

The effects of micro- and macro- habitat variables on tent construction in the tent-roosting bat *Artibeus watsoni* on the Osa Peninsula, Costa Rica.

Abstract

Bats spend half of their lives in their roosts, which play vital roles in the life histories of the bats that occupy them. More than half of all bat species roost in foliage. Within the Neotropics, 17 species of bat are known to modify foliage into structures referred to as “tents”. Of these species, Thomas’s fruit eating bat (*Artibeus watsoni*) uses the widest range of plant species for roosts, constructing five different tent types. However, the factors influencing the distribution and quantity of tents are not fully understood for this species. The aims of our study were to investigate whether [1] micro-habitat characteristics influence the number of tents on individual plants and [2] macro-habitat features influence the frequency of plants used for tent-roosting in the surrounding landscape. Our results demonstrate that the distribution of tents was influenced by proximity to fresh water, with 48.8% of tents within 100 m of fresh water. Additionally, *A. watsoni* constructed tents in sheltered habitats with a high cover abundance of trees. These types of habitat areas should be targeted for conservation efforts to conserve this species.

Keywords: Chiroptera; *Dermanura watsoni*; Thomas's fruit-eating bat; bat roost; roosting requirements; roosting ecology; roost selection; tent-building.

Introduction

Bats spend more than half of their lives in their roosts (Kunz and Lumsden, 2005; Altringham, 2011). Consequently, morphological, physiological and behavioural characteristics of many bat species have evolved as a result of their roosting ecology. Roosts play vital roles in the life histories of their occupants. They, for example, facilitate complex social interactions, mating, hibernation and the rearing of young (Kunz and Lumsden, 2005). At the same time, roosts provide protection from adverse weather conditions, aid in the conservation of energy and provide refuge from predators and parasites (Kunz and Lumsden, 2005; Rodríguez-Herrera, Medellín and Timm, 2007; Altringham, 2011). Of the more than 1,400 extant bat species currently identified (Simmons and Cirranello, 2020), more than half roost in some form of plant structure in an obligatory, or facultative, manner (Kunz and Lumsden, 2005). Twenty two species roost in leaves modified by the bats (known as tents). Of these species, 17 are found in the Neotropics (Rodríguez-Herrera, Medellín and Timm,

2007). The protection and understanding of roosting requirements is paramount to their conservation, particularly against anthropogenic pressures which, according to the Food and Agriculture Organisation of the United Nations (FAO), are likely to increase as the human population rises from 7.6 billion to a predicted 10 billion by 2050 (FAO, 2018).

Artibeus watsoni is one of the most well studied species of ‘tent-roosting bat’. Whilst studies have outlined the leaf-selection for tent construction (Choe and Timm, 1985; Stoner, 2000), how the tents are constructed (Timm, 1987) and behavioural aspects of tent use (Chaverri *et al.*, 2007; Chaverri, Gamba-Rios and Kunz, 2007), these studies tend to focus only on one specific tent type and little research has been undertaken to investigate how habitat variables affect tent-roosting in *A. watsoni*. Research on Peters’s tent-roosting bat (*Uroderma bilobatum*) demonstrated that micro-habitat (i.e., number of coconut palms and bushes) and macro-habitat (i.e., distance to forest edge) variables influence the presence and abundance of tent roosts (Sagot, Rodríguez-Herrera and Stevens, 2013) but this has not been studied in other tent-roosting species. Given the importance of *A. watsoni* for seed dispersal, forest regeneration (Melo *et al.*, 2009) and to a lesser extent pollination (LaVal and Rodríguez-Herrera, 2002), there is a need to fill the knowledge gaps in the macro- and micro-habitat factors affecting tent-roosting in this species, to better design conservation strategies to protect it.

We hypothesised that [1] micro-habitat characteristics influence the number of tents on individual plants used for tent-roosting, and [2] macro-habitat features influence the frequency of plants used for tent-roosting in the surrounding landscape.

Materials and Methods

Study Area

We conducted the study between 4th of June and 21st of July 2018 in the Carate Wildlife Refuge which encompasses 123 ha of protected forest and beach habitats on the Osa Peninsula, part of the Osa Conservation Area (ACOSA), Costa Rica (SINAC, 2018b). Carate is situated on an ecotone, bordering the mature, primary, tropical forests located in, and just outside of, Corcovado National Park and the modified secondary tropical forests surrounding it, combined with highly disturbed areas that have been cleared for small roads (Sanchez-Azofeifa *et al.*, 2002). The ACOSA experiences an average of 5,500 mm of rainfall in mountainous areas and 3,500 mm of rainfall in coastal areas annually (SINAC, 2018a).

