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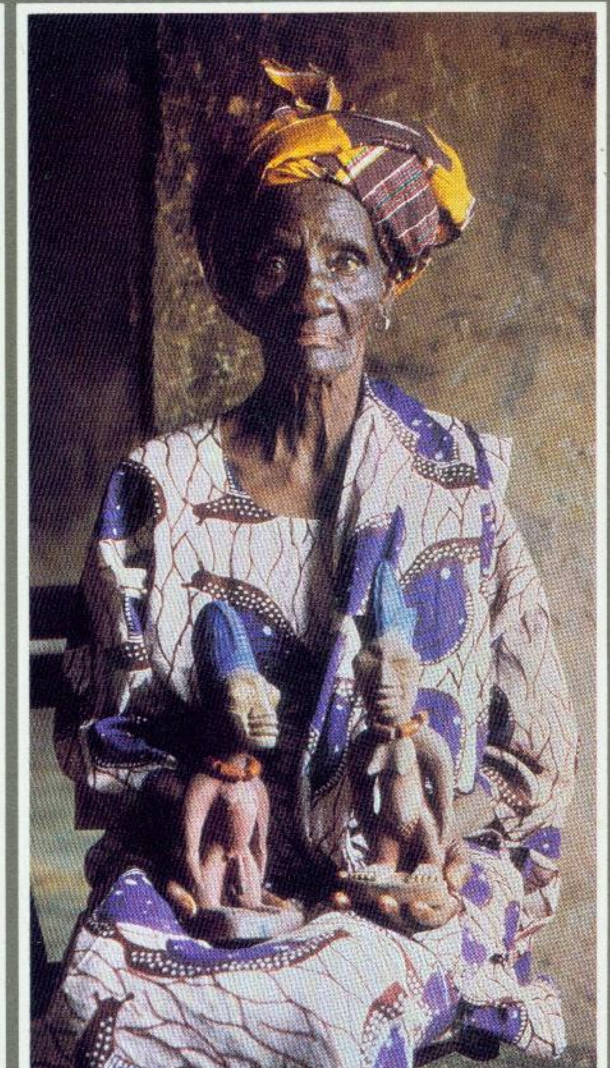

GREGARIOUS BUTTERFLIES □
YORUBA RITUAL □ DINOSAUR EVOLUTION □
TROPICAL ISLAND WATER BALANCE

James Mallet

Gregarious Roosting and Home Range in *Heliconius* Butterflies

Individual Heliconius *butterflies fly within a restricted area by day and roost gregariously at night. In preroosting gatherings, individuals "fan" already roosted conspecifics. Fanning does not have an aggressive function, as has been previously suggested; it is a courtshiplike behavior, although it never leads to mating. The behavior occurs with high frequency just before roosting and torpidity, rather than during the day when mating takes place. Individuals also fan dead individuals of their own and other species, and even crude cardboard models. Fanning is probably a means of testing for species-specific stimuli that enable individuals to aggregate.*

Roosts of H. erato *do not consist of discrete family groups; both teneral and older butterflies disperse among roosting groups. The home ranges of individual* erato *are independent of those of their roostmates, and frequently overlap with home ranges of individuals from other roosts. The loose population structure found in* erato *contrasts with that required for kin selection models of the evolution of warning color and unpalatability.*

There is little predation of Heliconius *near the roost, but foraging birds often disturb* erato *during the early morning, before the roosts disperse. The selective value of gregarious roosting is discussed.*

James Mallet *(The Galton Laboratory, Department of Genetics and Biometry, University College London, Wolfson House, London NW1 2HE, United Kingdom) studied* Heliconius *while at the Department of Zoology, University of Texas, Austin. The author has worked on the ecology, behavior, and genetics of heliconiine butterflies in Mexico, Costa Rica, Panama, Colombia, Venezuela, Guyana, and Ecuador. He is currently investigating the genetics of hybrid zones between races of* Heliconius *in Peru.*

Heliconius butterflies inhabit tropical forests and woods from the southern United States to Argentina. Their long wings, which allow a lazy, hovering flight, are usually black with gaudy patches of red, orange, yellow, white, or iridescent blue. The bright colors and slow flight of *Heliconius* act as signals that warn potential predators of their distastefulness (Boyden 1976, Brower et al. 1963), and most *Heliconius* species are müllerian mimics of other *Heliconius* or of distasteful butterflies in the subfamily Ithomiinae (Turner 1981).

After a brief teneral period, adult *Heliconius* are reproductively active for as long as six months, because they can collect and feed on protein-rich pollen (Dunlap-Pianka et al. 1977; Gilbert 1972, 1975). *Heliconius* collect pollen and nectar from a variety of flowers, but some species collect pollen almost exclusively from the vines *Psiguria* and *Gurania* (Cucurbitaceae) (Figure 1) (Boggs et al. 1981, Gilbert 1975). Marked individual *Heliconius* repeatedly return to the same clumps of *Psiguria* and larval host plants (*Passiflora*), and at night they roost gregariously at repeatedly used sites (Brown 1981, Cook et al. 1976, Mallet & Jackson 1980, Murawski & Gilbert in press, Turner 1981). Individuals fly, feed, and roost in what could be called a home range (Turner 1971a), a term

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Figure 1. Heliconius pachinus *visiting a flower of* Psiguria warscewiczii *at Sirena, Costa Rica. A blob of white pollen mixed with nectar can be seen on the butterfly's coiled proboscis.*

borrowed from studies of mammalian behavior (Burt 1943).

These seemingly complex behaviors of *Heliconius* suggested other possible parallels with the social behavior of vertebrates and social insects. If the individuals roosting together were closely related, as seemed likely from the limited dispersal movements of marked adults, social traits involving altruism and kin selection could have evolved (Benson 1971; Gilbert 1975, 1977; Turner 1971a, b). These speculations have been widely cited in reviews of the evolution of distastefulness and warning color (Brown 1981, Edmunds 1974, Harvey & Greenwood 1978, Hiam 1982, Wilson 1975). In fact, no previous studies combine data on gregarious roosting with accurate mapping of the daily movements of individual butterflies. The most detailed field studies of gregarious roosting are on *H. charitonia* (Beebe 1949, Cook et al. 1976, Edwards 1881, Jones 1930, Poulton 1931, Waller & Gilbert 1982, Young 1978, Young & Carolan 1976, Young & Thomason 1975), though some observations have been recorded from other species (Benson 1972; Turner 1971a, 1975). In an insectary, Crane (1955, 1957) studied courtship and mating of *H. erato* and other heliconiines, and observed gregarious roosting. In none of these studies was the relationship of roosting and home range behavior explored in any detail, and in only one previous study (Jones 1930) was more than one roost studied simultaneously.

