NOTES ON COMMUNAL ROOSTING OF *HELICONIUS CHARITONIUS* (NYMPHALIDAE) IN COSTA RICA

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Adults of the familiar neotropical butterfly *Heliconius charitonius* (L.) (Nymphalidae: Heliconiinae) form communal roosts to pass the night (Jones, 1930; Poulton, 1931). Individuals in a habitat come together to rest on a branch or dead vine and the same site may be used for roosting over a long period of time. It is known that in some species of *Heliconius,* a roost site may be used for several months (Benson, 1972). Owing to the lack of information on butterfly roosts in general and to the interest in *Heliconius* butterflies as organisms for investigations of phylogeny, population biology, microevolution, behavior, and chemical ecology (e.g., Crane, 1957; Emsley, 1963; Brower & Brower, 1964; Benson, 1971; Brown & Mielke, 1972; Ehrlich & Gilbert, 1973), we pursued a study of communal roosting in *H. charitonius* in central Costa Rica. The study consisted of documenting the membership and turnover in two different roosts in the same general region. Initially we believed that composition of the roosts was very stable in time, but as shown by our study, this turned out not to be entirely true.

Notes on the Roosts

Two roosts of *H. charitonius* were located in the rugged ridge-top terrain at "Cuesta Angel," a region of steep virgin wet forest about four km south of the village of Cariblanco, Heredia Province, Costa Rica. The first roost was discovered on 27 June 1972 in the immediate vicinity of "Site B" in the population study of Young, Thomason & Cook (In prep.); this was called the "wet season" roost (Roost A). This roost was on hanging dead creepers of *Mucuna* sp. (Leguminosae), located part way down the side of a very steep slope (Fig. 1); it was accessible for observation only by climbing down the slope on ropes and sitting on a small wooden platform constructed for this purpose. This observation deck was about 2 m beneath the roost in very dense grass.

The second roost (Roost B) was not discovered until 10 February 1973 during the variable dry season characteristic of this area. This roost was about 160 m from the first roost and situated on the crest of the ridge in thick secondary forest (Fig. 2), whereas Roost A was situated at the edge of primary virgin rain forest. Both roost sites consisted

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Fig. 1. Roost A of *Heliconius charitonius* was located at the edge of the primary growth forest on this steep slope. It was just left of the pair of *Cordia* trees, and under the shaded foliage. The observation deck is obscured by dense grass.

of dead creepers; Roost B was only about 1 m from the ground and thus very accessible for observation. We also discovered a third roost of *H. charitonius* on a very steep, dangerous slope about 200 m down the slope from Roost A; this roost was very inaccessible for study at close range, being about 20 m off the ground in a clump of vines among dense canopy vegetation. Owing to the high abundance of this butterfly at Cuesta Angel, there were undoubtedly many roosts in the area, but the very rugged terrain precluded any in-depth survey of several roosts. For these reasons, we confined our observations to Roosts A and B.

Departure of the butterflies from the roost in the morning generally occurred over a short period of time (15–45 min.) and took place either singly or in mass. The incidence of sunlight apparently triggers departure, and on overcast mornings with no rain, departures occurred at a later time. Upon leaving the roost, the butterflies insolated on the vegetation before attempting any prolonged flight. Arrival at the roost was more variable than departure, in one instance extending over a three

Fig. 2. Roost B of *H. charitonius* was on a cluster of dead creepers just to the left of center.

hour period. Light rain or overcast in the mid-afternoon hastened arrivals at the roost. On clear days, the butterflies arrived just before dusk, perhaps only coincidentally but just before the period of greatest bird activity in the area.

METHODS

The basic methodology employed was to capture, mark, and release individual butterflies either by (1) netting adults as they flew into the roost during the late afternoon and left during the early morning (as was used for Roost A), or by netting individuals throughout the day within the immediate vicinity of the roost (as was the case for Roost B). In this manner, we marked and observed butterflies associated with Roost A from 27 June–9 August 1972. During this six-week period, we visited the roost on 20 different days, despite the fact that after the tenth visit (11 July), a large branch fell next to the roost and broke some of the creepers used by the butterflies. The roost became virtually

Fig. 3. Marked and unmarked butterflies on Roost B; note marked individuals nos. 27, 34, and 45.

abandoned after this time. Our visits to this roost were generally confined to late afternoon (after 1550 C.S.T.) to observe arrival patterns of individual butterflies, and a check later that evening (usually after 2100) to make a total census of butterflies. Roost B was examined a total of *nine* different days over an *eight-week period*, ending into early April 1973 when the roost was no longer used. In this case, most observations were made early in the morning before the butterflies had left the roost. Occasionally late afternoon observations on the previous day were made in combination with the morning observations. In only one instance was an observation made of Roost B after nightfall.

