Macro and Microhabitat Associations of the Peter’s Tent-Roosting Bat (Uroderma bilobatum): Human-Induced Selection and Colonization?

Maria Sagot1,4, Bernal Rodriguez-Herrera2,3, and Richard D. Stevens1
1 Department of Biological Sciences, Louisiana State University, Baton Rouge LA 70803, U.S.A.
2 Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica
3 Reserva Biológica La Tirimbina, Sarapiquí, Costa Rica

ABSTRACT

Understanding species-specific habitat selection is essential to identify how natural systems are assembled and maintained, and how emerging natural and anthropogenic disturbances will affect ecosystem function. In the Neotropics, Peter’s tent-roosting bat (Uroderma bilobatum), known to roost in forests, has become abundant in human-modified areas. To understand how habitat characteristics in both intact forest and human-modified areas influence the presence and density of U. bilobatum, we characterized habitat use at two scales (macrohabitat and microhabitat) and used logistic and poisson regressions to determine which habitat characteristics best predicted the presence and density of U. bilobatum within each scale. Moreover, we performed a redundancy analysis to determine which habitat scale explained more variation. As these bats are obligate tent roosters, we used tent as a surrogate for bat presence and density. We found that both macrohabitat and microhabitat scales explained variation in presence and density. Characteristics of the microhabitat scale, however, had higher predictive power, revealing that U. bilobatum preferentially inhabits areas with high density of coconut palms. Coconut palms were introduced recently in the Neotropics and are found only in human-modified areas. Therefore, we hypothesize that U. bilobatum is expanding its range into these areas following the expanded distribution of this exotic plant species.

Abstract in Spanish is available in the online version of this article.

Key words: Chiroptera; Costa Rica; habitat selection; habitat scales; roost selection; tents.

Human-induced habitat alterations are ubiquitous. The wide distribution of mosaic landscapes consisting of configurations of intact and human-altered vegetation have forced many species to inhabit novel environments worldwide (McGarigal & Cushman 2002, Knowlton & Graham 2010). Little is known, however, about the effect of these rapid changes on natural populations (Wiens et al. 1993, Ims 1995). As a result, understanding habitat selection under contemporary scenarios, and especially how novel landscapes affect population dynamics, will inform a wide variety of ecological, evolutionary and conservation-related questions (Dunning et al. 1992, McRae et al. 2008, Knowlton & Graham 2010).

To detect organismal responses to altered landscapes, studies must be broad enough in spatial extent to incorporate multiple areas of suitable and unsuitable habitat (Hanski 1994). Although species-specific habitat preferences are widely known, such large-scale studies often preclude detailed investigation of individual behavior or population level demographics that are also major influences on population level patterns of habitat selection. Including such preferences that are associated with specific behavioral, morphological, and physiological adaptations may enhance understanding of how organisms improve fitness and success in particular habitats (Morris 1987). Moreover, animal populations can respond to habitat in both a coarse- and fine-grained fashion (Morris 1987). Coarse-grained characteristics can be defined by macrohabitat and are typified by broad, discrete habitat types (e.g., forest type, land use category) that vary at landscape scales. Fine-grained characteristics encompass heterogeneity within a particular habitat and are often defined by microhabitat characteristics (e.g., particular patches of habitat and/or, roost characteristics). To accurately examine habitat responses and reach relevant ecological conclusions regarding habitat use, different spatial scales should be considered (Morris 1987, Stapp 1997, Stevens & Tello 2009). Information on relevant scales can be used to study population dynamics and fitness and to propose education, management, and conservation strategies that merge human needs and ecosystem requirements of organisms.

Peter’s tent-roosting bat (U. bilobatum) provides an ideal species to explore response to human-modified habitats and the importance of incorporating different spatial scales while investigating habitat selection. U. bilobatum is one of the largest and more gregarious tent-roosting bats (those capable of constructing roosts called tents) with groups varying from 1 to 59 individuals, consisting mostly of females and their dependent young (Baker & Clark 1987). This fruit-eating bat promotes plant community diversity and secondary succession by facilitating seed dispersal, especially in small and medium forest fragments (Fleming & Heithaus 1981, Fleming 1988, Gorchov et al. 1993). Prior observations indicate that U. bilobatum is becoming more abundant in human-altered habitats, and may prefer to roost in
a number of introduced plant species (Timm & Lewis 1991, Lewis 1992, LaVal & Rodríguez-Herrera 2002). *Uroderma bilobatum* population density might respond to differences in abundance and distribution of plants in forest and human-modified areas, and these differences might have consequences for population growth and resilience to disturbances due to variation in reproductive success and sex ratios (Caro 1998). Changes in population dynamics of this important seed disperser due to differential roosting habits both in forests and human-modified habitats might have detrimental consequences to persistence of small forest fragments. Therefore, if humans facilitate use of non-native habitats, it is important to understand how this process might affect the roosting ecology of Peter’s tent-roosting bats.