In this study, the roosting habits and home ranges of a number of species of *Heliconius* are recorded. The following specific problems are investigated:

- how individuals gather together to form gregarious roosts;
- the relationship between gregarious roosting and home range, and the population structure of roosting groups; and
- evidence for and against hypotheses to explain gregarious roosting.

Study Sites and Methods

The author found and studied roosts of *erato* for the first time in Villa Garzón, Putumayo, Colombia, in 1977. In this area *erato* are extremely variable in color pattern because the town is in a narrow hybrid zone between highland and lowland races. Almost every individual was recognizable on the roosts and in flight, because of this color pattern variability, and it was in Villa Garzón that interactions between particular individuals were recorded. To test for the effect of color pattern on interactions between flying and roosting individuals, choice experiments were performed in which dead butterflies were pinned up as decoys in pairs near the roosts, and the number of flying individuals that approached each decoy was recorded.

The behavior of *Heliconius* was also studied at Sirena, Parque Nacional Corcovado, Costa Rica, in 1979 to 1981. The area around the park headquarters formed the study site, which consisted of beach habitat next to the Pacific Ocean, second growth near a horse pasture, and a grass airstrip. The area was surrounded by and interspersed with tall, tropical lowland rain forest. The trails in a 3-km^2 area were mapped, and numbered stations were positioned every 50 m. The trails were systematically walked at least once a week, and individuals of seven of the most common species of *Heliconius (erato, charitonia, hewitsoni, melpomene, pachinus, ismenius, hecale)* were captured, marked with unique numbers, and released. The date, time, and site of capture, and the mark number, sex, and wing wear of each individual captured were recorded (Gilbert 1984). Many visits of marked *Heliconius* to *Psiguria* flowers were also recorded without recapturing the butterflies.

Roosts are easiest to find between 1530 and 1745 hours (all roosting observations are relative to a sunset time of approximately 1800), when *Heliconius* begin to gather near their roost sites but still take to the air if disturbed. The species roost at different heights: *erato, melpomene,* and *charitonia* usually roost less than 2 m from the ground, whereas *hecale* and *ismenius* may roost above 10 m in the canopies of medium-sized trees, and *pachinus* and *hewitsoni* roost at intermediate heights (Mallet 1984a). The bulk of the observations were of *erato* because this species is

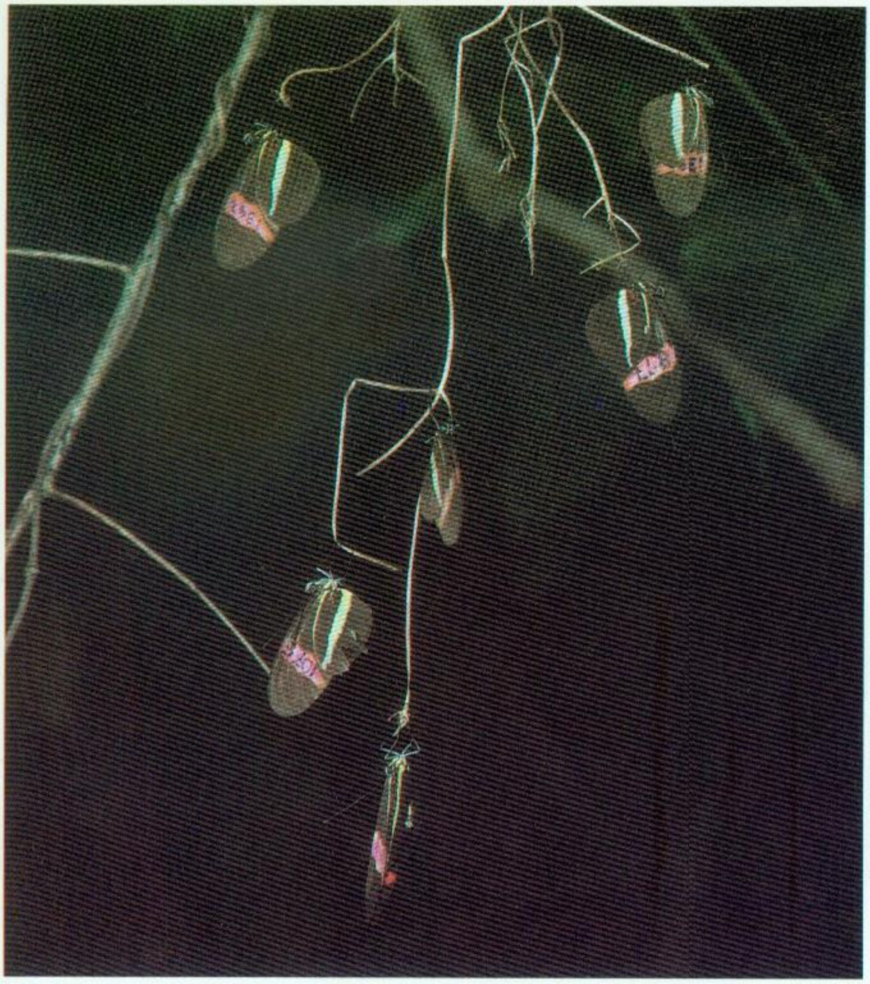

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Figure **2.** *A gregarious roost of* erato *at Sirena. The butterflies with their sides to the camera have all been marked; numbers can be seen on their forewing bands. A female (top right) shows how the underside forewing band is covered by the hindwing. Males nearby hold their forewings forward of their hindwings.*

quite common at Sirena (Gilbert 1984), and because its roosts can be found and easily observed in low vegetation. Binoculars were used to watch butterfly and bird activity at roost sites. In these observations, the author was behind vegetation and as far away from the roost as possible, while still allowing a clear view. Both morning (0530 to 0900) and evening (1600 to 1815) observations were made. In addition, each roost was visited after dark (1900 to 2100) on one or more nights every week, and the occupants identified with the aid of a flashlight.

Results

Roosting

Heliconius roosts consist of fine twigs or tendrils of dead vines, suspended in shady places and with much open space below and around them (e.g., Figure 2). The roosts are normally in deep shade where light is insufficient for green plant survival, and are for this reason free of the ants, centipedes, and other nocturnal predators so abundant on live vegetation in the tropics. Males predominate among individuals that gather at the roost sites, and all of the Sirena species of *Heliconius* had male-biased capture ratios during the day. The reasons for the approximately 2:1 male bias are not clear, as 1:1 ratios are produced in the laboratory (Mallet in press a).