We never attempted to net butterflies on the roost for marking, for fear of frightening away the insects. Twelve of the fifteen butterflies marked that were eventually seen on Roost A were initially captured in the immediate vicinity (with 15 m) of the roost, while the other three were caught a considerable distance (65–165 m) from this roost. But most of the marked butterflies seen on Roost B (31 of 42 individuals

TABLE 1. The census history of marked *Heliconius charitonius* on Roost A* (1972).

Individual No.	Age**	Date of Marking	Dates of Census*** June 29	June 30	July 3	July 10	July 11	July 12	July 18	July 19
2	Y	June 28	X							
3	M	June 29	X	X	X	X	X		X	X
4	M	June 29	X	X	X	X	X	X		
5	O	June 30			X		X			
6	M	June 30				X	X			
7	Y	July 1			X	X			X	X
8	Y	July 1			X					
9	M	July 3			X					
10	M	July 3			X	X	X	X		
11	Y	July 11					X			
12	M	July 19							X	
13	M	July 19							X	
14	Y	July 19							X	X
15	Y	July 19							X	
16	O	July 19							X	X

* An "X" is used to indicate the presence of an individual on the roost on a particular date when the roost was examined.
** "Y"—young or fresh; "M"—middle; "O"—old.
*** For each individual, the first entry is the first time the butterfly was seen on the roost.

first captured in the general area) had been marked before the roost was discovered, as part of a study by Thomason & Young (In prep.); all of these butterflies were captured within 30 m of the roost. Additional butterflies (11) were marked after being captured while leaving the roost.

Marking consisted of painting a small number near the center of the ventral side of each hindwing using white, fast-drying enamel paint ("Flo-paque"). Each butterfly so marked was recorded for freshness of wing condition ("age"), and only at Roost B, additionally for sex at the time of initial capture. A butterfly was always released immediately after marking. Unfortunately, the individuals of Roost A were not sexed. Resightings of marked butterflies on the roosts were made with binoculars; marked butterflies were seldom netted a second time. Usually an additional trained observer confirmed each resighting of marked butterflies on the roosts; night observations were done using a wide-beam flashlight and shining the light intermittently for short periods to minimize disturbance. For night observations on Roost A, two observers roped their way down the steep slope to the observation deck, which

TABLE 2. The census history of marked *Heliconius charitonius* on Roost B (1972–73).

Individual No.	Sex	Age	Date of Marking	Feb. 10	Feb. 12	Feb. 13	Feb. 15	Feb. 22	Feb. 24	Mar. 6	Apr. 2	Apr. 3
0	♂	M	Dec. 22		X	X			X			
2	♂	M	Dec. 22	X	X							
3	♂	M	Dec. 22		X							
6	♂	M	Dec. 22		X	X	X		X	X		
17	♂	O	Dec. 22				X	X				
18	♂	O	Dec. 22			X						
19	♂	M	Dec. 22			X						
20	♂	M	Dec. 22	X								
21	♂	M	Dec. 22	X	X	X	X	X	X	X		
23	♂	M	Dec. 22	X								
24	♂	M	Dec. 22			X						
27	♀	M	Dec. 29	X		X		X		X		
31	♂	Y	Dec. 29	X		X	X			X		
32	♀	O	Dec. 29					X				
33	♀	O	Dec. 30		X	X		X	X			
34	♀	M	Dec. 30		X	X			X			
35	♀	O	Dec. 30	X								
37	♀	O	Dec. 30	X								
39	♂	M	Dec. 30			X						
42	♀	Y	Jan. 5	X	X			X	X		X	
43	♂	Y	Jan. 6	X	X							
45	♂	Y	Jan. 6	X	X	X		X	X		X	
47	♀	Y	Jan. 6	X								
48	♀	O	Jan. 6	X		X	X					
52	♀	M	Jan. 6				X		X			

was about 25 m from the road above. It should be emphasized that it is very unlikely that observed absences of marked butterflies on the roosts at night were only apparent (i.e., not real) owing to the observers missing marked butterflies. All butterflies were coded with numbers on the hindwings, clearly visible at night. Furthermore, it was possible to get very close (within 0.5–1.5 m) of the roosts, thus eliminating inaccuracy in tabulating the marked butterflies present.