The aim of our study was to investigate what habitat characteristics influence the presence and density of *U. bilobatum*. Our objectives were: (1) to identify possible predictors of *U. bilobatum* presence at the local level; (2) to determine which scale (macrohabitat or microhabitat) best predicts *U. bilobatum* habitat selection; and (3) to determine the predictive power of habitat variables on density of tents and bats.

**METHODS**

**STUDY SITE AND SAMPLING.**—Fieldwork was conducted at two sites in Costa Rica between June 2007 and May 2009. Sites were selected because of different climate, vegetation, and anthropogenic influences. The Central Volcanic Cordillera separates both sites and is an important biogeographic barrier in Costa Rica (Janzen 1983). The first site is Sarapiquí, located in Heredia province, on the Caribbean versant (10°23' 55.88" N, 84°08’ 06.23" W). Elevation ranges from 37 to 187 m (see Sanford et al. 1984 for a more detailed description). The second site, Carara, occurs in Puntarenas province, in the Central Pacific region of the country (9°44’ 55.78” N, 84°37’ 1.29” W) (see Boza & Cevo 1998 for a more detailed description).

To assess abundance and distribution of *U. bilobatum* in forests and human-modified areas of Sarapiquí and Carara, we visited all plant species known to be used as roosts (*Cocos nucifera*, *Attalea rostrata*, *Musa acuminata*, *Cryosophila guarara*, *Carludovica* spp., and *Heliconia* spp.; Kunz & Lumsden 2003, Rodriguez-Herrera et al. 2007). Tents are conspicuous structures and can be observed from long distances. Moreover, *U. bilobatum* is the only tent-roosting bat known to construct tents in coconut palm (*Cocos nucifera*) and the palm *Attalea rostrata* (Kunz & Lumsden 2003). Therefore, all tents found in these two palm species were assumed to be built by *U. bilobatum*. Tents made in banana plants (*Musa acuminata*), guarara palms (*Cryosophila guarara*), hat palms (*Carludovica* spp.) and heliconias (*Heliconia* spp.) can be used by other tent-roosting bats (Rodriguez-Herrera et al. 2007). Nonetheless, those made by *U. bilobatum* can be distinguished by the size and configuration of cuts made in the leaf which are longer and less consistent than those made by other species. We searched for bats and tents in good condition in forested and human-modified habitats. Tents were considered in good condition when there was no sign of deterioration or physical damage, such as lack of leaflets or severe necrosis.

In the forest, we followed available trails (covering a distance of approximately 10 km, distance determined on a georeferenced map in ArcGIS 9.3.3; ESRI 2009) and randomly located ten 2 km transects per site. Spatial locations of random transects were selected from a georeferenced map of the area in ArcGIS 9.3.1 (ESRI 2009). Human-modified areas were defined as plantations, grassland, or urbanized sites. In these areas we followed available streets and roads, covering approximately the same distance covered in the forest (~30 km, distance determined on a georeferenced map in ArcGIS 9.3.2; ESRI 2009). To ensure similar effort at both sites, we searched for plants and tents that were located within 100 m from trails and roads. Numbers of bats were determined by observation. If tents were high, binoculars were used. *Uroderma bilobatum* roost in lines along the rachis when using coconut tents. Moreover, as individuals have two distinctive white stripes on their face and light penetrates through the leaflets, it is easy to distinguish individuals from beneath. We recorded the geographic location (geographic coordinates), number of tents, and number of bats for every plant visited.

We used the random number generator function in Microsoft Excel, to select 100 plants per habitat type with tents (including all plants where bats were found) and 100 plants without tents per habitat (forest and human-modified) in Carara. In Sarapiquí, no bats were found in the forest. Thus, data from this site consisted in 112 tents (including tents where bats were found) and 288 plants without tents. This was to obtain a balanced number of plants (total N = 800) because we found more plants used to build tents in human-modified areas than in the forest, and more in Carara than Sarapiquí.