Sampling Method

Over the course of the study period, we sampled six 1 km transects at least once per week for a period of six weeks. We searched for plants known to be used by bats for tent construction systematically within a 10 m belt zone on either side of the transect line, using binoculars for taller plants (Stoner, 2000). The selected transects were 1 km in length and homogeneous in habitat type. To gain data representative of the study area, we selected two transects that were in each of the highly disturbed, secondary and primary habitat types present.

Once host plant types were located, we systematically searched them visually for tents. For each tent, we recorded data that could be gathered from a distance (e.g. tent construction type, as per illustrations found in Kunz *et al.* (1994)). Tents were then approached carefully and in silence to avoid disturbing roosting bats, should they be present. If bats were present, some data (namely estimation of micro-habitat variables and tent measurements) could not be collected without potentially causing bats to abandon their roosts. *A. watsoni* is not the only species of tent-roosting bat known in the area, as we also observed *U. bilobatum* roosting nearby in Corcovado. However, tents constructed by *U. bilobatum* was distinguished from those of *A. watsoni* by the size and configuration of bite marks, being longer and less consistent (Sagot, Rodríguez-Herrera and Stevens, 2013; Villalobos-Chaves *et al.*, 2013).

Bat Identification

We counted and identified resident bats using external phenotypic features such as presence of dorsal stripe, colour of pelage and shape of tragus and by established habitual differences such as known tent construction type and using species distribution maps (Timm and LaVal, 1998; Reid, 2009; Kunz and Fenton, 2005). For the purposes of this study, the species of bats found in tents were presumed to be the architects (Stoner, 2000). We visited occupied tents daily after the initial encounter (except one occasion due to access constraints) until the tent in question was no longer occupied, at which point data that could only be gathered in the absence of bats were recorded.

Environmental Micro- and Macro- Habitat Variables

We collected micro-habitat data in the field by estimating the percentage cover of the surrounding vegetation within a 20 m radius of each plant that was used for tent-roosting. We measured the following variables: percentage cover of abundance of bushes (woody plants with a DBH of < 20 mm), trees (woody plants with a DBH of > 20 mm) leaf litter, herbaceous cover (non-woody plants) and open water (Sagot, Rodríguez-Herrera and Stevens, 2013).

For each tent found in good condition, we identified and recorded the species of host plant using field guides (Condit, Perez and Daguerre, 2011; Gargiullo, Kimball and Barbara, 2008). We measured the height of the modified leaf (in cm above ground) using a Tacklife laser distance measurer (range and incrementation: 40 m x 0.05 m), aimed at the centre of the leaf, where possible, from directly below with the rear of the device placed on the ground. If this was not possible (as was the case with some tents positioned on cliff edges) we used Pythagoras's theorem to calculate the height of the tent measuring the distance to a surface directly underneath the centre of the leaf and the hypotenuse (distance diagonally from the device to the centre of the leaf).

We used the same technique to measure the height of the plant used for tent-roosting (using the highest leaf). We also measured the number of tents per plant, number of those tents occupied, aspect of leaf (degrees), length of leaf from the point along the rachis where the leaf began to the very tip (cm), rachis diameter recorded using Vernier callipers along the thickest part of the rachis (mm) and width of leaf measured across the widest section (cm). Our survey method excluded unfinished tents and tents where measurements could not be collected safely.

We quantified macro-habitat data retrospectively using GIS. All plants that were used for tent-roosting were marked using a GPS device (model: Garmin GPS map 62s), and using QGIS software (QGIS, 2019) we measured: distance (m) to sea, distance (m) to nearest fresh water source (known rivers were mapped out using GPS racking) and elevation (masl). We measured the distance to the sea because It was not possible to measure distance (m) to forest edge in isolation from other habitats due to forest edge in all cases corresponding with the presence of the sea.