RESULTS

All of the 15 butterflies marked near Roost A were eventually spotted at least once on the roost. Although a total of 96 butterflies were marked

TABLE 2. Continued.

Individual No.	Sex	Age	Date of Marking	Feb. 10	Feb. 12	Feb. 13	Feb. 15	Feb. 22	Feb. 24	Mar. 6	Apr. 2	Apr. 3
53	♀	M	Jan. 6		X	X			X		X	
55	♀	O	Jan. 6				X					
60	♂	Y	Jan. 16				X					
61	♂	Y	Jan. 25	X	X					X	X	
62	♀	Y	Jan. 25		X	X		X				
63	♀	M	Jan. 25		X	X			X			
64	♂	Y	Feb. 10	X	X	X	X	X	X			
66	♀	M	Feb. 10				X	X	X	X	X	X
67	♀	Y	Feb. 10			X		X	X		X	
68	♀	Y	Feb. 10		X	X	X					
69	♂	Y	Feb. 10		X	X		X	X	X		
71	♂	Y	Feb. 24							X		
75	♀	Y	Feb. 24							X		
80	♂	M	Mar. 6							X		
81	♀	Y	Mar. 6							X		
82	♂	Y	Mar. 10								X	
83	♀	Y	Mar. 10								X	
1*	♂	Y	Jan. 16							X		
5*	♂	Y	Jan. 16							X		
11*	♀	Y	Jan. 17		X							
28*	♂	Y	Feb. 21					X				
89*	♀	Y	Feb. 11		X	X	X	X	X	X	X	X

* These last 5 entries are butterflies originally marked at other sites: Nos. 1*, 5* and 11* were marked at Site B in the study of Young, Thomason, & Cook (In prep.), about 160 m from Roost B, in the immediate area of the original Roost A. Nos. 28* and 89* were marked at Site D (*op. cit.*), about 150 m below Roost B, midway down the side of the ravine. Please note that the butterflies entered here are different from those in Table 1.

in the immediate vicinity of Roost B, only 42 were seen at least once on this roost. Of these 42 individuals, 19 were females and 23 were males, suggesting a sex ratio of 1:1 for roost membership with time. For Roost A, between 27 June and 10 July, there was an average of 13 butterflies on nights of observation. After 10 July, nightly attendance dropped greatly to an average of about 2 butterflies, beginning the night of 11 July which is the date the branch fell and destroyed some of the creepers used for roosting. There were no butterflies present on the roost for the last two dates of observation in early August. For Roost B there was an average of about 25 butterflies on the roost for the first seven nights of study, and for the last two nights, there were only five butterflies on each night.

TABLE 3. Mean percentage of resightings per marked butterfly over five or more census dates.*

Age Class	♀♀ N	♀♀ $\bar{x} \pm$ S.E. (%)	♂♂ N	♂♂ $\bar{x} \pm$ S.E. (%)	Total N	Total $\bar{x} \pm$ S.E. (%)
			ROOST A			
Young		———		———	3	32.0 ± 24.6%
Middle		———		———	5	59.0 ± 22.1%
Old		———		———	1	33.0%
Total		———		———	9	47.2 ± 25.5%
			ROOST B			
Young	7	41.2 ± 28.3%	10	35.5 ± –3.2%	17	37.9 ± 25.6%
Middle	6	44.4 ± 14.4%	10	25.5 ± 22.2%	16	32.6 ± 21.7%
Old	6	20.4 ± 13.5%	2	16.6 ± 5.6%	8	19.4 ± 12.1%
Total	19	35.6 ± 23.0%	22	29.3 ± 22.6%	41	32.2 ± 23.0%

* For those butterflies present in the population as marked individuals for 5 or more census dates. Mean percentage of resightings per marked butterfly is the average percentage that a given age group and sex were resighted on the roost.

Marked butterflies behaved identically to unmarked butterflies when on the roost (Fig. 3). Tables 1 & 2 summarize the census histories for all marked individuals of *H. charitonius* observed at least once on Roosts A and B respectively. It is striking that the temporal pattern of attendance is variable among individuals, despite large interruptions between dates of census. For example, 19 of the 42 marked butterflies seen on Roost B were seen only once, although 6 of these only were caught near the end of the study period (i.e., 6 March and 2 April). There is no particular pattern with respect to age as indicated by relative condition of the wings; "young" individuals are equally residential as "middle" individuals (Table 3). If we assume that the number of dates of observations on the roosts is sufficient for detection of temporal patterns of visitation over relatively short periods of roost existence, then it appears that roost membership from day to day is variable. Of the 69 butterflies marked at Site A by 10 February, 36 of these were seen on the roost at least once; of these 36 butterflies, 23 were seen one to three times on the roost while 13 were seen four to seven times (36%). If we define residentiality for an individual butterfly as it being present for 50% or more of the census dates, then 36% of the marked butterflies on the roosts were residents. Also, at Roost B, five individuals were marked at two different areas about 150 m from the roost (nos. 1, 5, 11 and 28 at one and no. 89 at another location). Of these, only no. 89 was seen more than once, becoming a highly residential member of the

