SELECTION OF ROOST SITES BY HONDURAN WHITE BATS, *ECTOPHYLLA ALBA* (CHIROPTERA: PHYLLOSTOMATIDAE)[1]

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Abstract. *Ectophylla alba* H. Allen (Chiroptera: Phyllostomatidae), the Honduran white bat, was found to alter the leaves of five species of *Heliconia* (*H. imbricata, H. latispatha, H. pogonantha, H. tortuosa,* and an undescribed species) for use as diurnal roosts. By cutting the side veins extending out from the midrib, the bats cause the two sides of the leaf to fold down around the midrib forming a tent. More tents were found on *H. imbricata* and *H. tortuosa* than on the other three species, but these were the most abundant species at the Costa Rican locality. The bats appeared to be selecting a specific size-class of leaves for tent construction rather than leaves of a particular species of *Heliconia*. Honduran white bats were found roosting in groups of 1–6 individuals. It appeared that a colony of bats roosts in a number of tents scattered within the forest. An hypothesis of leaf size selection, tent utilization, and evolution of tent construction is presented.

Key words: Costa Rica; Ectophylla alba; Heliconia; *Honduran white bat*; *Musaceae*; *Phyllostomatidae*; *tent-makers.*

INTRODUCTION

Ectophylla alba H. Allen, the Honduran white bat, a small stenodermine with black wings, was described in 1892 from a single specimen preserved in fluid and lacking a skull (Allen 1892). In 1898, Allen described the skull and dentition from a second specimen. *Ectophylla* apparently was not detected again until Casebeer et al. (1963) reported three specimens captured at Finca La Selva, Heredia Province, Costa Rica.

Essentially all of the published ecological data for *E. alba* are contained within two papers. Gardner et al. (1970) discussed the reproductive condition of 10 Costa Rican specimens, provided measurements, and commented on the distribution. They noted that seven of eight bats netted at one locality were in "second growth thickets interspersed with dense stands of *Heliconia* sp. . . ." Gardner and Wilson (1971) reported that native Costa Ricans mentioned "finding small clusters of these bats hanging from the undersurface of 'platanillo' or wild plantain leaves (*Heliconia* sp.)." All reported localities of record for this species are in the Caribbean lowlands from Honduras south to Panamá.

We observed several roosting *E. alba* in Costa Rica in the summer of 1974 and confirmed that these bats do indeed roost under *Heliconia* leaves. They actually alter the shape of the leaf to produce a tent by severing the tissue on either side of the midrib along most of the length of the leaf causing the two sides to droop and form a shelter.

A systematic search for *E. alba* and their tents revealed that several species of *Heliconia* were utilized as roosts. It also became apparent that the species of host plants vary considerably in the habitats where they are found and in the size of individual leaves. A modal height for a small forest species (*H. tortuosa*) is about 1 m, whereas that of the clearing species (*H. imbricata*) is about 5 m.

These observations led us to ask the questions: (1) What does a typical tent of *E. alba* look like? (2) Does *E. alba* preferentially select one species of *Heliconia* for tent construction? (3) Is a certain size-class of leaves preferred?

METHODS

This study was conducted at the Organization for Tropical Studies' field station at Finca La Selva, 1 km SW Puerto Viejo, Heredia Province, northeastern Costa Rica. The vegetation in the immediate vicinity of the study area is essentially virgin rain forest. It is classified as Tropical Wet Forest in the Holdridge Life Zone system (Holdridge 1967). Slud (1960), Holdridge et al. (1971), Sawyer and Lindsey (1971), and Fleming (1974) have described the vegetation and habitat types at La Selva. Much of the climax forest in the area surrounding La Selva has been cleared for agriculture.

From 11 to 19 July 1974 we searched Finca La Selva for roosting tents constructed by bats. Approxi-

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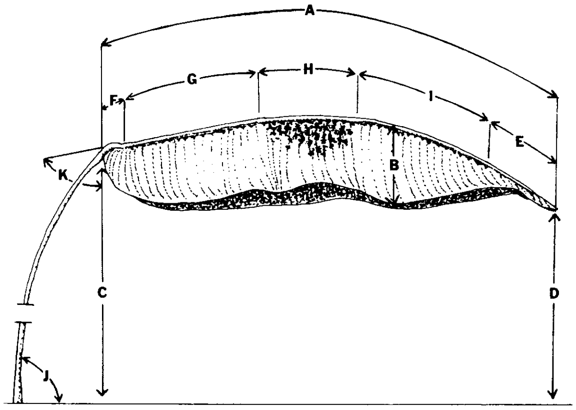

