Communal Roosting in Heliconius Butterflies (Nymphalidae): Roost Recruitment, Establishment, Fidelity, and Resource Use Trends Based on Age and Sex

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COMMUNAL ROOSTING IN *HELICONIUS* BUTTERFLIES (NYMPHALIDAE): ROOST RECRUITMENT, ESTABLISHMENT, FIDELITY, AND RESOURCE USE TRENDS BASED ON AGE AND SEX

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ABSTRACT. *Heliconius* passion-vine butterflies form communal roosts on a nightly basis as an anti-predatory defense. Although past studies have evaluated various components of this behavior, much remains unknown about many basic aspects of roost dynamics. To learn more about communal roosting I examined roost establishment, recruitment, roost-mate resource use, roosting participation in a population, and roost arrival, departure, and perch preferences in natural populations of *Heliconius erato petiverana* in Panama. My observations suggest that 1) younger butterflies are recruited more readily than older butterflies, 2) roosts are first established by a single butterfly roosting consecutively in the same location that later recruits butterflies, 3) males depart roosts earlier than females in the morning, 4) older butterflies tend to roost on the same perch in the same roost every night, 5) roost-mates share the same resource traplines, and 6) most butterflies in a population participate in roosts. These observations present an improved portrait of *Heliconius* roosting and raise several new questions about this behavior.

Additional key words: Aggregation, trapline, following behavior, butterfly memory, *Heliconius erato*

Since the late nineteenth century communal roosting in *Heliconius* Kluk (Nymphalidae) passion-vine butterflies has generated a great deal of scientific and popular interest (Edwards 1881). Many species from this genus assemble in communal roosts in which adults gather repeatedly in a particular location in their home range to roost for the night (Mallet 1986a), and a recent study determined this unique behavior provides predator deterrence through collective aposematism (Finkbeiner et al. 2012). Roost-mates are generally conspecifics, but occasionally include Müllerian co-mimics of other species (Mallet 1986a, Mallet & Gilbert 1995). *Heliconius* likely rely on memory to locate their roosts each night (Jones 1930, Turner 1975, Mallet 1986a), rather than pheromones or scent-marking which is commonly seen in other aggregating insects (Costa 2006). Many individuals stay loyal to their roost for several months and even until demise (pers. obs). It is proposed that communal roosting behavior in *Heliconius* is facilitated by unpalatability, slow reproductive rate (Erlich & Gilbert 1973), limited learned home range (Turner 1975, Mallet 1986b), and long lifespan due to pollen consumption (Gilbert 1972, Boggs et al. 1981).

A number of studies on roosting in *Heliconius* have evaluated the adaptive benefits, home range, spatial dynamics, roost assembly, fidelity, environmental elements, and origin of this behavior (Jones 1930, Turner 1975, Young & Thomason 1975, Young & Carolan 1976, Mallet 1980, Waller & Gilbert 1982, Mallet 1986a, Mallet & Gilbert 1995, Salcedo 2006, 2010a, 2011a, 2011b, Finkbeiner et al. 2012). Here I describe observations that address several key questions

about *Heliconius* roosting: 1) How are roosts established? 2) Do age and sex play a role in roost recruitment? 3) Are there trends in individual butterfly arrival, departure, or perch preference? 4) Do roosting butterflies share the same resources? 5) How many butterflies in a population participate in roosts? I addressed these questions through observations of natural roosts of *H. erato petiverana* Doubleday (Nymphalidae) in Panama in 2010.

MATERIALS AND METHODS

Field sites. All data were collected in Panama at the Smithsonian Tropical Research Institute Gamboa field station, located along the eastern side of the Panama Canal just north of the Chagres River, approximately 30 km north of Panama City. I chose this site based on the abundance and accessibility of *H. erato* butterflies and communal roosts. Data were collected from natural roosts during June through September of 2010 throughout the rainy season.

Age scoring and roost locating. Roosting and non-roosting *H. erato* butterflies collected in Gamboa were given unique numbers for identification using a Sharpie® permanent marker, with numbers written on the ventral side of the forewing pink band. Individuals were sexed and their ages were estimated based on wing wear (Erlich & Gilbert 1973, Karlsson 1987, Kemp 2000, Pinheiro 2009). I used a scale of 1–3 with (1) as young, (2) as middle-aged, and (3) as old. Although young butterflies sometimes have damaged wings and some older butterflies may have little wing damage, this method is generally reliable. To maintain consistency the same person scored all butterflies.