Statistical Analyses

We performed a chi-squared analysis in R (R Core Team, 2020) to assess distribution of tents and host plants over the three habitat types. To determine the effect of habitat variables on number of tents per tree, we used the *glm* function in R to run a generalized linear model (GLM) with a Poisson error structure (Zuur, Hilbe and Leno, 2013). In this model, we set the number of tents as the dependent variable with the percentage of cover of leaf litter, bush, water body, tree, canopy and herbaceous cover, as well as tree and canopy height as predictors. We excluded from this analysis three data points that were outliers and we did not include four variables in the Poisson GLM (i.e., altitude, distance from the sea, tree diameter and cover abundance of bare ground) that were strongly correlated with other variables in the

model. More specifically, altitude was correlated with cover abundance of trees whereas distance to sea correlated with tree diameter, cover abundance of bushes and cover abundance of fresh water. Similarly, tree height correlated with tree diameter and cover abundance of leaf litter correlated with cover abundance of bare ground. We used the *step* function in R to select the model with the best combination of predictors that best explained variation in the dependent variable. The GLM model was not over dispersed which confirmed its validity (Zuur *et al.*, 2013).

We categorised the micro-habitat variables into the following groups:

- aspect (degrees): 0-36, 37-72, 73-108, 109-144, 145-180, 181-216, 217-252, 253-288, 289-324, 325-360
- tent height (m): 0-50, 51-100, 101-150, 151-200, 201-250, 251-300, 301-350, 351-400, 401-450, 451-500, 501-550, 551-600, 601-650, 651-700
- blade width (cm): 0-25, 26-50, 51-75, 76-100, 101-125, 126-150, 151-175.
- rachis diameter (mm): 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12

For each variable, we ranked the categories from 0 to the maximum number of categories for that specific variable and used Spearman's rank correlation test to assess whether the number of plants hosting tents significantly increased, or decreased, as category values of micro-habitat variables increased/decreased.

Results

Bat Identification

We recorded a total of 117 tents on 61 individual host plants. These consisted of four architectural types (bifid, umbrella, apical and boat-style tents), constructed on five different host plant species (*Carludovica palmata*, *Anthurium ravenii*, *Heleconia* spp., *Musa acuminata* and *Cocos nucifera*). We recorded a total of 15 *A. watsoni* bats. Because bats encountered during counts from inspections of the same tents on subsequent days could not be identified individually, we considered the minimum count as the highest count from any given tent on any visit. We found *A. watsoni* in all tent types and in all species of plant.

The longest period for which a tent was continuously occupied was eight days (umbrella-style tents in a *C. palmata* along a primary transect); eight tents were used for one day only. The highest number of bats in a tent at one time was three. This occurred in the same tent with at least five individuals using the tent, as we observed three adults initially, with two

adults and one pup present on the subsequent day (apical-style tent in *A. ravenii* along a secondary transect).

Overall, bats occupied 12.12% of tents ([Table **Error! Reference source not found.**]). The transects with the highest percentage of occupancy and most tents were those in highly disturbed habitats, each with three different occupied tents, whilst primary habitat transects had the lowest percentage of occupancy with a single bat. The results of the chi-squared analysis showed no significant difference between the three habitat types for number of tents ($\chi^2 = 3.3729$; $(df) = 2$; $p = 0.1852$) or number of plants hosting tents ($\chi^2 = 2.5902$; $(df) = 2$; $p = 0.2739$).

[Table 1]

Environmental Micro- and Macro- Habitat Variables

The step-wise model selection procedure revealed that the best GLM model included: tree height, distance from nearest fresh water source, cover abundance of bushes, cover abundance of trees, cover abundance of canopy and cover abundance of water. This model shows that cover abundance of trees is the only significant positive predictor (Table 2) indicating the numbers of tents increased as the cover abundance of surrounding trees increased ([Figure 1]).

[Figure 1]

[Table 2]

Spearman's rank correlation analysis showed that altitude and distance from sea were not correlated with the number of plants ([Table 3]), yet the number of plants was negatively correlated with the distance from fresh water bodies ($r_s(10) = -0.69$, $p = 0.013$) with the number of plants used for tent building decreasing dramatically > 100 m from fresh water sources ([Figure 2]) and 48.8% of all plants hosting tents < 100 m of fresh water.

[Figure 2]

[Table 3]

Neither aspect, blade width, nor rachis diameter of the leaves were significantly correlated with the number of tents. However, there was a negative trend, albeit insignificant, with regard to tent height ($r_s(12) = -0.53$, $p = 0.051$) with tents more frequently around 151 - 200 (cm) from the ground ([Table 4]).

[Table 4]

Discussion

Our results demonstrate that tent construction by *A. watsoni* was dependent on habitat variables at both macro and micro spatial scales. Specifically, we found that the number of plants used for tent-roosting increased significantly within 100 m of fresh water sources whilst the number of tents used per plant increased with the percentage of cover abundance of trees within 20 m of the host plant.

