Roosting Ecology of the Tent-Roosting Bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in Southwestern Costa Rica[1]

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ABSTRACT

We described the plants used as roost resources by *Artibeus watsoni* in southwestern Costa Rica, assessed roost fidelity, and compared roosting ecology between two sites, Golfito and Corcovado, which vary in the degree of human influence. A total of 349 tents from 25 different plant species were used by *A. watsoni* as roosts; some plant species (*e.g.*, *Carludovica palmata*, *Asplundia alata*, *Heliconia imbricata* and *Calathea lutea*) were modified into tents with significantly higher frequency than others. The highest tents above the ground were observed in *Philodendron popenoei* and *Rhodospatha wendlandii*, whereas tents in *Philodendron grandipes* and *A. alata* were significantly lower than any other species. *Asplundia alata* and *R. wendlandii* also had the highest frequency of leaves modified per plant. Fidelity of bats to tents was low, although bats used several tents intermittently within a restricted area. Males generally were more faithful to tents than females, although not significantly so. This observation, along with indirect evidence of leaf modification, suggests that males are primarily responsible for tent construction. The two study sites differed in the plants used for roosting and in tent fidelity. Bats in Corcovado used a greater variety of plant species for tent roosting, whereas bats in Golfito were more faithful, suggesting that roosting resources were scarcer at the latter site.

RESUMEN

Enumeramos la plantas utilizadas como perchas por el murciélago constructor de carpas *Artibeus watsoni* en el suroeste de Costa Rica, determinamos fidelidad de perchas, y comparamos la ecología de perchas entre dos sitios con diferentes niveles de alteración humana, Golfito y Corcovado. Un total de 349 perchas de 25 especies de plantas fueron utilizadas por *A. watsoni*, y algunas especies (por ejemplo *Carludovica palmata*, *Asplundia alata*, *Heliconia imbricata* y *Calathea lutea*) fueron utilizadas con mayor frecuencia que otras plantas. Las perchas halladas a mayores alturas sobre el nivel del suelo fueron *Philodendron popenoei* y *Rhodospatha wendlandii*, mientras las perchas usadas en *Philodendron grandipes* y *A. alata* se utilizaron a alturas significativamente mas bajas. *Asplundia alata* y *R. wendlandii* también mostraron la mayor cantidad de hojas modificadas por planta. El promedio de fidelidad a las perchas fue bajo, sin embargo los murciélagos utilizaron perchas intermitentemente en un área relativamente restringida. Los machos fueron en promedio mas fieles a las perchas que las hembras, aunque no significativamente. Esta observación, junto con evidencia indirecta de modificación de hojas, sugiere que los machos son primordialmente responsables de la construcción de carpas. Los dos sitios muestreados mostraron diferencias en las plantas utilizadas como percha y en fidelidad de carpas. Los murciélagos de Corcovado usaron una mayor variedad de especies como perchas y fueron menos fieles a estas, pero en Golfito los individuos fueron mas fieles, aunque utilizaron menos plantas. Esto sugiere, por lo tanto, que el recurso de perchas es mas escaso en Golfito.

Key words: Artibeus watsoni; Corcovado; Costa Rica; Golfito; roosting ecology; tent fidelity; tent-making.

ROOSTS ARE EXTREMELY IMPORTANT RESOURCES FOR BATS, who spend almost half of their lives occupying them. Thus, it is not surprising that events associated with roosting have played a major role in the evolution of these mammals (Kunz 1982). Structures used by bats include caves, rock crevices, and diverse man-made structures, although more than half of the worldwide bat fauna use plants for roosting (Kunz & Lumsden 2003). Plants are probably widely used by bats because they are ubiquitous compared to structures such as caves, although the former provide little protection from predators and extreme climatic conditions (Kunz 1982).

Among plant-roosting bats, few species alter plant parts to improve their roosting conditions (Kunz & Lumsden 2003). However, some species appear to modify leaves and other plant parts

(*e.g.*, flower and fruit clusters and stems) to form structures referred to as "tents." At least 20 species of tent-roosting bats have been described, most of which belong to the New World family Phyllostomidae (Barbour 1932, Foster & Timm 1976, Koepcke 1984, Timm 1984, Brooke 1987, Timm 1987, Brooke 1990, Zortea 1995, Kunz & McCracken 1996, Tello & Velazco 2003). Three species of the family Pteropodidae (Balasingh *et al.* 1993, Bhat and Kunz 1995, Tan *et al.* 1997) and one member of the family Vespertilionidae (Rickart *et al.* 1989) have also been observed roosting in tents. To date, only one species (*Cynopterus sphinx*, Pteropodidae) has been observed in the act of tent-making (Balasingh *et al.* 1995).

Almost half the species known to occupy tents are members of the New World genus *Artibeus* (family Phyllostomidae). These bats use at least 34 species of plants belonging to nine different families, and are modified into six architectural styles, namely palmate umbrella, pinnate, apical, bifid, paradox, and boat tents (Kunz &

Lumsden 2003). The most commonly used plant families are Palmae and Araceae, which together comprise more than half the plant diversity used by these bats for roosting.