TABLE 1: Data representing frequencies of age and sex of butterflies from varying observations. Sample sizes differ since not all butterflies whose age was determined were successfully sexed. Significance values indicated by asterisks: * $p < 0.05$, ** $p < 0.0001$ with corresponding pairs in bold.

Observation	Young	Mid–Old Age	Males	Females
Overall in population				
n=110 aged, n=82 sexed	41%	59%	44%	56%
Overall in roosts				
n=58 aged, n=57 sexed	52%	48%	46%	54%
Recruited Butterflies**				
n=49 aged, n=29 sexed	**84%**	**16%**	52%	48%
Arrived to roost first				
n=97 arrivals by age				
n=93 arrivals by sex	55%	45%	46%	54%
Departed roost first*				
n=54 departures by age				
n=48 departures by sex	54%	46%	**65%**	**35%**
Preferred same perch*				
n=19 aged and sexed	**26%**	**74%**	58%	42%

I located roosts by following individual butterflies from foraging sites to their roosting locations in the late afternoon. These sites are usually within relatively close proximity due to the restricted home ranges of *Heliconius* (Mallet 1986b). Butterflies were captured and marked after departing their roosts in order to prevent them from associating the roost with danger (Young & Thomason 1975, Mallet et al. 1987). Identifying individual butterflies was important for detection of new roost recruits and monitoring roost fidelity.

Data collection. Here I follow the broader ecology literature in defining recruitment as the addition of new individuals to a population (Ricklefs 1979). Specifically, in the context of this study, recruitment refers to the addition of new individuals to a roost, and I refer to a recruit as a new roost-mate. In using the term recruitment it is worth noting that there is no implication that butterflies in established roosts are actively seeking out new roost-mates.

I evaluated roost establishment by monitoring single butterflies that roosted repeatedly in the same location. Individuals in existing roosts were noted nightly so recruitment could be monitored. Recruitment observations began one week after I located roosts to avoid counting existing roost members as recruits.

In order to look for trends based on individual, age, and sex, I made daily observations with binoculars during roost formation in the afternoon hours and during roost departures in the morning. Multiple roosts could be monitored by a single person in the morning and evening given proximity of some roosts to one another (<15 m); also butterflies in roosts under forest cover convened at roosts at least 30 minutes earlier in the afternoon and departed approximately 30 minutes later in the morning compared to butterflies whose roosts were along the forest edge, where more ambient light is available during crepuscular hours. This made it possible to collect data from roosts in both types of light environments in the same day.

Roost-mate traplines—i.e. foraging routes defined as repeated sequential visits to a series of feeding locations (Gilbert 1975, Ohashi & Thomson 2009)—were determined by following individuals during foraging periods to determine whether roosting individuals share the same resources. I estimated the frequency of roosting butterflies in a population based on how many individuals marked in a single locality were found at roosts. Roost recruitment, arrival, departure, and perching location based on age and sex were analyzed using a Chi-squared test for given probabilities. Middle- and old-aged butterflies (wing wear score of 2 or 3) were pooled together and categorized as "older" individuals in the analyses. It is important to note that butterfly age was recorded the first time an individual was captured, and that some individuals were still observed in roosts later in the season. For data analysis, their ages remained as the initial age recorded, however the initial age recordings do not affect the results for recruitment data but may inflate the number of young butterflies in roosts throughout the season.

RESULTS

Roost recruitment and establishment. Nine *H. erato petiverana* roosts located in Gamboa were observed in this study. Recruitment frequency averaged 1.23 new butterflies per week (SD = 0.92, n = 49 recruits over the course of 10 weeks), but while some recruits stayed at the roost, many appeared for only one night. Recruitment likely depended on the number of established butterflies in the roost, and roosts on average contained 4.3 butterflies (SD = 1.6, n = 233 observations across nine natural roosts). On five occasions I observed a new recruit following an established roost member to the aggregation, suggesting that recruits find new roosts by following behavior (as speculated by Waller & Gilbert 1982).

Younger individuals were recruited more readily than older individuals. Of 49 roost recruits, 84% were young —their wings had bright colors and minimal damage, compared to middle-aged and old individuals whose wings were faded and tattered with apparent edge damage ($\chi2$ = 22.225, d.f. = 1, p < 0.0001, n = 49 butterflies; Table 1). Within the *H. erato* butterfly population in Gamboa, only 41% were determined to be young (a total of 110 unique butterflies noted) providing support that the frequency of young roost recruits is independent of overall frequency of young butterflies in the population. I found, however, that there was no dominant age among all roosting butterflies ($\chi2$ = 0.069, d.f. = 1, p = 0.793, n = 58 butterflies; Table 1).