In both Colombia and Costa Rica, individual *erato* begin to congregate near their roost sites at about 1600, or earlier if the weather is cloudy. Laboratory populations of *melpomene* also roost earlier on cloudy days (Mallet 1978). After approaching several perches, a few individuals hang up by their tarsi from the roost, with their wings down and folded. Once one or two *erato* are on the roost, other individuals hover near the twigs and are especially attentive to twigs already occupied by conspecifics (Figure 3).

Fanning

Flying *erato* show various levels of interest in roosted conspecifics, ranging from brief approaches to hovering closely with probable antennal and wing contact ("fanning"), to grasping at the perch or the wings of the roosted butterfly with their tarsal claws ("clutching"). The recipients of these encounters may not react at all, but, if fanned or clutched, they often flap their wings vigorously ("fending off") without letting go of the perch. Young & Carolan (1976) watched similar interactions among roosting *charitonia.* Young & Carolan interpreted fanning as aggressive bids for perches.

If fanning has an aggressive function, it is extraordinarily inefficient: Of 597 observed fannings and clutchings at Villa Garzón, the fanner usurped the other party's twig in only 10 cases. In six of these 10 cases, the usurper did not remain on its hard-won twig, but flew off again, approached and fanned other individuals, and finally rested that night on a different twig nearby. Clutching contacts between a flying and a roosting individual are difficult to distinguish from attempts to hang up on a perch. In fact dead butterflies pinned near the roosts may themselves be used as perches by *melpomene* (Mallet 1978).

Both *erato* and *melpomene* approach and fan roosted members of other species of *Heliconius*, dead *Heliconius* pinned near the roost, and even black-and-white cardboard models (Mallet 1978), though they show most interest in live conspecifics. In *melpomene* the longest interactions occur when a male fans a female conspecific on a roost, and the male exposes his androconial patches in a sequence of movements similar to that shown during diurnal courtship (Mallet 1978). During fending off, *Heliconius* males flutter their wings and expose the androconial patches on their hindwings; females flutter their wings and expose anal scent glands in a behavior similar to that used in diurnal rejection of males (Gilbert 1976), except that it is performed upside down on the roost (Mallet 1978). In Colombia, male *erato* fanned more actively than females; males also fanned more females than males, whereas females fanned males and females in proportion to their abundance (Table 1). Fanning interactions peak at about 1745, when there is usually a rush to the roosts, just before all have roosted.

If fanning were actually courtship, as one reviewer has contended, mating should peak in the preroosting gatherings. In fact, *Heliconius* females are monogamous, or nearly so (Boggs & Gilbert 1979; Crane 1955, 1957), and mate during the mornings, at or very soon after female pupal eclosion (Gilbert 1972, Longino 1984, Mallet in press a). During more than 300 evenings, nights, and early mornings of watching roosts of *erato* in the wild, the author has never seen mating (see also Crane 1955:180); though a male *melpomene* was once seen unsuccessfully attempting copulation with a roosting female in an insectary (Mallet 1978). Fanning by females (Figure 3) may seem to have little relationship to courtship, but female Lepidoptera are now known to solicit mating (Mallet 1984b, Rutowski 1980), and the author has often observed female *Heliconius* in insectaries briefly chase other females as well as males (see also Crane 1955:179).

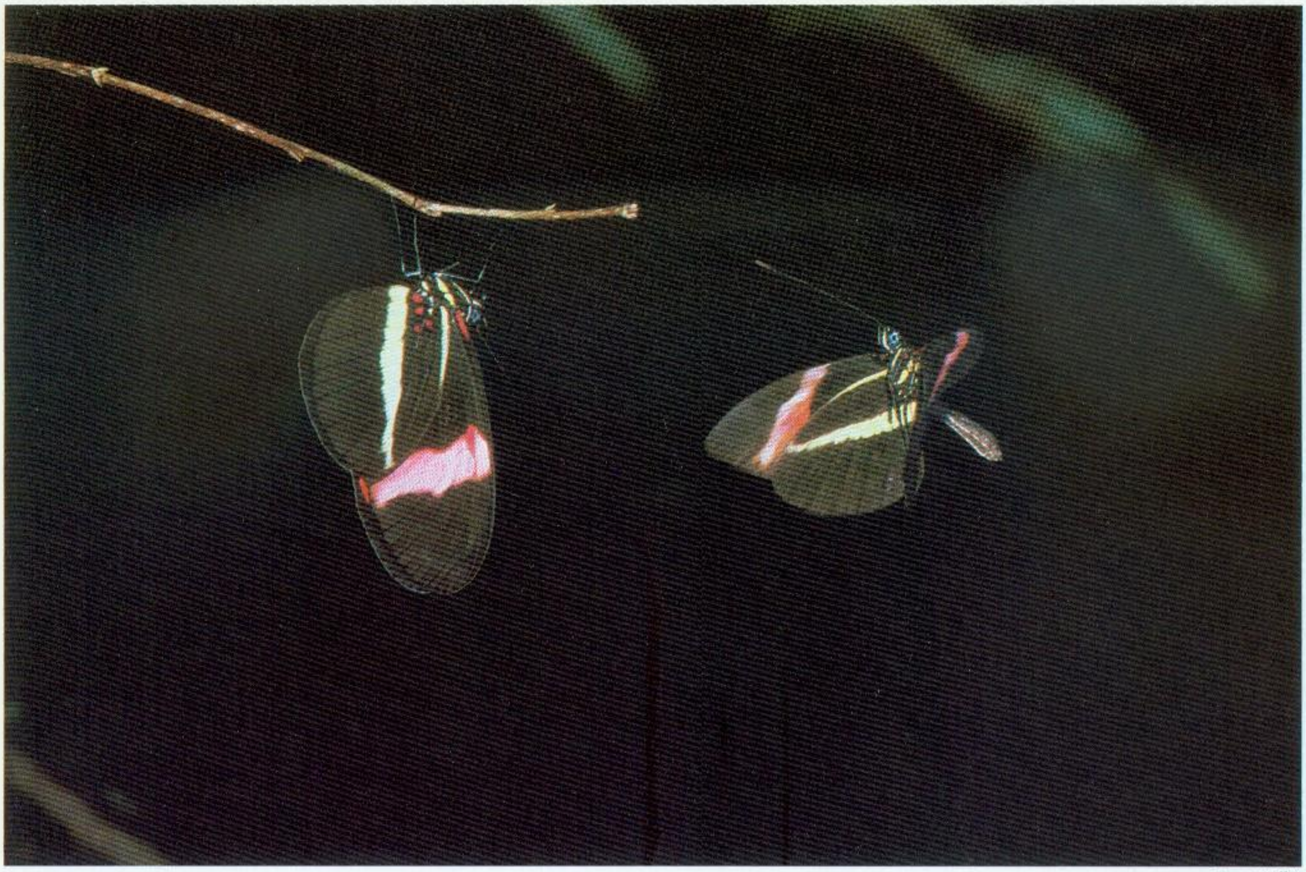

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Figure 3. A female erato *fanning a roosted male. Sirena, Costa Rica.*

