core and peripheral areas before resuming usual patrolling. Fig. 1 schematizes an ejection sequence in *H. sara*.

Evasive diving in intruding *H. sara* typically led to ground circling, which we interpret as an endurance contest to determine territorial possession. Although in the sequences we observed, territorial residents seemed always to expel invaders, extended contests, sometimes involving several butterflies, were witnessed just before and after changes in ownership. Twice in 1986 and once in 1987, an intruding *H. sara* was seen to attack a promenading resident which dove into the undergrowth. In each of these cases, the trespasser shortly left the area, and the submissive individual resumed patrolling, suggesting that downward dives may also aid less capable males in retaining territories, at least temporarily.

In *Heliconius leucadia*, agonistic territorial behavior seems less complex than in *H. sara*. After the initial rush at an intruder, the resident may expel it by simply following it off the territory from approximately ½ m below and behind. These tandem flights were often leisurely, and

TABLE 2. Behavior of *Eueides tales* during territorial interactions at Serra dos Carajás, Pará, Brazil during 1986 (n = 44) and 1987 (n = 31).

	Behavior of intruder			
	Interaction initiated by resident		Interaction initiated by intruder	
Behavior of resident	Slow departure	Rapid departure	Slow departure	Rapid departure
Chase or following	9	49	1	9
No chase or following	0	1	1	5

normally passed over bounding vegetation, sometimes attaining a height of 15–20 m before the resident suddenly and spontaneously disengaged. At Area 3 one resident often returned to the vicinity of its territory by means of spectacular 40-m-long glides.

Although more or less rapid, apparently aggressive expulsions were common in each of the three main species studied here, we did not observe spiraling pursuits of the type reported for other Lepidoptera (Baker 1983, Fitzpatrick & Wellington 1983). In *H. leucadia*, vigorous circular chases were accompanied by sounds of wing contact indicative of physical combat.

The leisurely exit of trespassing *H. sara* and *leucadia*, when being conducted from a territory by its owner, is almost certainly a form of appeasement behavior, behavior functioning to "inhibit or reduce aggression . . . where escape is impossible or disadvantageous" (McFarland 1981:17). Territorial defense in butterflies typically consists of direct combat, with the dominant positioning itself above its opponent and striking at it with its wings (Fitzpatrick & Wellington 1983, Wickman & Wiklund 1983). In the *Heliconius* studied by us, rapidly flying invaders may be vigorously pursued and perhaps hit by territory holders. In contrast, the slow ejections of heliconiines involve neither aggressive pursuit nor physical combat, and slow intruder movements, perhaps in concert with other behavior, seem to signal submission and stimulate "escort" behavior. Serious challenges are apparently resolved by endurance contests (within a context of appeasement) in *H. sara* and by brief but violent combats in *H. leucadia*.

Trespassing *Eueides tales* usually fled from a territory with the resident in pursuit, although often an intruder left slowly with the resident merely following (Table 2). Less commonly, intruders initiated interactions by flying at residents, but these were usually attacked in return or withdrew rapidly without being chased or followed. When a trespasser being followed from a territory got more than about ½ m ahead of the resident, or entered into foliage, the owner normally dashed after it, which at times provoked a high-speed chase.

Intruding male *E. tales* sometimes evaded pursuit by alighting on leaves. In the seven instances of landing by escorted butterflies, the resident flew agitatedly around the point of last contact. However, only once did the resident find the perched intruder, and in this case dislodge it, apparently by butting and landing on it. In two instances, landing intruders succeeded in fleeing unmolested, and in four, they returned to the territory where the resident found and expelled each once again.