Within the genus *Artibeus*, *A. watsoni* uses more plant species for roosting than any other species previously reported. The distribution of this small bat (*ca* 10 g) ranges from Veracruz, México through Central America to Colombia. *Artibeus watsoni* is usually found below 800 m above sea level, in semideciduous and evergreen lowland forests, second growth, and fruit groves (Reid 1997). It feeds primarily on fruits, although to a lesser extent may consume insects and pollen (LaVal & Rodríguez-H 2002).

Tent-roosting behavior in *A. watsoni* was first observed by Chapman (1932), and since then at least 20 species of plants have been reported as being used by this bat. Boinski & Timm (1985) observed tents in *Anthurium ravenii*, *Asplundia* sp., *Carludovica palmata*, *Asterogyne martiana*, *Geonoma* sp., *Cocos nucifera*, *Heliconia imbricata*, *Heliconia latispatha*, *Musa x paradisiaca* and *Calathea insingis* attributed to *A. watsoni*. Timm (1987) reported that this bat also used leaves of *Geonoma congesta*, *Geonoma cuneata*, *Bactris wendlandia*,*Welfia georgii*, *Asplundia euryspatha*, *Carludovica drudei* and *Cyclanthus bipartitus*. Among these, *A. watsoni* seems to preferentially select leaves of *Anthurium ravenii* and *Asterogyne martiana* located at specific heights above the ground (Choe & Timm 1985), usually preferring plants with tall, long leaves and thick rachises (Stoner 2000).

A considerable amount of information has been published on aspects of the roosting ecology of *A. watsoni*, such as the plant species used for roosting, although several elements of its roosting ecology remain unknown. For example, there is no quantitative information regarding roost fidelity, and whether fidelity varies among sexes. Additionally, no studies have examined variation in the roosting ecology and how human-altered environments may adversely affect this species. Thus, the aims of this study were to (1) describe the plants used by this bat in southwestern Costa Rica, specifically observing potential preferences for plant species; (2) determine short- and long-term roost fidelity and to contrast this fidelity among juvenile and adult males and females; and (3) to compare the roosting habits of this species between two sites, specifically to evaluate possible human influence on the ecology of these local populations.

METHODS

STUDY SITES AND SPECIES IDENTIFICATION.—This study was conducted at two sites in southwestern Costa Rica, in the province of Puntarenas, from June 2003 through September 2004. One site is in the Corcovado National Park (8°28′, 83°35′), a 42,468 ha park, from sea level to 550 m elevation. The other site is the 2810 ha Golfito Wildlife Refuge (8°38′, 83°11′), from sea level to 505 m elevation. The Corcovado site was located around the Sirena Research Station, in areas with distinct stages of forest regeneration, namely late secondary and undisturbed primary forests. The Golfito site, located near the Playa Cacao sector, includes a mixture of fruit groves and early to late secondary forests. These two sites differ greatly in the levels of human disturbance and in the relative

abundance of bats, which are greater in Golfito. In addition, bat populations sampled at Golfito are restricted to approximately 6 ha of useful habitat, because adjacent areas are either completely modified by humans or are inaccessible because of difficult topography with steep elevation of up to 230 m. Conversely, the forest in Corcovado has experienced little or no human disturbance, and there are no obvious topographic or anthropogenic barriers to dispersal such as those found in Golfito. Therefore, at Corcovado bats were sampled in approximately 100 ha of contiguous forests.

We identified bats based on the characteristics proposed by Timm and LaVal (1998) and Timm *et al.* (1999). We distinguished *A. watsoni* from the very similar *Artibeus phaeotis* based on the presence of a third lower molar in the former, which is frequently observed in approximately 85 percent of the individuals (Timm & LaVal 1998). This small molar was also present in more or less 80 percent of our study animals, and most bats that did not have a third lower molar were later identified as *A. watsoni* because they were observed roosting with individuals that had the molar.

SAMPLING PROCEDURES.—We conducted extensive sampling of potential plants at both sites to locate roosts occupied by *A. watsoni*. If leaves were modified into tents, we approached them cautiously to determine presence of bats. If bats were present, they were captured with hand nets, being careful not to damage the tent. Captured bats were individually marked with numbered plastic wing bands (A.C. Hughes Ltd.) and measurements such as length of forearm, reproductive condition, age, and sex were recorded. Before releasing the bats, we marked tents with flagging tape and individually numbered tags, and subsequently recorded data on height of tent above the ground, number of leaves modified, plant species, and group size. We also recorded the location of the tent using a Global Positioning System (GPS).