Elicitation of Fanning

A peculiar feature of roosting *Heliconius* is that the females retract their forewings so that they are maximally hidden behind their hindwings; in contrast, males hold their forewings fully extended (Figures 2 & 4). This gender-specific roosting posture occurs in all *Heliconius* known to the author, but not in closely related genera such as *Dryas*. Female *Heliconius* maintain their posture only while there is some light; after dark, they relax their wings and appear malelike. At night, a flashlight shone at a roosted female will cause her slowly to reassume her sunset posture, and the same process happens naturally at dawn. Females may also take up this posture when perching upright during the day, and while egg-lay-

Table 1. Fanning Interactions Among *erato on 21 Evenings, Villa Garzón, Colombia, August through September 1977**

FANNINGS RECEIVED FROM MALE FANNERS ($\chi_1^2 = 76, p < 0.0001$):

	By Male Recipients	By Female Recipients	Total
Observed	216	269	485
Expected on basis of sex ratio	309	176	485

FANNINGS RECEIVED FROM FEMALE FANNERS ($\chi_1^2 = 0.20$, n.s.):

	By Male Recipients	By Female Recipients	Total
Observed	69	43	112
Expected on basis of sex ratio	71	41	112

TOTAL NUMBERS OF FANNINGS GIVEN ($\chi_1^2 = 80, p < 0.0001$):

	By Male Fanners	By Female Fanners	Total
Observed	485	112	597
Expected on basis of sex ratio	380	217	597

**Observations were made on 14 males and eight females.*

ing or mating, whereas resting or mating males always rest with forewings fully extended. Experiments show that pale forewing bands are important for inducing approaches, and that the female posture reduces the number of approaches by partially covering the forewing band (Table 2). The female posture may reduce wing wear caused by males' excessive fanning, or it may decrease the visibility of females to predators.

Disturbance of Roosts by Birds

On the morning of 7 January 1979 unidentified birds were seen disturbing a roost of *charitonia* near Gomez Farías, Tamaulipas, Mexico. The roost "exploded" into flying butterflies. After the incident, a single *charitonia* female was found beneath the roost, freshly killed and limp, with one wing missing and beak marks on the remaining wings. Her body was crushed but intact, apparently taste-rejected by one of the birds.

Predation on roosts of *erato* at Sirena was investigated by watching roosts with binoculars on a total of 51 mornings from first light until the roosts were vacated, and on a total of 26 evenings from 1600 to dusk. In a total of 240 butterfly-mornings, 55 butterflies were disturbed by 21 birds and one fruit bat, and, in a total of 129 butterfly-evenings, 10 butterflies were disturbed by three birds and one *Anolis* lizard. The vertebrates that disturbed the butterflies were species that do not usually catch flying insects. Many feed on fruits, seeds, or nectar (though most of them supplement their diet with arthropods). These include doves, a hermit hummingbird, a bananaquit, a tanager, a saltator, sparrows, and the bat. Insectivores, e.g., antbirds, warblers, yellow-billed caciques, and *Anolis,* also disturbed the roosts, but they normally glean insects from foliage, or search for prey in rolled leaves or hollow stems. (The species of birds and disturbance rates are given in Mallet 1984a.)

Leaving the Roost

Roosted individuals spend the whole night on the roost unless they are disturbed by storms or animals. The eyes of roosting *Heliconius* do not

Table 2. Approach or Fanning by *erato* to Decoys, Villa Garzón, Colombia, August 1977

APPROACHES TO UNALTERED *ERATO* DECOYS:*

Roost Site	Date	Male with Forewing Band Displayed	Female with Forewing Band Partially Hidden	Statistic Used to Test for Preference, and *p* Value
B	23 August	7	2	binomial, $p = 0.18$
C	23 August	31	1	$\chi^2_1 = 28.1, p < 0.001$

APPROACHES TO ALTERED *ERATO* DECOYS:†

Roost Site	Date	Controls	Experimentals	Statistic Used, and *p* Value
B	24 August	18	5	$\chi^2_1 = 7.3, p < 0.01$
B	25 August	8	0	binomial, $p = 0.0078$
C	24 August	35	0	$\chi^2_1 = 24.6, p < 0.001$
C	25 August	30	5	$\chi^2_1 = 17.9, p < 0.001$

Each row represents a single evening's observation period at a roost from about 1630 to 1815 hours. Paired choice experiments were controlled for the effect of orientation; if a particular choice was arranged left to right, the other of the pair was arranged right to left. χ^2_1 *tests were used to test for deviations from a 1:1 choice ratio (if sample sizes were too low, a two-tailed binomial test was used).*

**Dead males in male roosting posture (forewing band displayed) versus dead females in female roosting posture (forewing band partially hidden).*

†Dead males in male posture with pale forewing bars blacked out by marking pen (experimentals) versus dead males in male posture with forewing bands untouched, but with black parts of underside marked black (controls).

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Figure 4. A female sara *(left) roosting with a male* wallacei *(no. 5, right). Different species of* Heliconius *sometimes roost together, and often (as in this case) these are müllerian mimics. Villa Garzón, Colombia.*

reflect flashlight beams (in contrast, nocturnal mammals and nocturnal or crepuscular brassolid and hesperiid butterflies have this eyeshine), which suggests that *Heliconius* lack the ability to adapt to night vision. In the morning, individual *erato* leave the roosts one at a time or, if a butterfly disturbs its roostmates, in small groups. They perch solitarily in nearby open areas, with wings open and their dorsal surfaces toward the sun (if it is shining). After basking, they fly off singly, and begin to forage at *Psiguria* or other flowers.