On five occasions an attacked butterfly, rather than flee or retaliate against its aggressor, assumed a descending gliding flight with its wings partially folded. This posture, apparently starting with the attacked individual, seemed to be copied by the attacker which trailed about 20–40 cm above and behind in descending flight. As the butterflies drifted downwards, the lead individual sometimes switched places by darting swiftly behind the trailing one, or one chased the other back up to patrolling altitude, initiating another descent, or chased it off the territory in an expulsion. Although sample sizes are small, data from 1987 suggest that glide chases may occur more frequently when invaders challenge residents (3 times in 7 attacks) than the converse (2 times in 25 attacks). One of the two observed cases of a resident *E. tales* losing its territory to an intruder followed an intruder-initiated attack and 4–5 glide sequences. Glide chases in *E. tales* seem to be ritualized territorial pursuits and, like ground circling in *H. sara,* may constitute assessment behavior that helps resolve disputes in lieu of potentially injurious combat.

Territorial defense. Territorial defense in the heliconines studied at Carajás was concentrated in the late morning (Table 1) with *Eueides tales* and exceptional *Heliconius sara* continuing as late as 1245 h. At Area 1 where territorial males of all three species flew, *H. leucadia* promenaded somewhat lower (about 3–4.5 m from the ground) than *H. sara* (4–5 m) and *E. tales* (5–6 m). The percentage of time spent in promenade flight ranged from less than 50% in *sara* to more than 90% in *tales* (Table 1). *Eueides tales* seemed to glide more than the two *Heliconius* species, perhaps assisted by its smaller size and the generally stronger breezes higher up and around mid-day.

During defense, territory owners typically clashed with conspecifics from 3 to 12 or more times/h, depending on the frequency of intrusions (Table 1). Intruders were almost always successfully intercepted; we have only one record of a probable intruder *H. leucadia* crossing a territory apparently unseen by the perched resident.

Each species had territory holders that rarely lost contests. In *H. sara,* one territory owner marked in 1986 and two marked in 1987 were observed to win all of their 52 conflicts with intruders (Table 1). One of these (1987, Area 4) additionally ejected another male that had set up a territory during a temporary absence. A resident briefly observed at Area 5 also dispossessed a newcomer that took over its territory after it was captured for marking. The two individually recognizable *H. leucadia* won the 97 clashes with trespassers, and in addition, each twice evicted newcomers that took up residence when the owner was away. A marked *E. tales* won 33 of its 34 territorial clashes, and of the 23 conflicts involving unmarked butterflies in 1987, only 1 was for certain lost by the resident butterfly. Reconquest of territories from subsidiary residents was not observed in *E. tales*.

The two *Heliconius* species usually returned to defend the same territory on successive days. The marked *H. leucadia* at Area 1 was observed defending on all nine visits over 19 days, and the Area 3 resident on all six visits over the last eight days we were at Carajás. The latter stayed in Area 3 at least 20 days after marking. On the last day of observation, the Area 3 resident patrolled for only 7 min, and the Area 1 butterfly did not appear. The *H. sara* at Area 3 defended on all seven visits made over the 11 days following marking. An *H. sara* at Area 4 apparently abandoned the territory after being marked, but returned in the role of owner 10 and 11 days later. Similarly, a butterfly at Area 6 took up residence 15 days after it was marked. The marked *E. tales* that returned to defend the Area 1 territory in 1987 was among the defenders present during visits made on three of the four days following marking. On day 4 it was evicted by an intruder and did not reappear on day 5.

The limited nature of territories is indicated by the rapidity with which newcomers reoccupied those left vacant. Three *Heliconius sara* removed from territories at Areas 4, 5 and 6 at N-1 were replaced in 3, 11, and <30 min, respectively. Three others taken from territories at Areas 1 and 2 were replaced by unmarked *H. sara* on the same or following days. On 7 of the 15 occasions in which an identifiable *H. leucadia* left or was removed from a territory (including final daily departures), another individual took up patrolling within 10 min. On the five occasions in 1987 that a *Eueides tales* territory became vacant before noon, a new resident took up promenading within 7 min. Territorial *E. tales* netted in 1986 were also rapidly replaced by newcomers.