The sex ratio of the recruits whose sex was determined was equal ($\chi2$ = 0.0345, d.f. = 1, p = 0.853, n = 29 butterflies; Table 1), as was sex ratio of all butterflies observed in roosts whose sex was determined ($\chi2$ = 0.439, d.f. = 1, p = 0.508, n = 57 butterflies; Table 1). With one exception, all roosting females observed were previously mated, as inferred from the characteristic anti-aphrodisiac odor that is present only after a female has mated (Gilbert 1976, Estrada et al. 2011). The next evening, however, the virgin female from the previous night had been mated. I observed a single mating event at a roost where a male from an established roost brought with himself, in copulation, a young female to the aggregation (Fig. 1). Copulation continued until nightfall and the female remained at the roost throughout the night but after departing in the morning she never returned to the roost. On three separate occasions a *Heliconius hecale* Fabricius (Nymphalidae) butterfly joined a roost for one night only, and I observed the same with a *Mechanitis* sp. Fabricius (Nymphalidae) butterfly. With respect to *Heliconius* mimicry, *H. hecale* and *Mechanitis* are members of the silvaniform 'tiger' mimicry ring, which has a

morphologically distinct wing pattern differing in appearance from the 'red' mimicry ring that *H. erato* belong to (Mallet & Gilbert 1995). Four different *H. erato* roosts had regular roost membership from hybrids between *H. erato hydara* Hewitson (Nymphalidae) and *H. erato petiverana* (Fig. 2). I also found libellulid and aeschnid dragonflies at *Heliconius* roosts multiple times, perching for the night on nearby twigs.

For one month, I monitored two solitary butterflies that chose to roost in the same location nightly. Eight days after one of these individuals had been roosting consistently in the same location, it was followed to the roost by a new butterfly. Nearly two weeks later there was a third butterfly recruited to the same roost. This suggests that roosts are established when new butterflies join single individuals that already roost consecutively in the same place. The other solitary individual observed continued to roost alone and did not gain any roost-mates.

Butterfly arrival and departure. Butterflies generally arrived at their roosting sites two hours before sunset, but individuals whose roosts were under forest cover arrived as early as three hours before sunset on cloudy days, which was often during the rainy season. In the early afternoon during a rain shower I observed two individuals at their roost at 2:00pm, more than four hours before sunset. They appeared to be using the roost as a retreat, unless low ambient light from the heavy rain clouds triggered early roosting behavior (Salcedo 2010a). Later they departed to forage once the rain stopped and returned to the roost again before dusk. In the mornings, butterflies generally left their roosts within an hour and a half after sunrise, but on cloudy mornings butterflies stayed at the roost up to two and a half hours past sunrise. On rainy mornings many butterflies did not leave their roosts at all.

Particular butterflies always arrived first to their roosts in the afternoon while other butterflies were repeatedly the last to leave in the mornings. There was no relationship between first roost arrival and age; middle-aged and old butterflies did not arrive to the roost earlier than younger butterflies ($\chi2$ = 0.835, d.f. = 1, p = 0.361, n = 97 roost arrivals; Table 1). Roost arrival did not depend on sex either ($\chi2$ = 0.527, d.f. = 1, p = 0.468, n = 93 roost arrivals; Table 1). I found no difference between first departing butterfly and age ($\chi2$ = 0.296, d.f. = 1, p = 0.586, n = 54 roost departures; Table 1), however I found a trend between departing butterfly and sex: males tended to depart roosts first in the morning ($\chi2$ = 4.083, d.f. = 1, p = 0.0433, n = 48 roost departures; Table 1).

Using observations from three roosts over the course of 54 nights, 61% of all roosting butterflies chose the

FIG. 1: Two mating *H. erato* butterflies at a communal roost. The male (labeled 5B upside-down) is on the left and the female is unmarked.

exact same perch to rest on each evening. There was no difference between perch choice and sex ($\chi2$ = 0.474, d.f. = 1, p = 0.491, n = 19 butterflies; Table 1), although older butterflies were more likely to roost on the exact same perch, compared to young butterflies ($\chi2$ = 4.263, d.f. = 1, p = 0.039, n = 19 butterflies; Table 1).

Roost-mate traplines. Trapline observations of butterflies from three neighboring roosts in a forest patch showed that butterflies shared the same resources, even if they were not all members of the same roost. They visited a series of *Lantana camara* Linnaeus (Verbenaceae) plants throughout Gamboa in the same order in the morning hours (Fig. 3), and by the afternoon they had reversed the trapline network to return to their roost for the night. None of these resources were visible from any of the three roosts.