Home Range and Roost Fidelity in *erato*

In 1980, as many as seven *erato* roosted at a site between the southwestern corner of the Sirena horse pasture and the airstrip. These included: two butterflies (e.g., Figure 5A) that repeatedly flew across the airstrip and adjacent forest to visit flowers of *Psiguria* in a small tree-fall, one that repeatedly crossed the airstrip but remained at *Lantana* flowers near the western edge of the strip (Figure 5B), two that repeatedly visited *Psiguria* and other flowers at the southern edge of the horse pasture (Figure 5C, D), and one that visited *Psiguria* at the northwestern corner of the pasture (Figure 5E).

At the time of the observations in Figure 5A–E, individuals from two separate roost sites near the beach (Figure 5F, G), and at a roost site near the south end of the airstrip (Figure 5H) were also repeatedly seen feeding at *Psiguria* in the forest tree-fall. One of these (Figure 5F) was seen moving to and fro between two *Psiguria* sites on each of three consecutive days; this kind of behavior has been termed "traplining" by Janzen (1971) and Gilbert (1975). These individuals usually roosted with conspecific roostmates that were never seen to enter the tree-fall (Mallet 1984a). Clearly, roostmates do not hold communal, exclusive home ranges, nor is there any evidence for territoriality. These conclusions are firmly based: Only a few individuals with more than 20 sighting or capture records are figured here, but the home ranges of many other *erato* from other roosts confirm these results (Mallet 1984a).

The home ranges of the individuals in Figure 5A, F–H are unusually large, probably because these butterflies must traverse a large stretch of forest to the tree-fall *Psiguria* sites. The average home range movement is about 100 m, like those in Figure 5C, D (see also Mallet 1984a, in press a; Murawski & Gilbert in press). The record home range movements that the author has observed were by a female *hewitsoni*. This butterfly repeatedly moved more than 1.2 km each way between her roost site and a larval host plant *(Passiflora pittieri)* on which she laid eggs during the day. These movements are unusually long for *hewitsoni*.

On average, *erato* return to the previous night's roost 72% of the time, but some individuals are extremely faithful to particular roost sites, while others may often switch among roost sites. Data for one roosting group are shown in Table 3. For example, individual no. 11345 (Figure 5B, Table 3) switched among four separate roost sites. In Jones' (1930)

Table 3. Fidelity of *erato* Roosting at Southwest Corner of Pasture, Sirena, Costa Rica, June to July 1980

Individual No. (Sex)	No. Nights Roost Unchanged	No. Nights Roost Changed	Home Range Diagram
1812 (♂)	26	2	Figure 5A
1858 (♂)	10	0	Mallet 1984a
11412 (♂)	28	2	Mallet 1984a
11345 (♂)	9	16	Figure 5B
11085 (♂)	11	2	Mallet 1984a
11009 (♂)	28	4	Figure 5C
1930 (♂)	8	8	Mallet 1984a
11076 (♂)	14	2	Mallet 1984a
1906 (♀)	15	2	Figure 5D
11078 (♂)	20	6	Figure 5E
Total	169	44	

Average fidelity = $169/(169 + 44) = 79\%$; *homogeneity test of individual fidelities:* $\chi^2_9 = 49.4$, $p < 0.001$; *homogeneity test (excluding individuals with expected values* < 5*):* $\chi^2_4 = 35.9$, $p < 0.001$

words, many of these butterflies "maintained more than one establishment." Neither sex nor age can explain these fidelity differences (Table 4). Apparently individual butterflies have "personalities."

Since individuals that are faithful to the same roost have different home ranges, the environment of the roost site alone cannot be forcing the daily movements: Individuals have a home range in the true sense of the term that Burt (1943) applied to mammals. When Jones (1930) moved the roost twigs of *charitonia* a few meters away and replaced them with different twigs, the butterflies returned to the old site and roosted on the new twigs rather than seeking out the original twigs. This experiment was repeated using Colombian *erato* during the present study, with the same result. Therefore *Heliconius* likely use memory, rather than scent-marking, to guide their movements between roost sites and foraging areas, which may be 1 km apart. In contrast, newly emerged *Heliconius* can have no memory of roosting or foraging sites. At Sirena, teneral *erato* frequently moved beyond the home ranges of their parents before setting up their own home ranges, and joining or founding a roost site (Mallet 1984a, in press a). Foreign individuals can join established roosts. In Colombia, eight *erato* were transferred 5 km to a site with known roosts: Half were repeatedly recaptured; three of these were observed roosting gregariously with the residents.

Comparisons Among Species

All known species of *Heliconius* have restricted home ranges (Gilbert 1984, Murawski & Gilbert in press), but they differ strongly in the extent to which they roost gregariously. Some species, such as *charitonia* (see front cover) and *sara*, cluster tightly, with individuals roosting many to a twig, often holding onto each other's legs. In contrast, *erato* usually roost close together, but often with only one to a twig tip at Sirena (Figure 2). In Mexico and Colombia, *erato* may roost in large groups containing at least some linear nontouching arrays of as many as five individuals per twig (Figure 6). On the other hand, *hewitsoni* (Figure 7) roosts gregariously with individuals separated by distances as great as 1 m; the same is true of *melpomene* and its close relatives *pachinus*, *cydno*, *ismenius*, and *hecale*.

Species also differ in the size of their roosting groups, and in the proportion of individuals that roost gregariously (Table 5). The *melpomene* group of species is less gregarious than the *erato* group of species (see Brown 1981 for phylogeny). The measures of gregariousness used in Table 5 likely depend partly on population density, so it is remarkable that

Table 4. Roost Fidelity of *erato*, Sirena, Costa Rica, June to August 1980 ($N = 50$)