The similarity in time intervals between expulsions and that required to reoccupy a vacant territory suggests that most intruders are floating males seeking territories. Intrusion rates in *H. sara* and *H. leucadia* seemed to decline during the morning (Figs. 2 and 3), perhaps because floaters took up searching for mates in other habitats.

Territorial heliconiines usually dashed after any large butterfly passing by. With non-conspecifics, chases normally terminated when the owner came within 10–30 cm of the intruder. Butterflies pursued in this manner included a number of heliconiines, including the other territorial species, and pierids. Heterospecific interactions between similarly patterned *H. sara*, *H. leucadia* and *H. wallacei* Reakirt often included mutual "on-and-off" chasing that, in the first pair of species, sometimes occurred across a territorial boundary in Area 3. We interpret this case of interspecific territoriality as a nonadaptive result of imperfect species recognition (Murray 1971). The *H. sara* and *H. leucadia* at Area 1 simultaneously occupied broadly overlapping territories without markedly interfering with one another. Both *E. tales* and *H. sara* darted after falling leaves, and one of the latter pursued a large bee, and another flew 8–10 m upwards eight times in succession in the direction of lesser yellow-headed vultures (*Cathartes burrovianus* Cassin) gliding low overhead. Apparently a combination of color, apparent size, form, and movement stimulates inspection flights in *H. sara* without the intervention of physical proximity or chemical stimuli.

In 1987, the marked territorial *H. sara* at Areas 3 and 4 each once courted and was rejected by a female, and a marked male patrolling Area 5 was seen to chase a probable female. Before systematic observations were begun, a recently emerged female *H. sara* was found copulating in undergrowth immediately adjacent to Area 5. The marked *H. leucadia* at Area 3 was also observed courting a female. In one encounter, which may represent a courtship flight, the other marked *H. leucadia* at Area 1, rather than follow the intruder from behind, flew 30 cm almost directly below it with rapid wing beats and darting flight reminiscent of the ascending expulsion flight of *H. sara*. The pair rose approximately 20 m directly overhead before drifting out of sight behind trees. The resident returned 14 min later, ousted an unmarked individual that had taken up promenading in the meantime, and resumed patrolling. In 1986 a courtship involving a male *E. tales* of unknown status was observed at Area 1.

Territoriality in other heliconiines. Territorial behavior in *Eueides aliphera* was noted in 1967 in a weedy coffee field 5 km S of San Vito, Puntarenas Province, Costa Rica. One of the several *E. aliphera* present on 27 April, flying about 1 m above the vegetation, seemed especially pugnacious, and dashed after *Heliconius charitonia* (L.), *Hypanartia lethe* (Fabr.), and on three occasions after other *E. aliphera*, in 18 min of observation. A male *E. aliphera* color-marked at the site 5 days later was re-encountered defending a territory at the same place on the six visits made over the next 19 days. This *E. aliphera* won all combats with natural intruders (Table 1) in addition to one with an apparently territorial male that was experimentally herded onto the marked butterfly's territory. The resident attacked and chased this insect into the underbrush. In encounters with other species, the territorial *E. aliphera*