FIG. 1. Sketch of a typical tent formed by *E. alba* on a leaf of *Heliconia* showing the measurements taken from each tent. A—total length of leaf; B—width of leaf from midrib; C—height from base to ground; D—height from tip to ground; E—length of uncut tip; F—length of uncut base; G—distance from basal cut to punctures; H—width of punctures; I—distance from punctures to cut tip; J—angle of petiole; K—angle of leaf. See text for further explanation of measurements.

mately 10 km of trails on the property were checked as were all likely looking patches of *Heliconia.* For each *Ectophylla* tent, the species of *Heliconia* was identified and the following measurements were taken: total length of leaf (A), width of leaf from midrib to margin at widest point (B), height from base of leaf to ground (C), height from tip of leaf to ground (D), length of uncut tip of leaf (E), length of uncut base of leaf (F), distance from basal cut to puncture clusters (G), width of puncture clusters (H), distance from punctures to cut tip (I), angle of petiole (J), and angle of leaf midrib (K) (Fig. 1). To determine the relative abundance of each species within the primary study area, we identified to species and counted the individual *Heliconia* plants on a 2-km transect through the forest. Measurements were taken from all unfurled *H. tortuosa* leaves ($N = 40$) and a sample of 49 unfurled *H. imbricata* leaves on the random transect to determine the range of variability in leaf size for each species. None of these leaves had been altered to form tents. Four measurements from each leaf were incorporated by means of the following formula into a single value that represents the relative size and orientation of the leaf:

$$\text{height (C)} \times \text{length (A)} \div \text{width (B)} \times \text{angle (K)}.$$

A relative value for size of each leaf that had been converted into a tent was also calculated in like manner. The distribution of *E. alba* tents in each species of *Heliconia* relative to the abundance of the species in the forest was tested by chi-square analysis.

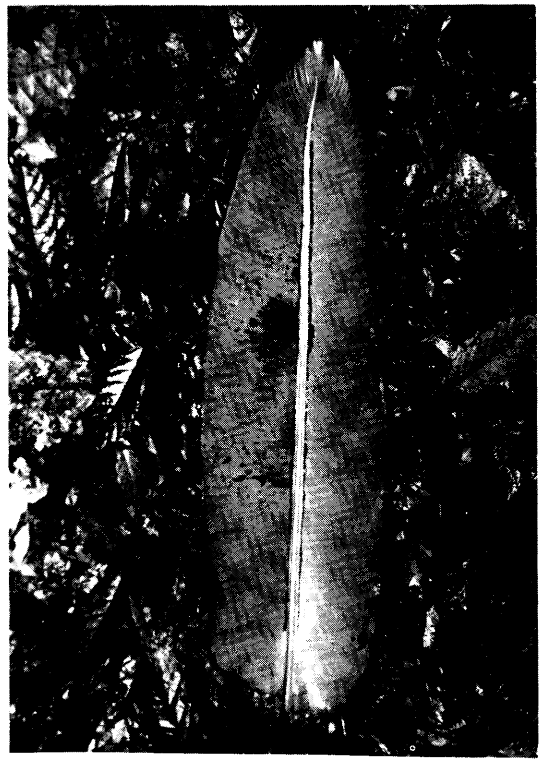

FIG. 2. Undersurface of *H. imbricata* leaf that has been cut along midrib by *E. alba* to form tent.

RESULTS AND DISCUSSION

Tents

To create a tent from a *Heliconia* leaf, *E. alba* severs the side veins and interconnecting tissue that extends at right angles from the midrib (Fig. 2). The two sides of the leaf thus collapse downward, hanging beneath the midrib (Fig. 3). Veins and interconnected tissues are not completely severed so that the sides of the leaf provide some support for the entire length of the cut. However, most of the structural support of the sides resides in the uncut basal and terminal sections of the leaf. The cuts do not extend either to the tip or to the base of a leaf (Table 1). The side veins are cut at a distance of roughly 5 mm from the midrib. Cutting the leaf destroys the majority of the vascular bundles, which probably accelerates death of the leaf.

Each leaf has an area near the center of the tent where both sides are punctured with numerous small holes. In all cases where bats were observed in the tents, they were hanging in the center of the punctured areas (Fig. 4). It is our hypothesis that the punctures are created by the claw of the pollex, perhaps when the bats land, enter the tent, or change position within the tent.