roost (Table 2). For Roost A marked butterflies, individuals nos. 3, 4, 7 and 10 showed high residentiality (Table 1).

The average number of resightings for each individual on the roost (Table 3) is another useful statistic for estimating residentiality or lack thereof. There is a general tendency for females to be residential slightly more than males, although this difference was only statistically significant for the "middle" category of both sexes, as indicated by a *t*-test ($t = 1.85$ for 14 degrees of freedom at $p = .05$) for the Roost B data. Tests of significance for differences in residentiality with increasing age within each sex were inconclusive, although it appears that older butterflies are resighted fewer times than young ones.

DISCUSSION

It is not known why individuals of *H. charitonius* roost communally. It is known that the butterflies are capable of detecting yellow color (Swihart, 1971), and this could be the appropriate visual mechanism causing adults to be attracted to one another during the late afternoon, the "capacity for sociability" of Beebe (*in* Jones, 1930). It was frequently observed that the butterflies arrive at a roost in small groups as well as singly, so individuals can be "recruited" to a roost site through visual contact with other individuals in the areas. Benson (1972) noted that flying aggregations of *H. erato* (L.) form during the late afternoon just before communal roosting.

In dense populations of *H. charitonius* such as the one at Cuesta Angel, there are undoubtedly many roosts within the area occupied by the adult population, and the prolonged absence of some marked butterflies seen at times on roosts, especially young butterflies, could be indicative of (1) instances of these butterflies sleeping singly away from the roost, or of (2) a high frequency of exchange in which these individuals associate with a number of roosts in the area, or leave the home area completely for a period of time, as was the case for four of the last five entries in Table 2. Communal roosting is a known social behavior pattern of *H. charitonius* (Jones, 1930) and our data suggest that the fidelity of individuals to a roost may be high. The pattern is one of some individuals being very residential at a roost, while other individuals are considerably less faithful; such a pattern, that correlates neither with sex nor age to any convincing degree, may be indicative of genotypic differences among individuals. In this context, it would be very interesting to determine if highly residential individuals with respect to roosting are also individuals that have high home range tendencies or low mobility (Benson, 1971). Despite the fact that many adults may exhibit home range behavior within the vicinity of Roost

B (Young, Thomason, & Cook, in prep.), the failure of many of these marked butterflies (54/96) to show up on the roost during the study period, plus the large number of individuals seen only once on the roost, suggests further that multiple roosts occur within an area of home range movement. Jones (1930) found substantial exchange of individuals among roosts of *H. charitonius* in Florida. As in our study in Costa Rica, both Jones (1930) and Poulton (1931) also observed large roost size for this species; roost size was close to 30 butterflies in some cases. The size of roosts of *H. charitonius* seen in the present study were much larger than the roosts of *H. erato* observed in Costa Rica by Benson (1972).

However, the greatly reduced percentage of resightings of "old" marked butterflies suggests that the mortality of older individuals also contributes to the failure of butterflies to be observed consistently on the roosts. In a capture-mark-release population study of the butterfly here, conducted over several successive months, it was found that old individuals are the ones recaptured the least number of times, and they tend to disappear within a very short time (Young, Thomason, & Cook, in prep.). In those instances where a marked butterfly is seen on a roost infrequently at long intervals it is difficult to explain why this is the case since there were long gaps in the nightly schedule of observations. It may be a regular habit of the butterflies to spend most of their time on a given roost, but due to the presence of a large number of roosts in the area, individuals occasionally transfer to another and then perhaps transfer back to their original roost. But since observations were not continuous and not on several roosts simultaneously, it is not possible to interpret the data further. More field study is clearly needed to distinguish among these alternative explanations of absences of marked butterflies from roosts. It is clear from the data that butterflies may be absent from roosts and further studies are needed to explore the reasons why this is so.