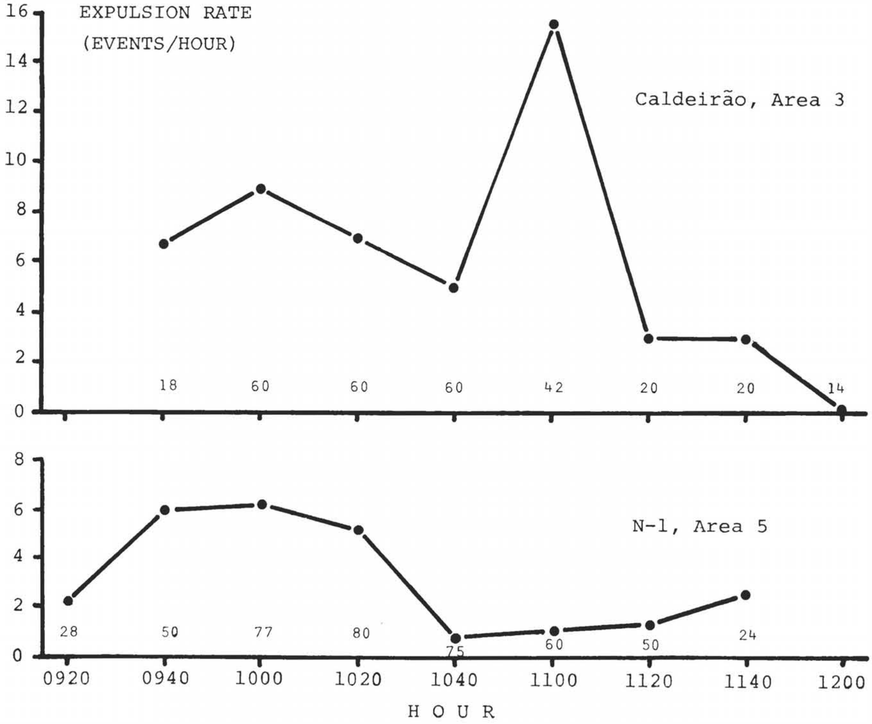

FIG. 2. Expulsion rates for territorial *Heliconius sara* at Serra dos Carajás, Pará, Brazil. Results grouped for intervals of 20 min. Numbers above abscissa show minutes of observation in time interval.

immediately turned away; however, conspecifics were vigorously pursued with pairs usually rising 10–15 m into the air and speeding off the territory. After flying well outside the patrolled area—pairs sometimes flew out of sight—the resident disengaged and returned to the territory. All chases were energetic, and "escorting" analogous to that recorded in other heliconiines was not observed.

The marked butterfly arrived on the territory as early as 0830 and 0910 h, and departures were as late as 1433 h during sunny weather. On one afternoon, the *E. aliphera* flew off the territory and over the canopy of neighboring forest about 50 m away three times during cloudy periods, and returned to patrol during intervening sunny spells.

The territory of the marked *E. aliphera* contained larval food-plant (*Passiflora oerstedii* Mast. *in* Mart.) with immature stages. An *E. aliphera* observed in August 1985 near Serra Norte, Brazil, promenaded above a roadside tangle of *Passiflora* vines on which *E. aliphera* larvae were also feeding. The territories of other heliconiines studied at Cal-