From the selected plants, we described habitats at macro and micro scales. Macrohabitat was defined as discrete habitats in the landscape based on land use (human-modified/forest), site (Carara vs. Sarapiquí), and distance to the forest (measured from a georeferenced map of the areas in ArcGIS 9.3.1; ESRI 2009). Microhabitat characteristics were measured in a 20 m diameter plot around the 800 plants selected for analyses. Variables measured were: amount of herbaceous cover, number of bushes (woody plants with a dbh less than 20 cm), number of trees (woody plants with a dbh larger than 20 cm), average tree diameter at breast height (dbh), tent height, plant height, plant species (represented by dummy variables in analyses; Suits 1957), and average light penetration measured with a quantum light meter (Hydrofarm West, model 2053), taken at cardinal points. Density of bats was determined as the number of individuals divided by the area of the 20 m diameter plot (bats/314 m²) and as plants can have multiple tents, tent density was defined as the number of tents per plot (tents/314 m²).

**ANALYTICAL METHODS.**—Macrohabitat scale. To predict bat or tent presence based on macrohabitat, we performed two separate stepwise multiple logistic regressions (Crawley 2007). We removed from the model the non-significant and collinear variables using a model selection under the stepwise AIC procedure implemented in the package bootstepAIC (Venable & Ripley 2002, Austin &
Tu 2004, R v.2.10, R Development Core Team 2009). This test uses a bootstrap procedure (1000 bootstrap samples) to return the variables that significantly contribute to the model (Venables & Ripley 2002, Austin & Tu 2004). The procedure simulates a new dataset by subsampling with replacement, then refitting the model using the new dataset and running the stepAIC algorithm. After 1000 iterations, we tallied how many times each variable was selected. Only variables selected in 100 percent of the iterations were included in the analyses (Venables & Ripley 2002, Austin & Tu 2004, R v.2.10, R Development Core Team 2009).

To determine effects of distance to forest, site, and land use on density of bats or tents, we conducted two separate analyses of covariance (ANCOVA) where density of bats or tents was the response variable, site and land use were two categorical explanatory variables, and distance to forest was a continuous covariate. We removed from the model the non-significant variables using the function ‘step’ from the package Stats (R v.2.10, R Development Core Team 2009), which tests all terms to see whether they are needed in the minimal adequate model. The selection criterion used was AIC (Crawley 2007). Because in this case we were only interested in using macrohabitat (site, habitat and distance from the forest) to predict higher densities of bats or tents, this analysis was conducted only for plots where we found both bats and tents. Analyses were conducted in R (v.2.10, R Development Core Team 2009).

Microhabitat scale. To determine ability to predict the presence/absence of bats and tents based on microhabitat, we again performed a stepwise multiple logistic regression (Crawley 2007) where presence/absence of bats and tents were used as response variables and microhabitat characteristics were predictor variables. We also performed the model selection procedure as described in the macrohabitat scale analyses and repeated regressions with variables selected by this procedure. We used Poisson regression to predict variation in density of bats and tents based on microhabitat because residuals were not normally distributed. As in this case we were interested in predicting higher densities of bats and tents based on microhabitat scale variables, Poisson regression was performed only for plots where we found both bats and tents. Analyses were conducted in R (v.2.10, R Development Core Team 2009).

Relative predictive abilities of different scales. To determine relative ability of each habitat perspective to predict the presence/absence and density of bats or tents, we performed variation partitioning based on redundancy analysis (RDA; Legendre & Legendre 1998). We were interested in unique variation explained by a particular scale (e.g., macrohabitat or microhabitat) after controlling for the other scale. To obtain the relative ability of each habitat component to predict densities of bats or tents, we selected only plots where we found both bats and tents. We further subdivided microhabitat scale into two different components: (1) structural, characterized by variables describing the area surrounding the roosts (amount of herbaceous cover, number of bushes, number of trees, and average dbh) and (2) roost, characterized by variables describing roost characteristics (tent height, plant height, plant species). By subdividing microhabitat, our goal was to ascertain the importance of roosts compared with other microhabitat variables in predicting the presence and density of *U. bilobatum*. Variables were standardized for the analyses using the function ‘standardize’ from the package dscl in R (v.2.10, R Development Core Team 2009), which rescales numeric variables to have a mean of 0 and standard deviation (sd) of 0.5, so that the scaled regression coefficient corresponds to a change from mean −1*sd to a mean +1*sd. Binary variables are rescaled to have a mean of 0 and a difference of 1 between their categories. Variation partitioning analysis was conducted in VarCan (v.1, Peres-Neto et al. 2006).