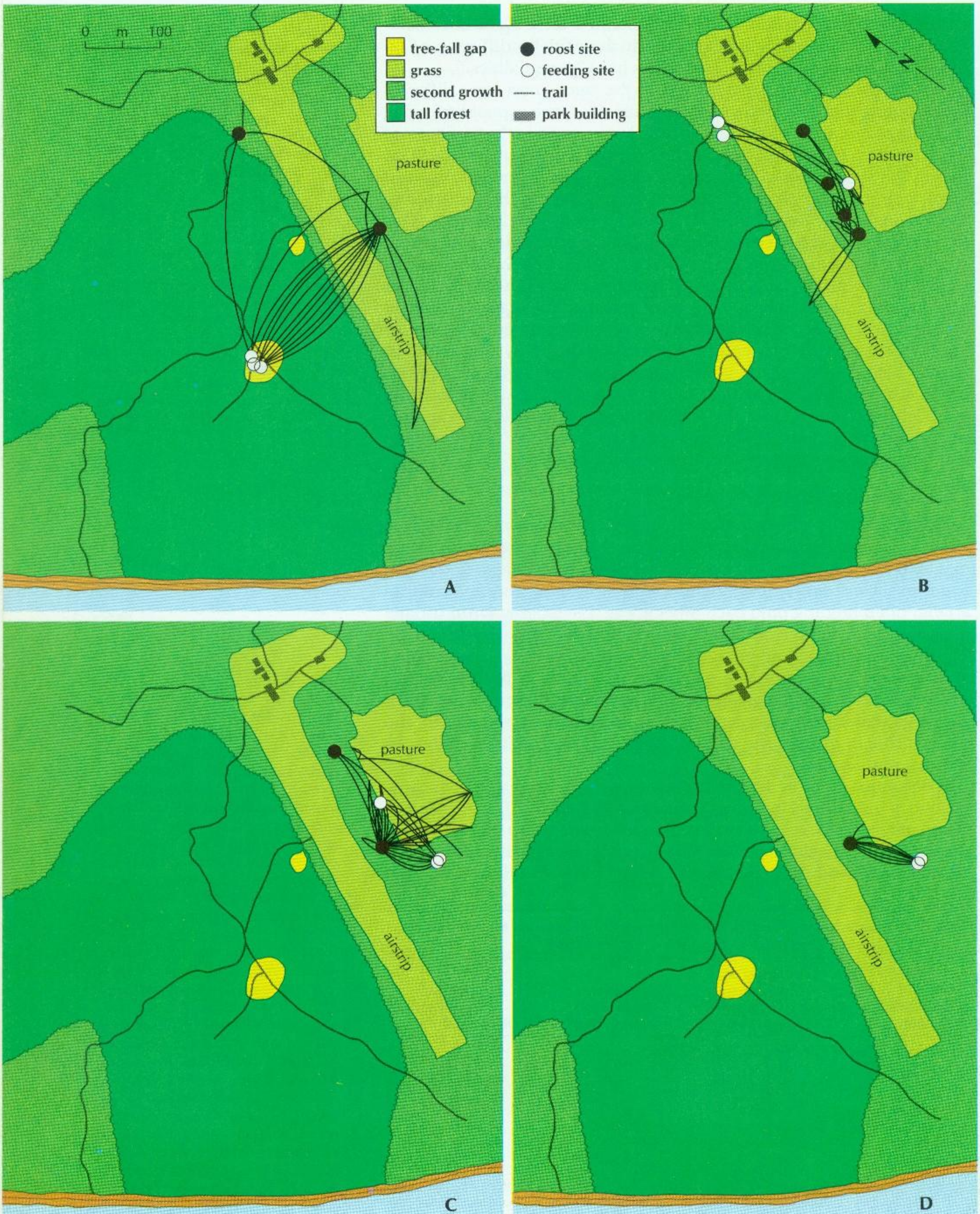
Overall average:	72%
By sex:	
Males	72%
Females	73%
By wing-wear class:	
Fresh	73%
Intermediate	72%
Worn	68%

Fidelity (Table 3) is calculated by dividing the total number of nights with no change of roost site by the total number of nights for which a change could have been observed. Individuals for which a change of roost site could have been observed on less than 10 nights have been excluded. Differences in fidelity between sexes, wing-wear classes, or roost sites were not significant. However, individuals within these categories were highly heterogeneous (see also Mallet 1984a).

Table 5. Gregariousness of Different Species of *Heliconius*, Sirena and Llorona, Corcovado, Costa Rica, 1979 to 1981

Species Group Species	Proportion of Individuals Seen Roosting Gregariously at Least Once	Mean No. Individuals Roosting Together	Total No. Individuals Observed Roosting
melpomene group			
ismenius	0.29	1.3	14
hecale	0.62	2.5	29
pachinus	0.44	1.8	57
melpomene	0.42	1.5	33
erato group			
charitonia	0.86	2.8	14
erato	0.88	4.1	397
sara	0.83	3.0	12
hewitsoni	0.87	3.9	54

*Figure **5** (overleaf). Home range maps of* erato, *Sirena, Costa Rica, June to August 1980. Feeding sites indicate nectar and pollen from* Psiguria, Lantana, *and* Tournefortia. *Second growth near park headquarters is very diverse for* Passiflora *spp., and supports many* Heliconius *spp. Each curved, black line connects roosting records, diurnal captures, and sightings in sequence: **A**, no. 1812* erato *(male), based on 12 diurnal and 29 roosting events over 34 days; **B**, no. 11345* erato *(male), based on 14 diurnal and 25 roosting events over 51 days; **C**, no. 11009* erato *(male), based on 20 diurnal and 39 roosting events over 96 days; **D**, no. 1906* erato *(female), based on 7 diurnal and 18 roosting events over 54 days; **E**, no. 11078* erato *(male), based on 4 diurnal and 25 roosting events over 27 days; **F**, no. 1579* erato *(male), based on 41 diurnal and 6 roosting events over 71 days; **G**, no. 1809* erato *(male), based on 14 diurnal and 25 roosting events over 38 days; **H**, no. 11408* erato *(female), based on 10 diurnal and 10 roosting events over 39 days.*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tree-fall gap
grass
second growth
tall forest
roost site
feeding site
trail
park building
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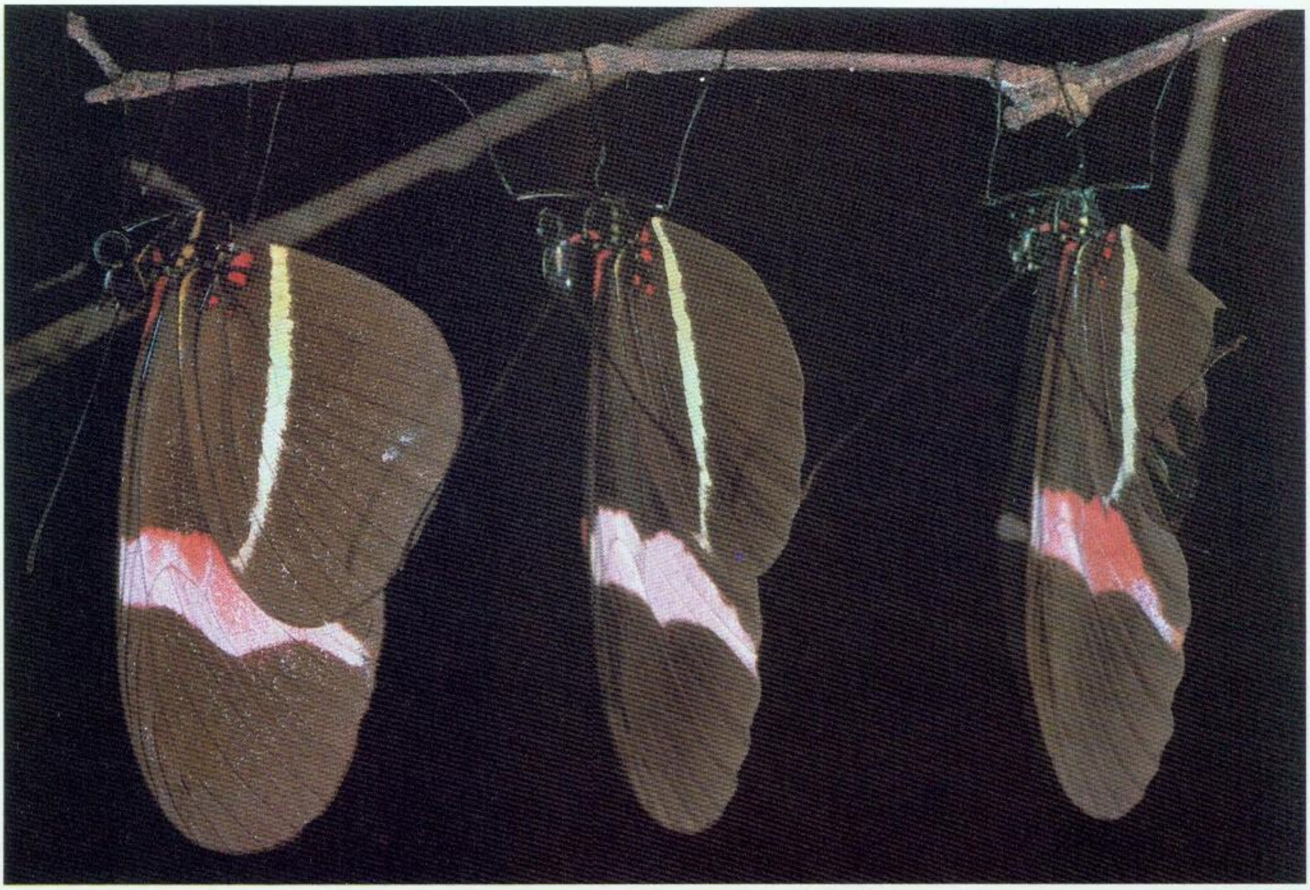