Because we may have overlooked tents using the above method, we also used radiotelemetry to complement our visual sampling. We fitted a total of 50 bats with radiotransmitters (Holohil Systems Ltd., Woodlawn, Ontario, Canada, model BD-2 and BD-2N; 0.47–0.51 g; 3.9–4.25% of the bat's body mass) during the 16-mo study period (June 2003–September 2004). Radiotransmitters were attached to adult males and females, and to a few volant juveniles using Skin Bond Cement. All juveniles foraged on their own, although one was still nursing and roosting with its mother, and the other two were already fully weaned and not roosting with other bats.

We used radio receivers (TRX-1000S, Wildlife Materials, Inc.) with three-element Yagi antennae to locate roosting bats during the day. We approached each occupied tent carefully to record the number of bats that occupied the roost. We placed a numbered tag near the tent, not on it, to avoid alerting the roosting bats, and then recorded the tent measurements specified above. Bats were located in their tent roosts as long as the radio transmitter remained active and attached to the bats for 5–17 d.

ROOST FIDELITY.—We determined roost fidelity by tracking radio tagged bats on a daily basis. Three behavioral categories of tent use were established: *STAY*, if bats remained in the same tent the day after initial observation; *MOVE*, if the bat moved to a previously

unoccupied tent; and *RETURN*, if the bat changed roost but returned to a previously used one. Fidelity was estimated using the following index:

$$F = \frac{[2(STAY) + 1(RETURN) - 1(MOVE)]}{STAY + RETURN + MOVE}$$

where *F* is a measure of fidelity of a single bat, *STAY* is the number of days a bat stayed in a single roost, *RETURN* is number of days the bat returned to previously used tents, and *MOVE* the number of times the bat was found in a different tent than the previous day, divided by the total number of observations. This index assumes that bats expressed higher fidelity when they stayed longer in a single tent than when the same tents were used intermittently. *F* can thus assume values of −1 (complete infidelity) to 2 (complete fidelity). Because bats seldom returned to the tent where they were initially captured, we recorded the behavior of bats beginning from the second day.

STATISTICAL ANALYSES.—We used one-way ANOVA to test the effect of plant species on group size, number of leaves modified and tent height. If significant, Tukey's pairwise comparison at $\alpha = 0.05$ was used to identify differences among plant species. Multiple linear regression was used to test for differences in roost fidelity among males and females, and between adults, subadults, and juveniles. Additionally, we used one-way ANOVA to test for site effect on tent height, number of modified leaves, and group size, and an independent samples *t*-test to determine if there were differences in roost fidelity among sites. Finally, we used Spearman's rank correlation coefficient to test for similarity in plant species used by the bats between the two study sites (Krebs 1999). If not statistically correlated, we further explored differences among the two study sites in plant species richness using the rarefaction method. This method is used for estimating the number of species expected in a random sample of individuals (Krebs 1999), thus allowing us to determine the estimated number of plant species used by the bats if sampling at both sites would have been the same. Rarefaction curves were generated separately for both study sites using EcoSim 7 (Gotelli & Entsminger 2004) and plotted together for further comparison. Values reported are means ± SD, and significance was assessed at an α of 0.05.

RESULTS

PLANTS USED FOR ROOSTING.—A total of 338 tents representing 25 plant species were used by *A. watsoni* during the 16-mo study period (Table 1). Thirty-six percent of the plant species used belonged to the aroid family Araceae, 12 percent to the palm family Arecaceae, and 12 percent to Heliconiaceae. All other plant families are represented by less than two species, although one of these families, Cyclanthaceae, is represented by almost 30 percent of the tents observed. The most commonly used plant species were *Carludovica palmata*, *Asplundia alata*, *Heliconia imbricata* and *Calathea lutea*. Others, such as *Pentagonia tinajita* and *Myriocarpa longipes*, were used only once.

In addition to the roosts included in Table 1, where use by *A. watsoni* was confirmed by capturing or radio tracking the bats, we also observed occupied tents in *Cocos nucifera*, *Pleiostachya pruinosa*, *Philodendron* sp., and *Calathea* sp. It is possible that the bats we observed were *A. watsoni* because of their small size, absence of a dorsal white line, and because we found them in areas where other similar tent-roosting bats were absent or very rare.

Tent architecture did not differ from the styles described for *A. watsoni* (Kunz *et al.* 1994; Kunz & Lumsden 2003, Table 1). Apical tents were observed in all aroids, in *Calathea* spp., *Artocarpus communis*, *Piper* sp., *Pentagonia* spp., and *M. longipes*. *Asterogyne martiana*, *Astrocaryum standleyanum* and *Asplundia alata* were modified into bifid tents and *Cryosophila guagara* and *Carludovica palmata* were modified into palmate umbrella tents. Finally, all species of *Heliconia* and *Musa* were modified as boat tents. Thus, of the 25 species used by *A. watsoni*, 16 were modified into apical tents (64%), 3 were bifid (12%), 2 were palmate umbrellas (8%) and 4 were modified into boat tents (16%).