**RESULTS**

A total of 7597 individual plants used as roosts by *U. bilobatum* were sampled across both study sites. We found tents in 10 percent of sampled plants (*N* = 764) corresponding to 6 different species (Table 1). These 764 plants contained a total of 1606 tents, of which only 14 percent (*N* = 228) were occupied (Table 1). Habitat information was obtained for 107 of the 228 occupied tents. At both sites combined, we found a total of 588 bats occupying 228 tents. The median group size per tent was 2 (range 1–58).

**Macrohabitat scale: predicting presence and density of bats and tents.**—Bats. Regression analysis indicated differences among plots regarding bat presence or absence based on land use, site, and distance to the forest; however, explained variance was low (*R*² = 0.020; *df* = 245; *P* < 0.001). Overall, plots containing bats were more numerous in human-modified habitats

<table>
<thead>
<tr>
<th>Plant taxa</th>
<th>Attalea rostrata, Caribudoria sp., Cocos nucifera, Cryosophila</th>
<th>Guanarara, Heliconia sp., Musa acuminata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>Carara</td>
<td>Sarapiqui</td>
</tr>
<tr>
<td>Habitat type</td>
<td>Human-modified</td>
<td>Human-modified</td>
</tr>
<tr>
<td>Number of plants</td>
<td>1828</td>
<td>3355</td>
</tr>
<tr>
<td>Plants with tents</td>
<td>267</td>
<td>425</td>
</tr>
<tr>
<td>Number of tents</td>
<td>543</td>
<td>801</td>
</tr>
<tr>
<td>Number of bats</td>
<td>336</td>
<td>224</td>
</tr>
</tbody>
</table>

**Table 1.** Number of plants, number of plants with tents, number of tents, and number of bats, of the species *U. bilobatum* found after sampling similar areas (determined by a georeferenced map on ArcGIS v9.3), at two different habitat types (forest and human-modified) in Carara National Park and surrounding areas on the Pacific slope, and Sarapiqui in the Caribbean slopes of Costa Rica.
of Carara. No plots containing bats were found in the forest of Sarapiqui. Moreover, regression between bat density and macrohabitat variables showed that site was the only significant factor (Fig. 1A). Higher densities of bats were found at Carara (0.900 ± 3.000 (SD) ind/plot in Carara vs. 0.420 ± 1.300 (SD) ind/plot in Sarapiqui; \(R^2 = 0.110; F_{1,103} = 5.092; P = 0.002\)).

**Tents.** Logistic regression indicated that tents are not distributed randomly among land use categories, site, and distance to the forest; however, explained variance was low (\(R^2 = 0.020; df = 796; P = 0.003\)). ANCOVA indicated that there was an effect of site on tent density, but it depended on distance to the forest (10.1 ± 1.4 tent/km\(^2\) in Carara and 13 ± 1.2 tent/km\(^2\) in Sarapiqui; \(R^2 = 0.050; F_{1,10} = 5.091; P = 0.006\); Fig. 1B).

**Microhabitat Scale: Predicting Presence-Absence and Density of Bats and Tents.**—**Bats.** Microhabitat characteristics explained 22 percent of variation in the presence/absence of bats (\(R^2 = 0.220; df = 245; P < 0.001\)). For both sites, areas with more bats contained higher numbers of coconut palm, *C. nucifera* (Beta coeff. = 3.710; \(P < 0.001\)) for tent construction that ranged in heights from 8 to 15 m (Beta coeff. = 0.342; \(P < 0.001\); Fig 2A) and possessed many tents with heights between 5 and 10 m (Beta coeff. = −0.153; \(P < 0.001\); Fig. 2B). Tree diameter also contributed significantly to explained variation (Beta coeff. = 0.0017; \(P = 0.001\)). Microhabitat characteristics explained 14 percent of the variation in density of bats (\(R^2 = 0.140; df = 106; P < 0.001\)). At both study sites, higher densities of bats were found in habitats with higher numbers of coconut palm, *C. nucifera* (Beta coeff. = 0.600; \(P < 0.001\)) with heights that ranged from 8 to 15 m (Beta coeff. = 0.103; \(P = 0.003\)) and tents with heights ranging from 5 to 10 m (Beta coeff. = 0.0043; \(P = 0.05\)), fewer trees of large diameter (Beta coeff. = −0.010, \(P = 0.003\)), few bushes (Beta coeff. = 0.021; \(P = 0.009\)), and abundant light penetration (Beta coeff. = −0.001; \(P < 0.001\)).