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*Figure **6.** Roost of* erato *showing a linear array of three individuals; near Gomez Farias, Mexico.*

charitonia, which is rather scarce at Sirena, is so gregarious. On the other hand, the three commonest species — *hecale, ismenius*, and *pachinus* (Gilbert 1984) — are among the least gregarious, although their opportunity for finding conspecifics should be greatest.

Discussion

The Function of Fanning

The fanning and fending off behaviors of *Heliconius* are little more than modified courtship and mate rejection (themselves an exchange of species-specific signals), which may act as a means by which butterflies can identify (using pheromones?) and roost near other members of their own species. This second use for courtship behavior would account for the males' greater fanning tendencies, and their tendency to fan females more than males. Members of different species of *Heliconius* sometimes roost together (Figures 4 & 7), but when this happens they usually segregate into subgroups by species, suggesting that they have some means of detecting conspecifics. Crane (1957:141–142) also concluded that gregarious roosting evolved through modification of courtship behavior.

Structure of Roosting Groups

The dispersal of teneral adults, the movements of older adults among roosts, the overlap in the daily home ranges of individuals from different roosts, and the ability of foreign individuals to join gregarious roosts, together, show that the gregarious roosts and home ranges of *erato* are not defended or exclusive territories of family groups, as they are in many social insects and vertebrates. There is plenty of interchange among roosting groups, and there is no evidence for tight inbreeding or kin structuring in the groups (contra Hiam 1982). Genetic studies, which show high levels of heterozygosity within populations and little local differentiation, also confirm a lack of inbreeding (Mallet in press b, Turner et al. 1979). Far from being kin groups, many gregarious roosts include more than one species (Figures 4 & 7).

Function of Gregariousness

Mating Hypothesis

As noted above, *Heliconius* rarely, if ever, mate on the roosts, so roosts are very unlikely to be aggregations that facilitate mating, even though courtshiplike behavior occurs on the roost.

Information Center Hypothesis

If *Heliconius* are able to follow one another, it could be sensible to roost near others that can lead them to food. Originally developed for birds (Ward 1965, Ward & Zahavi 1973), this information center hypothesis predicts that gregarious roosting will be favored in flock-foraging species, when food is superabundant but available in patches for short periods, so that little selection prevents knowledgeable individuals from leading their roostmates to food.

Heliconius do not fit this stereotype at all. By day they forage singly for larval and adult host plants. These are patchily distributed, but each patch produces only a small quantity of resource (pollen and nectar by *Psiguria*, new shoots suitable for eggs by *Passiflora*) at more or less constant rates (Gilbert 1975). The author has seen adult *charitonia* following each other in flight, but only in the evening when roosts are being formed, rather than early in the morning when the roost breaks up and individuals travel to foraging areas. In contrast, *erato* forage singly and were never seen following one another (except for courtship chases or other brief encounters). The consistently different home ranges of roostmates (Figure 5A–E) strongly suggest a lack of communication among individuals on the roost.

Gilbert (1975) points out that *Psiguria* flowers are inconspicuous and probably difficult to find, so that information exchange at the roost might be useful for *Heliconius*. However, *erato* individuals from at least four different roost sites were able to find the same tree-fall *Psiguria* flowers, often 500 m or more from where they spent the night (Figure 5A, F–H). Any similarity between the home ranges of roostmates could be due to the limited number of resources within flying distance of each roost, rather than to communication among roostmates. This may explain the nearly exclusive use of a *Psiguria* plant in observations of *charitonia* from a single roost (Waller & Gilbert 1982). If roosting gregariously is important for obtaining information on *Psiguria* sites, it is surprising that the *melpomene* group, whose species are most specialized on *Psiguria* pollen (Boggs et al. 1981), roost less gregariously than the more catholic *erato* group. In conclusion, there is no support for the hypothesis that *Heliconius* roosts are centers that individuals use to gain information about food, though the possibility that information may sometimes be transmitted cannot be excluded.