Tents of *E. alba* were found in five species of

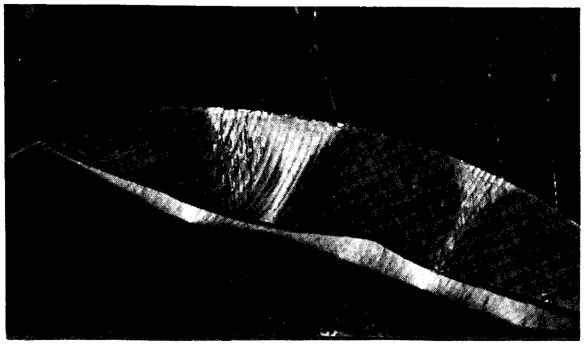

FIG. 3. Typical tent on *H. tortuosa* altered by *E. alba.*

FIG. 4. Colony of six *E. alba* roosting in a tent on *H. tortuosa.* Details of cut veins may be seen.

Heliconia: *H. imbricata, H. latispatha, H. pogonantha* (= *H. rostrata*), *H. tortuosa,* and *H.* sp. (undescribed) having a "red sword-like" flower (taxon no. 17 currently being described by G. S. Daniels and F. G. Stiles in a revision of the *Heliconia* of Costa Rica). Means or individual measurements are provided in Table 1 for the tents discovered in each of these five species of *Heliconia*. In general, tents on the various species of *Heliconia* were similar in dimension.

Selection of plant species

No observations of plant genera other than *Heliconia* being utilized for tent construction by *Ectophylla* were made at La Selva and elsewhere. Nevertheless, it seems unlikely that the Honduran white bat restricts its roost sites to the five species of *Heliconia* listed above. There are 9 species of *Heliconia* at La Selva and a total of 35 species in the genus is known to occur in Costa Rica. Furthermore, the five species we found with tents were also the species most commonly encountered.

Twenty-six *Ectophylla* tents were examined. *Heliconia imbricata*, the most common species at La Selva, contained 14 tents; *H. tortuosa*, the second most abundant species, had 9 tents. The three other species of *Heliconia* were relatively uncommon and only a single tent was located in each. We compared the distribution of tents on each species of *Heliconia* to the relative abundance of these species in the forest with a chi-square test. A chi-square of 1.997 ($p < 0.05$) indicates that *E. alba* chose leaves of each species in approximately the same ratio as they occur in the forest.

The frequencies of each relative size value for *H. tortuosa, H. imbricata,* and the tent leaves are plotted in Fig. 5. *Ectophylla alba* apparently selects for roost construction a size-class of leaves that is larger than the average *H. tortuosa* leaf, but smaller than the average *H. imbricata* leaf. The single tents found on *H. latispatha, H. pogonantha,* and the undescribed *H.* sp. also were within this size class.

TABLE 1. Data (means or individual measurements) collected from 26 tents constructed by *Ectophylla alba* on five species of *Heliconia*. Measurements for the first nine columns are in cm

Total length of leaf (A)	Width of leaf from midrib (B)	Height from base to ground (C)	Height from tip to ground (D)	Length of uncut tip (E)	Length of uncut base (F)	Distance from basal cut to punctures (G)	Width of punctures (H)	Distance from punctures to cut tip (I)	Angle of petiole (J)	Angle of leaf (K)	Relative size value
					H. imbricata ($n = 14$)						
103.6	16.5	161.5	192.0	25.3	17.1	33.5	19.8	27.4	74°	63°	0.62
					H. tortuosa ($n = 9$)						
82.3	13.4	155.4	173.7	19.2	5.8	25.0	16.5	17.4	73°	58°	0.80
					H. pogonantha ($n = 1$)						
51.8	12.2	134.1	134.1	6.1	1.5	15.2	12.2	15.2	45°	98°	0.19
					H. latispatha ($n = 1$)						
73.2	13.7	256.0	253.0	13.7	4.6	15.2	19.8	24.4	78°	50°	0.90
					H. sp. (undescribed) ($n = 1$)						
97.5	15.2	173.7	198.1	15.2	3.0	33.5	15.2	33.5	75°	73°	0.50