**Tents.** Microhabitat characteristics explained 87 percent of the variation in the presence/absence of tents (\(R^2 = 0.870; df = 796; P < 0.001\)). Presence of tents was associated with plants with heights that ranged from 8 to 15 m (Beta coeff. = −0.451; \(P < 0.001\)), tents with heights that ranged from 5 to 10 m (Beta coeff. = 1.948; \(P < 0.001\)), and few or no bushes (Beta coeff. = −0.014; \(P < 0.001\)). Microhabitat variables explained 20 percent of the variation in density of tents (\(R^2 = 0.200; df = 310; P < 0.001\)). Higher densities of tents were associated with the presence of *C. nucifera* (Beta coeff. = 0.255; \(P < 0.001\)), *C. guaguara* (Beta coeff. = 0.723; \(P < 0.001\)), and *Cariniana* sp. (Beta coeff. = −0.612; \(P < 0.001\)). Higher density was also associated with habitats with few or no bushes (Beta coeff. = −0.002; \(P < 0.001\)).

**Relative Importance of Scales in Predicting Presence and Density of Bats and Tents.**—**Bats.** Microhabitat and macrohabitat variables combined explained 22 percent of the variation in terms of presence/absence of bats (\(R^2 = 0.220; P < 0.001\); Fig. 3A). Microhabitat accounted for more unique variation (11%) than macrohabitat (5%) with 6 percent jointly accounted for by both sets of variables.

Micro and macrohabitat combined explained 23 percent of the variation in terms of bat density (\(R^2 = 0.230; P = 0.030\); Fig. 3B). Macrohabitat accounted for more unique variation (13%) than did microhabitat (10%).

**Tents.** Micro and macrohabitat combined accounted for 64 percent of the variation for in the presence/absence of tents (\(R^2 = 0.640; P = 0.001\), Fig. 3C). Microhabitat accounted for 62 percent of unique explained variance while macrohabitat explained 1 percent.

Micro and macrohabitat combined accounted for 21 percent of the variation for in density of tents (\(R^2 = 0.210; P = 0.001\); Fig 3D). Microhabitat had the highest predictive power in explaining tent density (18% of unique variation), while macrohabitat explained 2 percent of unique variation.

**Relative Contribution of Roost, Structural, and Macrohabitat Components.**—**Bats.** All three components (macrohabitat, structural, and roosts) combined explained 22 percent of the variation in terms of the presence/absence of bats (\(R^2 = 0.220; P < 0.001\); Fig 4A). From this explained variation, roost characteristics had the highest predictive power (11%
unique variation). Macrohabitat explained 8 percent of unique variation. Structural characteristics accounted for only 1 percent of unique variation.

All three components combined explained 23 percent of the variation in bat density ($R^2 = 0.230$; $P = 0.030$; Fig 4B).

Macrohabitat accounted for most of the explained unique variation (13%). The roost component accounted for 7 percent, and structural component 3 percent.

**Tents**: The three components combined accounted for 63 percent of the variation for presence/absence of tents.
(R^2 = 0.630; P = 0.001, Fig. 4C). Only the roost component accounted for significant unique variance (60%).

The three components combined accounted 19 percent of the variation in density of tents (P = 0.001; Fig. 4D). The roost component had the highest unique predictive power in explaining tent density (13%). Structural accounted for 2 percent, while macrohabitat explained only 1 percent of unique variation in density of tents.