It was common to find multiple roosts in visible range of each other (typically ≤15m) in a given part of the home range. When individual *H. erato* were exercising pre-roosting behavior they often interacted with one another before dispersing to their preferred communal roosts. On multiple occasions I observed a butterfly from one roost following a butterfly to another roost, then eventually returning to its preferred roost before dark.

Roost participation and fidelity. Of 110 total marked *H. erato* in the Gamboa *Heliconius* population, I found at least 66 in roosts, providing evidence that, at minimum, over half of the butterflies within a population choose to participate in communal roosts. From the nine roosts used in this study, eight roosting butterflies (out of 66) moved between roosts. Most only

moved once and did not return to their previous roosts, however two individuals (during different evenings) moved between three different roosts that were in close proximity.

DISCUSSION

Roost recruitment and composition. Most of the *H. erato* butterflies within the Gamboa population participate in roosts, which supports the apparent adaptive benefits associated with communal roosting (Finkbeiner et al. 2012). Roost recruitment occurred regularly, and younger butterflies were recruited more often than older butterflies in a population, which was probably a result of older butterflies already being committed members of specific roosts. Even though the young:old ratio of roosting butterflies is close to equal, some individuals were recorded in roosts when they were recruited but aged over the course of the season. As was observed, roosts are likely established when a butterfly follows and roosts with a single butterfly that had been roosting consecutively in the same location, then eventually more individuals are recruited over time. Since I observed four roosts to have a *H. erato hydara* hybrid member, racial wing pattern differences may have little effect on recruitment, although Salcedo (2010a) suggested that altered wing patterns in *H. erato petiverana* interfere with roost formation.

My observation that dragonflies roost with *H. erato* butterflies is probably not a result of limited roost substrate, since many dry branches were available in these sites to support other aggregations or single roosting perches. Both dragonflies and damselflies have been documented to form communal roosts (Parr & Parr 1974, Miller 1989, Rehfeldt 1993, Switzer & Grether 2000). It could be possible that other insects in

FIG. 2: A *H. erato hydara*–*H. erato petiverana* hybrid roosting between two *H. erato petiverana* butterflies. The hybrid lacks the large yellow hindwing band.
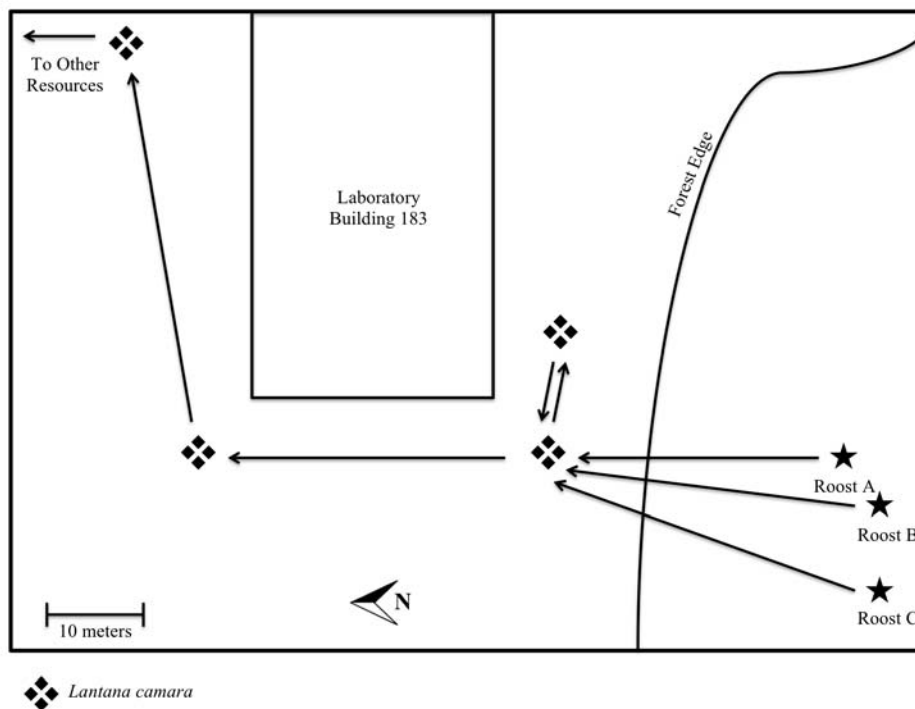
FIG. 3: Map of butterfly traplines from three neighboring roosts (A, B, C). Traplines are indicated by arrows and scaled according to distance measurements based on a Garmin GPS system. Traplines were reversed by butterflies upon return to the roosts in the afternoon. GPS coordinates for site: 9° 06' 58.26" N, 79° 41' 54.24" W.