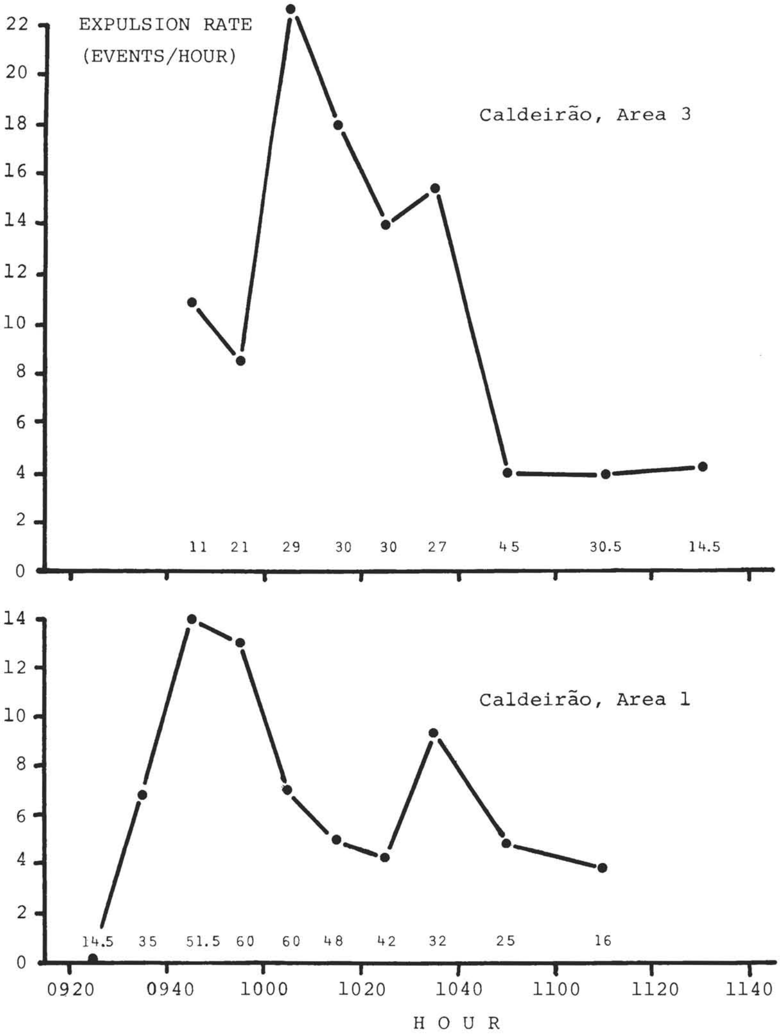

FIG. 3. Expulsion rates for territorial *Heliconius leucadia* at Caldeirão, Serra dos Carajás, Pará, Brazil. Results grouped for intervals of 10 or 20 min. Numbers above abscissa show minutes of observation in time interval.

deirão lacked larval food-plants, although at N-1 an *H. sara* host, *Passiflora* (*Astrophea*) sp., was abundant next to Area 5. This situation seems fortuitous.

Territoriality probably occurs in other heliconiines. In January 1968 near Huixtla, Chiapas, Mexico, two well separated *Eueides isabella* (Cramer) were briefly observed while tracing 10–15-m-long paths over low vegetation in a roadside ravine. Each shared its space with a single similarly behaving *E. aliphera*, although the latter flew somewhat lower (1 m vs. 2 m) above the vegetation. On approaching within 2–3 m of each other, one butterfly would occasionally dash at the other without chasing it. *Heliconius ricini* (L.) promenades in Trinidad (W. W. Benson field notes), and at Caldeirão appears to defend spaces over the forest canopy. *Heliconius antiochus* (L.) at Caldeirão is both aggressive and site-tenacious, and may be territorial. However, *Eueides vibilia* (Godart) promenading near N-1 did not fight or expel closely approaching conspecifics. Seitz (1913) reported promenading to be especially well developed in *E. aliphera*, *E. isabella* and *Philaethria dido* (L.). We have detected no sign of promenading or area defense in *Heliconius erato* (L.), *H. melpomene* (L.), *H. wallacei*, *Eueides lybia* (Fabr.), or *Dryas iulia* (Fabr.) at any locality.

DISCUSSION

The heliconiines studied here are clearly territorial. Conspecific males rarely remained together in a promenade area longer than the few seconds necessary for the resident to find and expel the encroacher. In the absence of an owner, territories were rapidly taken over, and the time for this to occur was comparable to the average interval between intrusions, suggesting that most intruders are territory-seekers. In three species, both residents and invaders seem to possess a repertory of species-specific behaviors for use during territorial confrontations.

Territoriality in butterflies seems based on male defense of encounter sites where chances of mating are high (Baker 1983, Wickman 1985b, Courtney & Anderson 1986). The territorial heliconiines studied by us probably also defend rendezvous points. Although we observed few courtships and no matings by known territorial males, female heliconiines seem often to mate only once (Crane 1957, Gilbert 1976), and their rarity is expected in long-lived insects that mate infrequently (Alcock 1983). The places defended by *Heliconius sara*, *H. leucadia* and *Eueides tales* are humid, sunny, and seem protected from wind, and possibly attract receptive females. *Eueides aliphera* defends more exposed sites, and its territoriality may be in part based on the despotic control of host-plant patches where females are likely to emerge.