Sexual behavior was not observed for individuals on roosts, and judging from the condition of adults, it is likely that both mated and virgin females partake in roosting with males; the reduced amount of sunlight at the time of roost formation probably precludes any courtship activity. Poulton (1931) noted that individuals of both sexes of *H. charitonius* roost together, with an approximately 1:1 sex ratio.

Some recent studies (Turner, 1971; Ehrlich & Gilbert, 1973; Benson, 1972; Thomason & Young, in prep.) have demonstrated that adults of some species of *Heliconius* exhibit home range movements. Both home range behavior and communal roosting limit the tendency for indi-

vidual butterflies to move out of some portion of the habitat containing sufficient resources. The population in which individuals exhibit home range movement forms one or more roosts, and exchange among the roosts may be high, depending upon (1) dispersal tendencies of different genotypes, (2) population density, and (3) the spatial and temporal distribution of adult resources (preferred flowers—cf. Brown & Mielke, 1972). Ehrlich & Gilbert (1973) observed changes in the home range movements of individuals of *H. ethilla* Godart on Trinidad when an important food plant was accidentally cut down during their experiment.

It has recently been argued that the combined characteristics of limited home range movement and communal roosting in *Heliconius* are found in unpalatable species (Benson, 1971). Since *H. charitonius* is phylogenetically close to *H. erato*, a highly unpalatable and mimetic species in some localities (Brower & Brower, 1964), it is strongly suspected that *charitonius* is also unpalatable (W. W. Benson, pers. comm.).

Even though some individuals in an area exhibit substantial residentiality at a roost (Table 2), there must be a complex of environmental factors that makes roosts temporary to some degree. An accidental damaging of perching sites may result in butterflies abandoning a roost site completely (Roost A on 11 July). One of us (A.M.Y.) has seen a small group of toucanets shake creepers containing a roost during the late afternoon, resulting in many butterflies settling individually on nearby vegetation and not returning to the roost that night. Also, the occasional appearance of individuals on the roost that were marked considerable distances away (nos. 1, 5, 11, 28 and the highly residential no. 89) could be the result of accidental passive displacement by strong winds and even of attempted predatory attacks in the usual home range area of such individuals. However neither of these events were observed to take place when observations were being conducted. If there are large differences in the size of the assumed home ranges of individuals, this in turn could influence residentiality: individuals with large home ranges may show a greater tendency to be transient among different roosts from night to night. It is clear, though, from our preliminary study, that communal roosting in *H. charitonius* in a dense mountain population in Costa Rica reflects the tendency for many butterflies to be residential for a given roost, even over relatively small distances in the habitat between roosts. Further studies should document the locations of other roosts and measure individual exchange among roosts and the relation of such movement to home ranges. But it is also evident that other species of *Heliconius* in similar or the same habitats exhibit very different adult

movement behavior: at Cuesta Angel, *H. cydno* is found in the same habitats as *H. charitonius* but it neither exhibits communal roosting nor home range behavior of the type seen in the latter species (Young, 1973).

SUMMARY

(1) Using the method of capture, mark, and recapture, the composition and individual residentiality (or turnover) of two roosts of the neotropical butterfly *Heliconius charitonius* L. at one mountain locality in central Costa Rica were investigated. One of the roosts was studied during the wet season (June–August 1972) and the other during the following dry season (February–April 1973). The roosts were situated about 160 m from one another, though at different times.

(2) Our working hypothesis was that the composition of a roost should be stable through time, with the exception of occasional new recruits through eclosion in the area. In general, we found this to be the case, but with some evidence of considerable transiency among some individuals on each roost. Thus roosts of this butterfly are less stable than usually assumed in the literature for *Heliconius*.

(3) Based on our observations of the larger roost, we found that about 36% of the marked butterflies seen on that roost which were marked early in the study in fact returned on 50% or more of the nights of observation, suggesting a high degree of residentiality among certain individuals. The degree of residentiality could not be correlated in any convincing way with sex or age of individuals. However, there is a tendency for old butterflies to disappear faster from roosts, suggesting they have died. Owing to large gaps in the observation records, it is not possible to confirm the suggestion that *H. charitonius* individuals spend most of their time at one roost but occasionally transfer to other roosts in the area, and then perhaps transfer back to the original roost.

(4) The temporary component of roost membership over short periods of time (weeks) is very likely due to several factors including (a) the tendency for certain individuals to spend the night at different roosts, or singly away from the roost, but in the general area, (b) accidental wanderings into the vicinity of other roosts, and (c) tremendous variation in the size of home ranges assumed to be possessed by individual butterflies.

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