Group size of bats did not differ significantly among plant species ($F_{14} = 1.32$, $P = 0.194$), but the number of leaves modified per plant varied significantly among some species ($F_{14} = 17.55$, $P < 0.001$; Fig. 1), as did tent height between roosts from different species ($F_{14} = 6.52$, $P < 0.001$; Fig. 1). For example, *A. alata* (3.18 ± 1.97, $N = 44$) and *Rhodospatha wendlandii* (3.10 ± 1.85, $N = 10$) averaged more modified leaves per plant than *C. palmata* (1.46 ± 0.63, $N = 43$) and *H. imbricata* (1.30 ± 0.64, $N = 42$). Additionally, *Cryosophila guagara* (4.71 ± 3.02 m, $N = 19$), *Philodendron popenoei* (5.90 ± 2.55 m, $N = 5$), *Philodendron pterotum* (4.18 ± 2.34 m, $N = 25$) and *R. wendlandii* (4.95 ± 1.57 m, $N = 10$) were modified into tents at greater heights in the understory than species such as *A. alata* (1.47 ± 0.53 m, $N = 46$) and *Philodendron grandipes* (1.23 ± 0.29 m, $N = 26$), which were among the lowest tents above the forest floor. A tent used by a satellite male in *Philodendron auriculatum* was the highest recorded at both study sites, and was located at approximately 12 m height. The lowest tents were found at 1 m, and were mostly observed in *A. alata* or *P. grandipes*, although a few tents of this height were recorded in terrestrial members of *A. ravenii*.

ROOST FIDELITY.—Bats in Golfito and Corcovado exhibited little short-term fidelity to tent roosts (0.99 ± 0.80, range = −1.0–2.0), although a few bats showed complete fidelity to their roosts. Neither sex nor age had a significant effect on roost fidelity ($R^2 = 0.02$, $F_{2,47} = 0.49$, $P = 0.61$), although females exhibited lower fidelity (0.90 ± 0.87, $N = 33$) than males (1.14 ± 0.67, $N = 17$), and juveniles had higher fidelity (1.12 ± 0.69, $N = 4$) than subadults (0.3, $N = 1$) and adults (0.99 ± 0.82, $N = 45$). Sample size for juveniles and subadults was too small to make statistically meaningful comparisons.

Long-term roost fidelity was not assessed for all tents recorded, although we did observe that leaves modified in plants such as *Carludovica palmata*, *Cryosophila guagara,* and *P. pterotum* were used as roosts for periods of more that 16 mo. In contrast, we found that tents located in banana-like plants, such as *Heliconia* spp.*, Calathea*

TABLE 1.   *Plant species, number of tents marked and previous reports on plants used for roosting by* Artibeus watsoni.

Plant family	Plant species	Total marked	Tent style	Previous reports
Araceae	*Anthurium ravenii*	9	1	Boinski and Timm (1985), Choe and Timm (1985)
	Monstera adansonii	1	1	
	Philodendron auriculatum	1	1	
	Philodendron sagittifolium	1	1	
	Philodendron grandipes	26	1	
	Philodendron popenoei	5	1	
	Philodendron pterotum	26	1	
	Rhodospatha wendlandii	10	1	
	Spathiphyllum wendlandii	2	1	
Arecaceae (Palmae)	*Asterogyne martiana*	7	2	Boinski and Timm (1985), Timm (1987), Kunz *et al.* (1994), Stoner (2000)
	Astrocaryum standleyanum	10	2	
	Cryosophila guagara	20	3	
Cyclanthaceae	*Asplundia alata*	47	2	
	Carludovica palmata	46	3	Boinski and Timm (1985), Choe and Timm (1985), Choe and Timm (1985)
Heliconiaceae	*Heliconia imbricata*	42	4	
	Heliconia latispatha	6	4	
	Heliconia sp.	6	4	
Marantaceae	*Calathea lutea*	35	1	
	Calathea inocephala	4	1	
Musaceae	*Musa x paradisiaca*	26	4	Boinski and Timm (1985), Timm (1987)
Moraceae	*Artocarpus communis*	1	1	
Piperaceae	*Piper* sp.	3	1	
Rubiaceae	*Pentagonia tinajita*	1	1	
	Pentagonia wendlandii	2	1	
Urticaceae	*Myriocarpa longipes*	1	1	

Tent style: 1 = apical; 2 = bifid; 3 = palmate umbrella; 4 = boat (Kunz *et al.* 1994).

spp., and *Musa* sp., remained usable for short periods, sometimes less than 1 mo.