Predator Satiation Hypothesis

Because *Heliconius* are unpalatable and warningly colored, any naive predator attacking a group is likely to eat only a few of the individuals. It should rapidly appreciate the butterflies' unpalatability and learn to avoid the remaining roostmates on the same and subsequent encounters

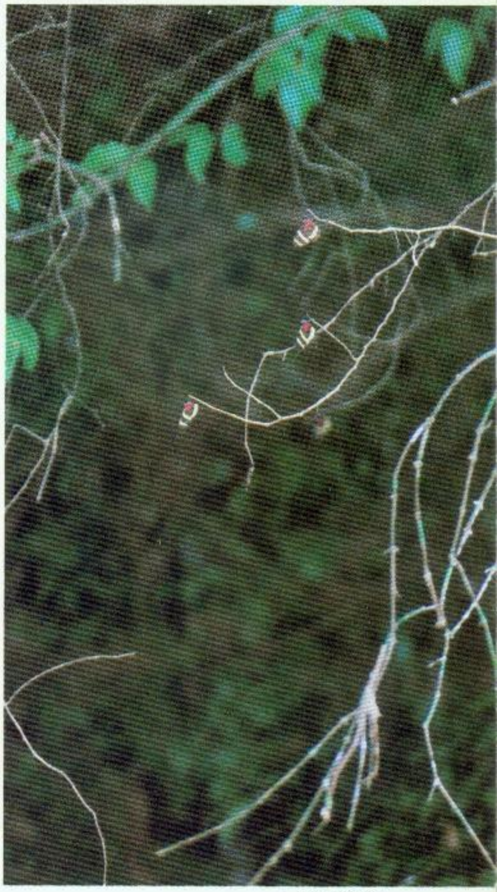

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Figure 7. Mixed-species roost of Heliconius, *showing extensive spacing between individuals. The individual at the top is a* pachinus; *the rest are* hewitsoni. *As in Figure 4, the two species roosting together are müllerian mimics.*

with the roost. A low per-individual attack rate should result within a gregarious roost, because fewer naive predators will find gregarious butterflies than they would solitary butterflies scattered about in a number of predators' territories (Turner 1975).

This hypothesis seems likely, but it requires that predation of roosting *Heliconius* exists, and that this predation be more intense on smaller groups (for a demonstration using the very large overwintering roosts of the Monarch butterfly, see Calvert et al. 1979). Although an anecdote shows that birds attack *charitonia* near the roost in Mexico, no predation on *erato* was seen in Costa Rica in many hours of observation. On average, each *erato* was disturbed once every 4.3 mornings and once every 13 evenings. These disturbance rates are surprisingly high, since animals must come very near the roost, or actually contact the perches, to cause the butterflies to fly off. Clearly, opportunity for predation is ample, especially if some roosts are sited in the territories of birds more likely to attack butterflies, such as tyrannid flycatchers and jacamars. The tendency for müllerian mimics to roost together (Figures 4 & 7) (Mallet 1984a) could be explained if visual predators attack *Heliconius* at or near the roosts. Important predation might also result from night-active predators, such as gleaning bats, but no observations confirm or deny this possibility. Further observations will be needed to establish whether predation on roosts is common, and whether it can account for the evolution of gregariousness.

Avoidance of Disturbance

John Smiley has suggested that *Heliconius* may benefit from roosting near conspecifics for a different reason. Roosts are fragile and very liable to destruction by falling branches, or by large nocturnal animals which are not themselves insectivorous. At Sirena, peccaries, brocket deer, a tapir, and a jaguar have been seen during roosting observations. Once a bat swerved near the perches of a roost at night, causing some *erato* to fly out and blunder into a spider's web. The spider immediately killed these butterflies and wrapped them in silk. If disturbed at night, *Heliconius* fly up blindly and usually cling to the first object they contact. If the new perch is on green vegetation, this must expose them to patrolling night-active invertebrate predators such as centipedes, ants, and spiders.

Smiley suggests that a *Heliconius* can reduce the risks of nocturnal roosting if it hangs up near other individuals: If the roost is already occupied, the site must be relatively safe, since the other occupants have probably roosted there for some nights. This hypothesis seems reasonable, but it would be difficult to distinguish this advantage from a predator satiation advantage without watching the roosts all night. Both potential advantages might even act simultaneously.

A Neutral Hypothesis

While little evidence has been produced for any advantage of gregariousness in *Heliconius,* evidence for any disadvantage is equally sparse. Behavior involved in aggregating at the roost site differs only slightly from diurnal courtship and mate-rejection. The roosting aggregations could conceivably be by-products of normal courtship tendencies. However, this neutral hypothesis explains neither why unsuccessful courtship reaches a sudden peak just before the butterflies become completely torpid, nor why different species vary so much in their gregariousness. The *erato* group, whose males indulge in "pupal rape" (Gilbert 1975, 1976), might be expected to be less gregarious than the *melpomene* group whose males actively court their females; instead the former group is more gregarious than the latter (Table 5). Also, the mutual leg-clinging behavior by tens of individuals of *sara* and *charitonia* (see the cover) has no parallel in mating behavior, and is a complex, specialized behavior that must surely have been caused by natural selection.

Conclusions

This study confirms that gregarious roosting and diurnal behaviors of *Heliconius* are remarkably complex. Airborne *Heliconius* near the roost usually fan roosted individuals. This interaction depends on color pattern features of the recipient; pheromones may also be involved. Fanning is similar to diurnal courtship behavior, but differs in that mating never ensues. The author suggests that fanning is required for species recognition on the roosts.

Newly emerged butterflies disperse widely, but older individuals have relatively fixed home ranges, and repeatedly return to the same foraging and roosting sites. This homing behavior is almost certainly learned. *Heliconius* do not forage in flocks, and roostmates seem to have completely individualistic daytime flight paths. Some individuals disperse among roost sites, and roostmates do not have home ranges or territories that they hold exclusively, as is the case with many social insects and vertebrates. The rather loose population structure of *Heliconius* contrasts with suggestions that kin selection might promote the evolution of altruism within roosting groups.

Why *Heliconius* roost gregariously at all remains a puzzle. The observations presented here suggest that avoidance of disturbance and predation are likely reasons. Any theory that explains gregarious roosting should also explain why *Heliconius* species differ so much in their gregariousness, and why some individuals roost singly, even within the most gregarious species. It is also not clear why female *Heliconius* use their hindwings to cover their forewing markings on the roost. The female posture seems to require energy, as it is relaxed after dark. This suggests that it has some advantage, but if so, what makes the posture less advantageous to males? Obviously there is still much to be understood about the behavior of these unusual butterflies. To resolve these questions, new hypotheses may be required, as well as further observations, experiments, and comparative work.

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