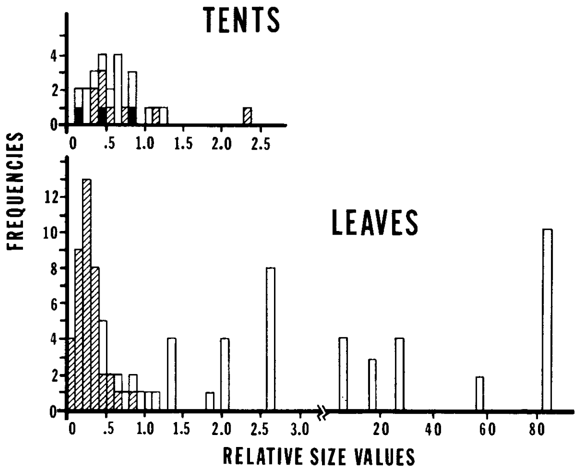

FIG. 5. Size distribution of 25 leaves of *Heliconia* that had been altered (upper histogram) by *E. alba* to form roosting tents compared to a random sample of unaltered (lower histogram) leaves of *H. imbricata* and *H. tortuosa*. Open bars represent *H. imbricata*, diagonal lines represent *H. tortuosa*, and black bars (upper only) represent single altered leaves of *H. latispatha, H. pogonantha,* and *H.* sp. (undescribed). Both histograms are drawn to the same scale.

Observations on Ectophylla alba

We observed 14 individuals of *E. alba* roosting under tents of cut *Heliconia* leaves during this study. Bats were found in groups of six, four, and two, and two bats were hanging singly. Additionally, six *Ectophylla* were captured in mist nets at La Selva. The cluster of four bats contained two adult males and two adult females; one of the single bats was an adult male. Bats in the other tents were not handled.

Colonies or individuals apparently were not restricted to roosting in a single tent over an extended period of time. Bats were observed using the same tent for more than 1 day on only two occasions. The colony of six bats was observed first on a clone of *H. imbricata* containing three tents, apparently of different ages. One tent was fresh, another was beginning to die, and the third was largely decomposed. The bats roosted for 2 consecutive days in the freshest tent. That tent was empty on the 3rd day, but a tent ≈ 75 m away, which previously had been unoccupied, contained a colony of six *Ectophylla* (presumably the same six bats). On the 4th day six bats were found on the original clone, but roosting in the middle-aged tent. For diurnal roosts, then, it appears that each colony of bats uses a series of tents that may or may not be constructed from closely associated leaves.

Evolution of tent construction

Only three other bats, all stenodermines, *Uroderma bilobatum, Artibeus watsoni,* and *Artibeus cinereus,* were known previously to be tent-makers. The first two are found sympatrically with *E. alba* in Central America. Barbour (1932) first reported that some bats may sever the veins of a leaf to produce a shelter. He noted that *U. bilobatum* did so by cutting the side veins in the leaves of an introduced palm, *Prichardea pacifica.* Chapman (1932) independently discovered that *A. watsoni* constructed tents by making cuts similar to those of *Uroderma*, but in a native palm, *Geonoma cuneata* (= *G. decurrens*), on Barro Colorado Island, Canal Zone. Goodwin and Greenhall (1961) have subsequently reported that *A. c. cinereus* roosts under palm leaves that have been cut similarly to those altered by *Uroderma.* Thus, the three previously known tent-makers utilize palm leaves and construct tents that are similar in design to those of *Ectophylla.* However, none has been studied in an attempt to determine which leaves are selected, why a tent is constructed, or how the system evolved.

For tent construction, *E. alba* appears to select leaves that grow approximately horizontal. This preferential selection provides the bats with some protection even before they alter leaf shape. The long, broad leaves of *Heliconia* serve as an efficient umbrella to protect the bats from rain and sunlight, both of which are already reduced by the forest canopy. Smaller leaves would probably not have enough strength to support the weight of the bats and larger leaves, growing more nearly vertical, would not provide such effective umbrellas.

Additional protection against terrestrial predators (such as opossums or snakes) accrues to the roosting bats because they are generally out of reach of a predator on the ground and the stems are not rigid enough to support the weight of most predators; thus potential predators jarring the flexible *Heliconia* leaves would inadvertently warn the bats. We observed that roosting bats readily took to flight when a tent leaf was jarred. Perhaps greater safety from terrestrial predators during roosting was a major selective force in the original choice of *Heliconia* leaves as roost sites. The bright white color of these bats, although presumably adaptive, provides little cryptic concealment.

Heliconia leaves that were naturally folded in a manner similar to the tent leaves were found occasionally. Such naturally folded leaves would provide better protection from the sun and rain than would normal leaves, but the folded leaves are usually older and hence would not provide shelter for any length of time. Such a leaf could be detrimental if it was weak and broke off easily under stress, for example, during a thunderstorm or an attack by a predator. By modifying a young, vigorous *Heliconia* leaf, *Ectophylla* appears to be creating an efficient roost site that may remain usable for a relatively long period.

Selection of size-class and angle of leaf is important to the effectiveness and longevity of the tent, and thus conveys a definite selective advantage for the bats.

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