DIFFERENCES AMONG THE TWO STUDY SITES.—Plant species used by *A. watsoni* between the two study sites, Golfito and Corcovado, were not significantly correlated ($R^2 = 0.33$, $P = 0.10$). Species richness of plants used for roosting was greater in Corcovado for any given number of tents sampled (Fig. 2). For example, if the number of tents sampled at each site is 50, then plant species used as roosts in Corcovado and Golfito would be 15 and 11, respectively, and when sample size increases to 100, plant diversity increases to 18 and 13. Plants used as roosts by *A. watsoni* in Corcovado, but not in Golfito, include *Philodendron auriculatum, Philodendron sagittifolium, Mon-stera adansonii, C. guagara, Heliconia latispatha, Heliconia* sp., *M. longipes, Pentagonia tinajita, Philodendron pterotum,* and *Piper* sp. (Fig. 3). Plant species used in Golfito, but not in Corcovado, were *A. communis, Spathiphyllum wendlandii,* and *Pentagonia wendlandi.* Other plants, such as *Asplundia alata, Asterogyne martiana, Astrocaryum standleyanum,* and *H. imbricata,* were used at both sites, although a greater number of tents were recorded in Corcovado. In contrast, *Calathea lutea, Carludovica palmata,* and *Musa* were more commonly used in Golfito.

Golfito had significantly fewer modified leaves per plant (1.72 ± 1.04, $N = 119$) than Corcovado (2.06 ± 1.44, $N = 186$, $F_{2,47} = 5.15$, $P < 0.05$; Fig. 4), but these leaves were occupied by significantly larger group sizes (2.72 ± 1.62 bats per tent, $N = 119$, $F_{2,47} = 10.59$, $P < 0.01$; Fig. 3) when compared to group
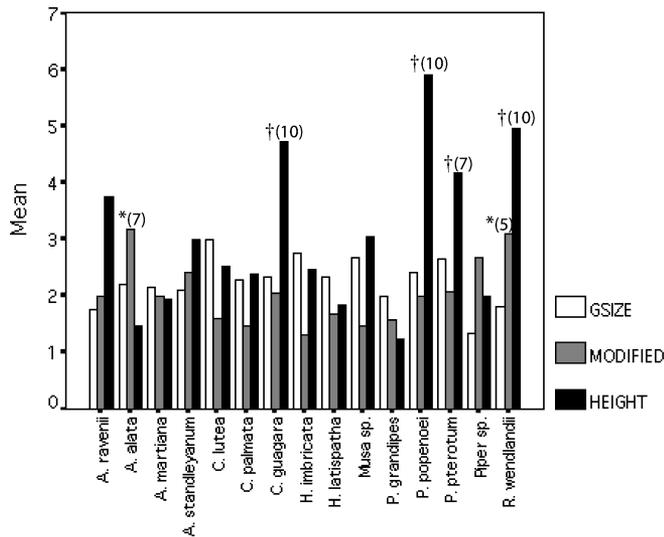
FIGURE 1.   Average group size (GSIZE), number of modified leaves (MODIFIED) and tent height (HEIGHT) of the 15 most common plant species used by *Artibeus watsoni* in southwestern Costa Rica. Examples of significant differences among species in number of modified leaves per plant and tent height are represented by the symbols * and †. The number in parentheses indicates how many species have significantly less modified leaves or how many have significantly lower tents. Complete species names are provided in Table 1.

FIGURE 2.   Rarefaction curve for plant species used as roosts by *Artibeus watsoni* in Corcovado and Golfito.

sizes in Corcovado (2.19 ± 1.24 bats per tent, $N = 191$). Average tent height did not differ between sites (Golfito: 2.61 ± 1.35 m, $N = 117$, Corcovado: 2.70 ± 1.81 m, $N = 191$, $F_{2,47} = 0.25$, $P = 0.61$). Short-term roost fidelity was significantly different between the two sites ($t_{48} = 3.04$, $P < 0.01$), and bats in Golfito exhibited significantly greater average fidelity (1.38 ± 0.59, $N = 20$) than in Corcovado (0.72 ± 0.83, $N = 30$).

DISCUSSION

PLANTS USED FOR ROOSTING.—We observed that *A. watsoni* in southwestern Costa Rica preferentially uses leaves for tent construction in four plant species: *Carludovica palmata*, *A. alata*, *H. imbricata* and *Calathea lutea*. The total number of tents used from these four species represents over 50 percent of the total roosts recorded. Our finding differs from that of Choe and Timm (1985), who also conducted their study at the Sirena Research Station. They observed that *Anthurium ravenii* was the most common plant species used for roosting by *A. watsoni*. Nonetheless, in our study, tents in *A. ravenii* represent <1 percent of the total roosts recorded. We believe that Choe and Timm (1985) may have overestimated the use of *A. ravenii* by *A. watsoni* because they did not confirm the presence of bats in each roost. At the field station where these studies were conducted, other tent-roosting species are known to use *A. ravenii*. Thus, it is essential to confirm the identity of bats in particular tents when assessing roost preference. Other studies conducted in Corcovado National Park (see Timm 1987) agree with our results
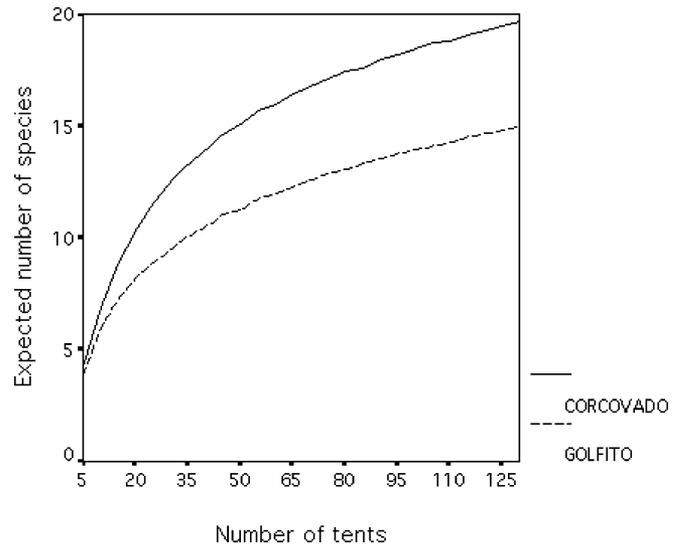
in that some of the most common plant species used by *A. watsoni* include *Heliconia imbricata* and *Carludovica palmata*.