**DISCUSSION**

At Carara, *U. bilobatum* was more common in human-modified areas where introduced coconut palms (*C. nucifera*) are more abundant, and was less common inside the forest, where it uses native species, namely guagara palm (*C. guaguara*) and the palm *A. rostrata*. At Sarapiqui, *U. bilobatum* is also more common in human-modified areas, again, corresponding with higher density of *C. nucifera*. Moreover, it was absent inside the forest. We presume that this might be related to the fact that plants such as *A. rostrata* and *C. guaguara* are naturally rare or nonexistent in the area. After dividing the microhabitat scale into structural and roost components, we found that structural components were poor predictors of presence and density of *U. bilobatum*. In addition, characteristics of the roost component (plant height, tent height, plant species) have the greatest ability to predict the presence and density of tents. There is usually substantial variation in natural environments and correlations that are only low or moderate are not uncommon in ecological work (Hill & Lewicki 2007). Despite substantial variation, it is important to highlight that we were able to explain a substantive amount of the variation in the presence and density of bats and tents. Although some of the R^2 values found were low, patterns in habitat use by *U. bilobatum* emerged, indicating that habitat characteristics influence distribution of bats and tents.

**TENTS VERSUS BATS AS PREDICTORS OF HABITAT SELECTION.**— Macro and microhabitat scales were better predictors of tent presence and density than bat presence and density (Fig. 3). The fact that we could only predict small amounts of variation in bat presence or density is likely related to a smaller bat sample size compared to tent sample size. Nonetheless, *U. bilobatum* is an obligate tent-roosting bat (Baker & Clark 1987, Timm & Lewis 1992, Kunz & Lumsden 2003, LaVal & Rodriguez-Herrera 2002, Rodriguez-Herrera et al. 2007). Thus, the presence of tents reflects the presence of bats. Moreover, although tent-roosting bats that occupy tents of short lifespan, such as *Ectophylla alba*, build and inhabit one tent at a time (Rodriguez-Herrera et al. 2007), the bats that use tents of longer lifespan, such as *U. bilobatum*, may build many tents of similar size and use one as a primary roost.
species that build tents of long lifespan, as is the case of *U. bilobatum* and *Dermanura watsoni* are known to build and utilize multiple tents for short periods of time (Lewis 1992, Storz et al. 2000, Kunz & Lumsden 2003, Chaverri & Kunz 2006, Campbell 2008, Sagot & Stevens 2012). Some groups switch between tents on a weekly or even daily basis (Lewis 1992). This nomadic behavior is more common in tent makers that use long lasting tents (Sagot & Stevens 2012). Because of this, it is not uncommon to find empty tents that were occupied the day before and *vice versa*. This nomadic behavior makes it more difficult to predict the presence of bats based only on the presence of groups. Moreover, as refuges are one of the most important factors impacting bat survival and fitness (Kunz & Lumsden 2003), the mere presence of tents can be considered a good predictor of habitat use by *U. bilobatum*. Because these tents are ephemeral, presence of tents in good condition reflects recent habitat use.

**Importance of scale in habitat selection.**—Organisms can respond to their environments at multiple scales (Morris 1987). Associations at one habitat scale may influence and constrain relationships at broader or finer scales; however, investigators addressing habitat selection have often conducted their studies at single and frequently quite different scales (Wiens 1989, Orians & Wittenberger 1991, Gorrensen et al. 2003). Not surprisingly, failure to appreciate scaling differences among organisms has lead to mixed results and disagreement.

Because roost sites are a critical resource that most bats are committed to for long periods of time, roost characteristics (*i.e.*, roost component) often may be important determinants of habitat selection (Orians & Wittenberger 1991). Individuals can travel long distances from a safe roost to foraging sites and many species fail to reproduce if adequate roosts are not available, even if food supplies are abundant (Orians & Wittenberger 1991). Thus, it is not surprising that roosting habits influence local and global distribution, population density, foraging and mating strategies, social structure, and seasonal movements (*e.g.*, Altringham 1996, Vonhof & Barclay 1996, Kunz & Lumsden 2003). By investigating habitat associations from macrohabitat and microhabitat scales, we found that microhabitat (specifically roost characteristics) often is the most important scale, which reflects distribution of plants for tent construction.