Territorial combat in heliconiines contrasts greatly with courtship. In *Heliconius sara* and related species, courting males hover above and in front of females (Crane 1957, pers. obs.). Territorial males fly below intruders or harass or "escort" them from behind. Owner behavior seems adaptive since intruders are denied searching foliage for receptive mates, taking the profit out of trespassing. However, trespassing and skirmishing may still benefit interlopers in assessing vacancies and discovering weak residents (Lederhouse 1982, Wickman & Wiklund 1983, Grafen 1987).

Promenading heliconiines fly slowly and seemingly with little effort through their territories. Butterflies are conspicuously exposed under such circumstances, and aposematic unpalatability in *H. sara* (Brower et al. 1963), and probably the other species studied, must compensate for much of the added risk of predator attack. Butterflies that are profitable prey may be selected to reduce conspicuousness by perching more, or to reduce catchability by patrolling territories using energetically costly acrobatic flight, or both.

Recent works on territoriality (Bitzer & Shaw 1983, Wickman 1985a, Dennis & Williams 1987, Shreeve 1987) equate Scott's (1974) terms "perching" and "patrolling" with territorial and nomadic mating strategies, respectively. Although this terminology is misleading when applied to a species such as *Eueides tales,* which spends more than 90% of its time in patrolling flight and combats, it is probably too intrenched to change. Promenading, *sensu* Seitz (1913), may be a useful alternative to designate site-faithful patrolling.

Given the prowess of resident *Heliconius sara* and *H. leucadia* in rivalries, unrestrained fights may be risky. The fact that intruders often flee, flying at what seems to be maximum speed, suggests that some chance of injury exists. The submissive stance of many intercepted intruders is noteworthy, and, combined with a less aggressive dominance of the resident, results in slow but safe and effective expulsions. To our knowledge these are the first reports of stereotyped appeasement behavior in butterflies, and one of the few among nonsocial insects (Fitzpatrick & Wellington 1983). They are also apparently the only known cases of relatively pacific dominance relations inserted in territorial behavior sequences.

The ground-circling behavior of *H. sara* seemed to help submissive individuals avoid ejection, and may be, as appears with the glide chases of *E. tales,* a ritualized contest used to decide territorial ownership. Whatever their precise origins and functions, these behaviors are clearly tied to presumably adaptive defense of territory.

Territoriality in *Heliconius sara* and *H. leucadia* is not simply explained by current hypotheses. In general, female attraction to encounter sites (and competition for them by males) is thought to stem from male rarity and the increased speed of mating permitted by their use (Shields 1968, Lederhouse 1982, Alcock & O'Neill 1986). However, nonterritorial male *H. sara* and *H. leucadia* were common in our study, and *sara* is frequently abundant throughout its range, suggesting that isolated females would be quickly found and mated and that rendezvous sites may be superfluous. On the other hand, the known territorial

Heliconius lay eggs in batches that give rise to synchronously developing groups of larvae. It seems likely that emergence of large broods of females in these species may commonly overtax mating capacity of local males and result in pulses of virgin females that might profitably seek mates at encounter sites. The importance of intrasexual competition among females is manifest in the use of what is apparently an aggregating sex pheromone by female pupae of *H. sara* (W. W. Benson field notes), similar to that of the related *H. charitonia* (Edwards 1881, Gilbert 1975) and *H. hewitsoni* Staudinger (J. T. Longino *in* DeVries 1987). Pupal pheromone production may aggravate mate shortages by concentrating males at pupation sites well ahead of mating. We believe that common heliconiines that lay solitary eggs would tend to have a more uniform production of, and a more assured rapid mating of, receptive females, and thus tend not to be territorial. Territoriality in *Eueides tales* and *E. aliphera* may be explained by current theory.

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