In the course of our study, we noted that *A. watsoni* selects plants for roosting based on two criteria: abundance and permanence. For example, plants from the family Heliconiaceae and Maranthaceae are common at both study sites, and are often observed in patches of hundreds of individuals. Thus, we believe that *A. watsoni* uses these plants most often because they are abundant. However, other abundant plant species such as *C. inocephala*, whose leaves deteriorate rapidly following modification, are not commonly chosen as roosts, and *A. watsoni* seems to use this plant species only
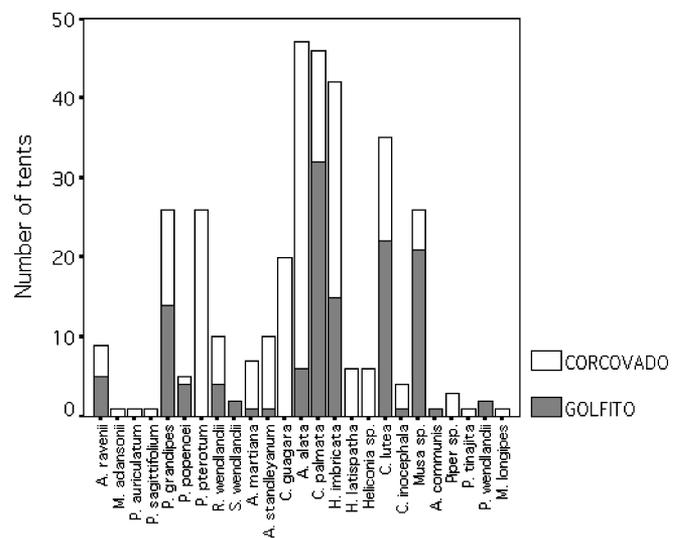

FIGURE 3.   Number of tents recorded for all plant species at both sites, Golfito and Corcovado. Complete species names are provided in Table 1.
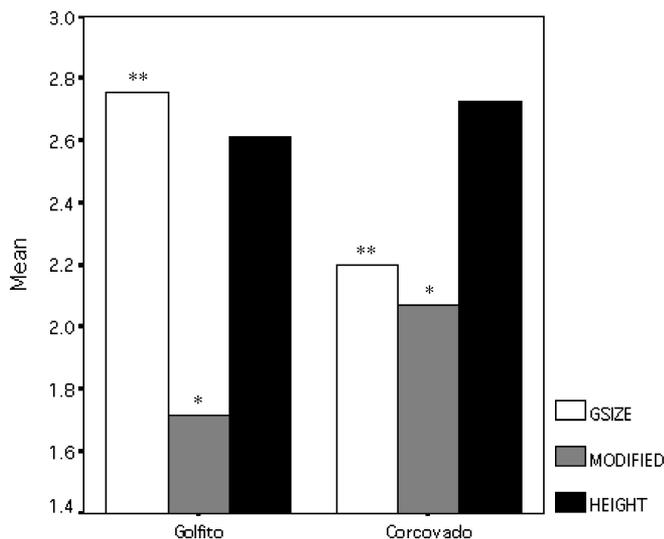
FIGURE 4.   Mean height of tents (HEIGHT), number of modified leaves (MODIFIED) and group size (GSIZE) for both sites, Golfito and Corcovado. *represents significant differences at $P < 0.05$, and **represents highly significant differences at $P < 0.001$.

in areas where more resistant leaves are not available. This low tent permanence of some plant species may not be influenced by the bats' leaf modification (Cholewa *et al.* 2001), but may be attributable to inherent poor leaf resistance. Other plant species that are uncommon at both sites, such as *C. palmata* and *A. alata*, are probably widely used because tents from these species persist for periods of more than a year. Thus, we suggest that *A. watsoni* prefers to modify leaves in plants that remain functional for long periods of time, minimizing the need for additional tent construction.