*Uroderma bilobatum* was found roosting in six different plant species that are morphologically similar (Fig. S1). The fact that *U. bilobatum* preferentially selects plants species with very specific leaf morphologies and heights (Kunz & Lumsden 2003) suggests that this bat uses a specific search image to find leaves for tent construction. Thus, given that tent-roosting bats construct tents only in specific plant species, it is reasonable to assume that their distribution and habitat use would be influenced by distribution of these plant species. Although abundances of bats and tents are higher in human-modified areas, *U. bilobatum* is not found far from forest patches (Baker & Clark 1987). Thus, we hypothesize that roosting in plants in human-modified areas, especially coconut palms (*C. nucifera*), reduces time and energy spent looking for plants in which to build new tents and allows use of multiple active tents in close proximity. Moreover, higher abundances of these plants, compared with native plants used in the forest, and similarities in their morphologies, can also facilitate finding suitable roosts. In addition, arboreal animals such as squirrels and capuchin monkeys, as well as birds of prey such as double-toothed kites, constitute a significant cause of mortality for tent-roosting bats (Boinski & Timm 1985, Souza et al. 1997) which might be reduced outside forest areas. Further investigation is needed to verify this point.

**Habitat colonization and human-induced expansion in *U. bilobatum.*—At a local scale, our results suggest that current distribution of *U. bilobatum* may be influenced by abundance of plants suitable for tent construction. Moreover, introduction of non-native plants such as *C. nucifera* appear to have facilitated expansion to areas where native plants are not present, filling gaps in local distribution. This palm is native to coastal areas of Southeast Asia (Malaysia, Indonesia, Philippines) (Chan & Elevitch 2006, Baudouin & Lebrun 2009) and was probably introduced into West Africa and the Caribbean (including the Atlantic and Pacific coasts of Central America) by European explorers (Harries 1978) or Polynesians (Baudouin & Lebrun 2009). Another recently introduced plant that now is widely used in human-modified areas by *U. bilobatum* is banana (*Musa acuminata*). This plant was also introduced from the Indo-Malaysian, Asian, and Australian tropics (Langdon 1993, Nelson et al. 2006). In addition, *Carludovica* spp. are used for tent construction both in forested, but mainly human-modified areas. They are native to South and Central America (Harling 1958), but have recently been used as both an ornamental and a crop plant (Harling 1958), thereby increasing in abundance in human-modified areas. Due to the rather recent introduction of these plants to Costa Rica, it is reasonable to assume that *U. bilobatum* historically roosted in native plants such as *Attalea* spp. and *Cryosophila* spp. Because the non-native plants have the preferred architecture for tent construction, upon their arrival to the Neotropics, *U. bilobatum* has recently switched to use these plants (*i.e.*, coconut palms).

**Implications for conservation.**—Although *U. bilobatum* is a widely distributed species, to our knowledge, this is the first study that presents a detailed description of habitat preference at different spatial scales and addresses how scale may have affected distribution and density of this Neotropical bat. We found that *U. bilobatum* is selecting habitat primarily based on microhabitat (roost characteristics), in particular presence of plants such as coconut palms (*C. nucifera*). Distribution of *U. bilobatum* may have been positively affected by geographic expansion of plants used for tent construction.

In the last decade, there has been an increased interest in species that inhabit human-modified areas (Chace & Walsh 2006). Although it is widely accepted that knowledge of urban species will comprise a significant component of future global biodiversity, the ecology and distribution of urban species remain poorly understood. While *U. bilobatum* is still present in forest patches, using native plants species as roosts, we have found that it has become abundant in human-modified areas such as yards, agricultural plantations, or cattle ranches. Although speculative, greater use of coconut palms in human-modified areas might be related to higher abundances of these plants, compared with...
native plants in forests. Differences in abundance of populations inhabiting these two different habitats can have direct consequences on effective population size \( N_e \), population growth rate and consequently, on the resilience of a population to exploitation and speed of population recovery (Caro 1998). This is because higher densities alter variation in reproductive success (Caro 1998). Moreover, tent-roosting can be the last dispersers of medium and large seeds in small forest patches (Melo et al. 2009). Because \( U. \) bilobatum is historically a very abundant species, we can presume that changes in habitat use by this bat can affect seed dispersal in small forest patches, where other mammals or birds have already disappeared. Understanding how different environmental characteristics affect distribution and density of these populations will be extremely important to define optimal management strategies able to assure long-term survival.

ACKNOWLEDGMENTS

We thank E. Alvarado, J. Arce, C. Chavarría, D. Mora, Carara National Park, CONAGEBio, Tirimbina Rainforest Center, SINAC and EZ for their helpful collaboration in Costa Rica. We are especially grateful to K. Montero for her crucial support in the field and valuable discussions and feedback.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Similarity between plant species in forest and human-modified areas, commonly used for tent construction by \( U. \) bilobatum.


LITERATURE CITED