addition to *Heliconius* join the roosts as a strategy to avoid predation since *Heliconius* roosts are aposematic (Gamberale & Tullberg 1998, Finkbeiner et al. 2012). This possible commensalism should be investigated further since very little is known about the potential existence of "cheater" animals in aposematic aggregations. It is important to note that non-co-mimic *Heliconius* species have been seen roosting together (Mallet & Gilbert 1995, E. I. Deinert, pers. comm.) and *H. hecale* and *Mechanitis* species have been observed in *H. erato* roosts but with irregular attendance (pers. obs.), however these butterflies are chemically defended whereas dragonflies typically are not.

There appears to be no difference in roost sex ratio, suggesting the benefits of roosting have no relationship to mating, unlike other gregarious and roosting animals where this behavior may play a role in mate finding (Parrish & Edelstein-Keshet 1999, Blanco & Tella 2009, Bijleveld et al. 2010). The idea that *Heliconius* roosting behavior and mating behavior are un-related is further supported by my single mating observation where a non-established roost member was brought to the roost in copulation, but was never recruited later to the roost.

The fact that all observed roosting females were already mated indicates the females are unlikely to mate again (Gilbert 1976) so males would have no benefit from using roosts to locate mates. The only observed sex-related difference was that males depart roosts earlier than females in the morning. These early departures by males may be related to patrolling for unmated females or female pupae (Deinert et al. 1994, Estrada et al. 2010), although further work would be required to confirm this. In *Heliconius sara*, only females arrive to the roost with large pollen loads that are digested overnight which could affect early roost departure due to metabolic constraints (Salcedo 2010b), however in *H. erato* most individuals (both male and female) arrived to the roost in the afternoon without a pollen load. Thermoregulatory ability could also be an important factor determining which individuals are able to depart the roost first (Clench 1966), but this may not be as necessary in tropical climates as it is temperate climates. In other butterflies, males are able to fly at lower body temperatures (Gilchrist 1990), and smaller individuals (in particular males) have a heightened rate of heat exchange suggesting they would have greater control

over heat gain while basking (Kemp & Krockenberger 2004). In *H. erato*, males are sometimes slightly smaller than females so it is possible thermoregulation is associated with roost departure trends in this species.

Individuals prefer specific perch sites. I observed that older butterflies tend to prefer the same perch within the same roost every evening, thus implying individual butterflies are capable of remembering specific roosting locations. Such a precise spatial preference may be gained over time as a result of repeated visits to the roost (Salcedo 2006). There is little evidence that *Heliconius* use pheromones or scent-marking to locate their perches in the roost (Jones 1930, Mallet 1986a, Salcedo 2010a), and perch preference is likely based on memory and visual cues.

Roost members share resources. That butterflies from neighboring roosts share the same traplines strongly suggests following behavior occurs regularly in butterflies between flowering plants. Following between resources by *Heliconius* has been noted by Waller & Gilbert (1982) and Pinheiro (2009). There is no evidence that butterflies use the roosts as information-sharing centers (Mallet 1986a, Finkbeiner et al. 2012) in which individuals would learn the locations of foraging sites by following roost-mates during morning departures. The butterflies could, however, have the same traplines based on coincidence, but there were other flowering resources in the area and not all resources in the trapline were visible from one another, nor were any resources visible from either of the roosts. These results are consistent with Waller & Gilbert's (1982) findings that roosting *Heliconius charithonia* butterflies generally use the same pollen plants that are within close proximity to their roost. On the contrary, it is important to note that Mallet (1986a) observed that roosting *H. erato* butterflies have a predictable tendency to visit different flowers.

These results improve our understanding of communal roost dynamics in *Heliconius*. I conclude that age is strongly associated with roost recruitment and perch preference within a roost, suggesting young butterflies join roosts more willingly than older butterflies, while older butterflies have more precise roosting preferences. Earlier male departure from roosts could indicate either that females require more time at roosts in the morning before foraging, possibly due to thermoregulatory or metabolic constraints, or that males prefer an early start on searching for resources. These findings suggest that communal roosting behavior in *Heliconius* butterflies is somewhat unusual for insects since such trends are typically seen in roosting vertebrates rather than in gregarious insects.

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