Adult and juvenile *A. watsoni* sometimes differed in the type of roosts they used. For example, volant juvenile males frequently occupied unmodified leaves, and subadult females used incomplete tents in plants that were typically not used by adults, such as *M. longipes* and *A. communis*. Young individuals less than 1 mo of age were always found roosting with their mothers, and thus seemed to occupy the higher quality tents used by adults. The tendency for young males and females to occupy low quality tents may be related to their need to establish a territory, so that young bats seeking a territory must first travel through areas where tents are already occupied by resident bats, and consequently must use whatever roost resources that are available.

We found significant differences in tent height and number of leaves modified per plant. For example, some climbers of the aroid family, such as *P. popenoei* and *R. wendlandii*, had significantly higher tents than the understory species *P. grandipes* and *A. alata*. This suggests that bats may not have particular preferences for tent height, but rather select roosts in a manner that represents availability of suitable leaves at restricted heights within a specific plant or habitat. Some plants also exhibited differences in the number of leaves modified per plant. For example, *A. alata* and *R. wendlandii* had significantly larger numbers of tents per plant, and *H. imbri-*

cata, *Musa*, *Carludovica palmata*, *P. grandipes* and *Calathea lutea* had fewer tents per plant. The number of tents counted per plant may reflect both tent persistence and leaf abundance. *Rhodospatha wendlandi*, for example, is a climber that sometimes has more than 30 leaves per plant clumped within a very small area on a tree trunk. Bats that construct tents probably take advantage of this and engage in substantial construction within a single plant. Conversely, *C. palmata* has few leaves per plant, and thus the number of potential tents per plant is more restricted. Tent permanence also may increase the chances of counting several tents in a single plant, as in the case of tents in *A. alata*, which appear to be usable for several years. Tents in *H. imbricata* and *C. lutea*, on the other hand, deteriorate so rapidly that they are no longer recognizable after 2 mo.

We expected to find differences in group size of bats among plant species, but our data provided no evidence for this. We assumed that larger tents of *Musa*, *H. imbricata*, *C. lutea*, and *P. pterotum* would contain larger groups, and that other tents, such as the small *Piper*, would only be able to support one or two individuals. Although group size generally increased in larger-leaved plants and decreased in smaller-leaved species, the relationship was not significant.

We found that roosts used by *A. watsoni* also were used by other tent-roosting species, such as *Vampyressa pusilla*, *Uroderma bilobatum* and *Artibeus jamaicensis*. We observed that a tent that was first used, and perhaps modified, by *V. pusilla* was later used by *A. watsoni*. Also, a tent used by *A. watsoni* was subsequently occupied by *U. bilobatum*. *Artibeus jamaicensis* was never observed roosting in a tent where we previously had seen *A. watsoni*, although the former was observed roosting in a very old tent located in an area where *A. watsoni* is very common. Tent-sharing has also been observed by others (Brooke 1987, Timm 1987, Timm & Clauson 1990, Timm & Lewis 1991, Kunz & McCracken 1996), and allows us to understand the important role that a common tent-making species such as *A. watsoni* may be playing for the entire tent-roosting assemblage.

Tent roosts may also be important for other organisms, such as wasps. We often attempted to capture what seemed to be a bat, only to find out that the bats were actually wasp nests. Timm & Clauson (1990) suggest that wasps may be an important factor reducing tent attractiveness, and once they occupy a tent the structure becomes almost unusable by bats. Nonetheless, we observed a roost that was alternatively used by a group of *A. watsoni* and wasps. We first captured a roosting group in this tent that was subsequently abandoned, only to be immediately occupied by wasps. The bats returned to the tent 8 mo later, when the wasps were still using the tent. One day after the bats had returned, the wasp nest was completely destroyed. This demonstrates that bats may reclaim tents that were occupied by wasps.

The number of plant species used for roosting by *A. watsoni* in this study greatly exceeded the number of previously reported plant species (reviewed in Kunz *et al.* 1994). We found, for example, eight new aroids, two new calatheas (*C. lutea* and *C. inocephala*), one new palm (*C. guagara*), and four new families: Moraceae, Rubiaceae, Piperaceae and Urticaceae. This list is further increased if we consider that tents of other plant species were observed in areas where

A. watsoni was very common, although we could not confirm that their leaves were used as tents by this bat species. Our results suggest that *A. watsoni* is the most generalist of tent-roosting species, and that methods such as radiotelemetry may be the best way to fully understand the roosting ecology of elusive tent-roosting bats that otherwise would be impossible to locate, mainly because visual sampling of tents may be biased toward more conspicuous roosts.

TENT FIDELITY.—Overall tent fidelity was very low, and bats seemed to often change roosts located within a restricted area. Several hypotheses have been proposed to explain why some bat species exhibit low fidelity to their roosts. For example, Boinski and Timm (1985) proposed that *A. watsoni* may often change tents due to predation pressure and Lewis (1996) suggested that parasite load may be an important factor influencing roost fidelity. Additionally, Lewis (1995) suggested that bats that occupy spatially abundant, less-permanent roosts are more likely to change roosts frequently. Avoidance of parasites may not play such an important role in the roosting ecology of this species because we observed that *A. watsoni* is rarely a host of ectoparasites. We did observe, however, that bats that were accidentally flushed from tents seldom returned to them and as a consequence exhibited low roost fidelity, providing evidence that predation pressure may play an important role in the roosting ecology of this species. Additionally, roost abundance seems to be an important factor influencing roost fidelity in *A. watsoni*, because in areas where roosts were extremely abundant, individuals showed lower fidelity, as has been observed in other species (Timm & Clauson 1990, Kunz & McCracken 1996, Vonhof & Barclay 1996, Willis & Brigham 2004).

We found no significant differences in roost fidelity among males and females, although males did show higher average roost fidelity compared to females. Storz *et al.* (2000) observed high roost fidelity among harem males in the short-nosed fruit bat (*Cynopterus sphinx*), which they attribute to a resource-defense strategy to secure access to breeding females. Likewise, Balasingh *et al.* (1995) noted that single males of the short-nosed fruit bat actively defended the tent which they constructed, and females subsequently occupied this tent. Increased male fidelity to tents suggests that males could be primarily responsible for tent construction. Our primary evidence of tent construction by males comes from observations we made one night while recording night activities of an adult male fitted with a radiotransmitter. We observed that the male had suddenly ceased flying at peak foraging time, and remained at the same place for 30 min, after which he resumed his foraging activities. The next day we located the male with a female and her pup roosting in a new tent constructed in the same place where the male had paused the night before. This behavior, along with frequent observations of solitary males in tents and nightly foraging activities where males return to tents more frequently than females, suggest that males of *A. watsoni* construct tents that function as a defendable resource used by females for rearing young and for males to gain mating access to females. Except for anecdotal observations, few published studies attribute tent construction to males. For example, Balasingh *et al.* (1995) observed a single male of *C. sphinx* in the act of roost

construction, and Muñoz-Romo & Herrera (2003) observed leaf-modification behavior by male *Artibeus lituratus*.

Although we did not collect specific data on long-term roost use, we did observe that bats used tents for periods of more than 16 mo. Notwithstanding, *A. watsoni*, and perhaps other species, may modify leaves in such a way that allows the plant to maintain water flow to damaged areas and thus remain suitable for roosting for relatively prolonged periods (Cholewa *et al.* 2001). We observed that even though bats seldom returned to tents where they were first captured, some of them return after some time, especially if no damage is made to the tent. This suggests the importance of preventing damage to a tent when attempting to capture roosting bats, because these tents remain an important resource even after bats have been captured in such structures.

DIFFERENCES AMONG POPULATIONS AT THE TWO STUDY SITES.—The roosting ecology of populations of *A. watsoni* in Golfito and Corcovado differed in several ways. First, the population at Corcovado used more plant species as roosts than bats at Golfito, and bats from Golfito exhibited higher fidelity and larger group sizes in tents. These differences between the two study sites may be explained by human activities and their effect on local resources and habitats. For example, the *A. watsoni* population in Golfito is restricted to only a few areas where roosting resources are available, such as lowlands near human settlements, which have been, and continue to be, severely modified for agricultural purposes. Additionally, humans have over-harvested plants that are important resources for *A. watsoni*, such as *Asterogyne martiana*. In contrast, Corcovado National Park has large interconnected areas of primary and late secondary forests, which have long remained unaffected by human activities. Thus, human modification of habitats in Golfito has reduced availability of native plants, such as *A. alata*, *H. latispatha*, *Philodendron pterotum,* and *Piper* sp., which would otherwise be frequently used by this bat for roosting.

Bat density was another difference between the two study populations that may influence the roosting ecology of *A. watsoni*. *A. watsoni* in Golfito has average population densities five times higher than Corcovado, probably as a consequence of low habitat availability and a subsequent population encroachment. As a result, fewer roosting resources at Golfito must be shared among a larger number of bats, thus leading to higher roost fidelity at this site. Additionally, increased population densities in Golfito most likely result in an increase in group size because of a higher encounter rate and fusion of groups, as suggested by Shankar Raman (1997) for axis deer.

These three differences between the study populations in Golfito and Corcovado, namely plant diversity used for roosting, roost fidelity, and group size, suggest that human activities may currently play an important role in the roosting ecology of *A. watsoni*. Although we do not know whether these differences may cause a negative impact on population dynamics of this very common tent-roosting species, it is possible that the same habitat modifications that affect *A. watsoni* may influence the roosting ecology of other less common bat species in a similar way. Understanding the potential threats of human activities on the roosting ecology of this and

other bat species thus becomes essential in developing appropriate conservation strategies for local bat assemblages.

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