Occupancy of tents by bats (average 12.12%) was similar to that observed in other studies (Rodríguez-Herrera, Medellín and Timm, 2007; Sagot, Rodríguez-Herrera and Stevens, 2013). Primary habitat transects had the lowest rate of occupancy. Our results differ from those of Chaverri *et al.* (2007) who found that roost fidelity is related to roost availability with less available roosting opportunities leading to higher rates of occupancy. Given that the home range of *A. watsoni* is small (ca. 3.6 ha) (Chaverri, Quirós and Kunz, 2007), the distance between some transects was such that a degree of overlap in the roosting range of individual *A. watsoni* was possible between neighbouring transects and, in some cases, between habitat types.

Habitat type had no significant effect on the number of tents or the number of plants with tents. Many non-independent variables may influence tent construction type and plant species used to construct tents even in the same area and habitat type (Choe and Timm, 1985;

Chaverri and Kunz, 2006b; Rodríguez-Herrera, Medellín and Timm, 2007; Villalobos-Chaves *et al.*, 2016; this study).

Plants selected for the construction of tents most frequently occurred within 100 m of fresh water sources, suggesting that distance to fresh water influences the selection of plants suitable for tent-building. In general, bat species richness and activity are higher around permanent or ephemeral water bodies (Razgour *et al.*, 2010). Various species of bat select their roosts based primarily on distance to water sources (Jenkins *et al.*, 1998; Evelyn, Stiles and Young, 2004; Korine, Daniel and Pinshow, 2013; Korine *et al.*, 2016). Bat activity around permanent water sources increases in periods of drought (Geluso and Geluso, 2012), hence proximity of roosts to water sources could decrease during Costa Rica's dry season. It could also decrease in the rainy season, when *A. watsoni* females become pregnant (Chaverri and Kunz, 2006a), because lactation increases the demand for water intake up to three times that of the norm required by female bats to successfully rear their young (Adams and Hayes, 2008). In support, we observed females with pups in tents near water. On the other hand, in rainforests the diversity of flora is dependent on proximity to water (Ghazoul and Douglas, 2010), therefore the distribution of tent types may be a consequence of the habitat requirements of individual plant species rather than plant preferences of *A. watsoni*.

We found a significant positive correlation between number of tents and the percentage cover of trees in the immediate habitat. By contrast, Sagot, Rodríguez-Herrera and Stevens (2013) found a negative correlation between the presence of tents in plants constructed by *U. bilobatum* and the amount of surrounding tree and bush cover, and a high density of tents on single plants with few, or no bushes, in the immediate area. *U. bilobatum* will readily roost in human modified habitats (Sagot, Rodríguez-Herrera and Stevens, 2013), whereas *A. watsoni* prefers to roost in natural forests (Ripperger *et al.*, 2015). Further, *U. bilobatum* and *A. watsoni* differ in their roosting ecology regarding the plant species they use to construct tents and where they build them. They also differ morphologically: *U. bilobatum* is larger (~ 3mm forearm and 11 mm head and body length) and heavier (~ 5 g) than *A. watsoni* (Reid, 2009) which may restrict its aerial agility, inhibiting its ability to manoeuvre through denser forest than the smaller and more agile *A. watsoni*. Thermoregulation may also explain the correlation between number of tents and tree cover. Tents constructed in *C. nucifera* by *U. bilobatum* are usually located in open habitats, allowing them to heat up more readily and save energy that would otherwise be expended through thermoregulation (Sagot, Rodríguez-Herrera and Stevens, 2013; Rodríguez-Herrera *et al.*, 2016). However, the pinnate-style tent

constructed by *U. bilobatum* is less efficient at retaining heat than that of the tents used by the Honduran white bat (*Ectophylla alba*) which are similar to those used by *A. watsoni*. The poor thermoregulatory qualities of tents constructed by *U. bilobatum* is related to their lack of roost defence, whereas *E. alba* females defend their roosting resources (Rodríguez-Herrera, Medellín and Gamba-Rios, 2005; Rodríguez-Herrera *et al.* 2016). *Artibeus watsoni* males also defend their roosts, and the territories surrounding them (Chaverri, Schneider and Kunz, 2008; Chaverri *et al.*, 2007). Moreover, *U. bilobatum* will roost in large groups (towards 50) and *E. alba* exhibit synchronized parturition (Brooke, 1990; Rodríguez-Herrera *et al.*, 2016), but *A. watsoni* roost in small groups with females often leaving the young in the tents whilst foraging (Chaverri *et al.*, 2007). This may limit the ability of *A. watsoni* to lower the cost of thermoregulation by huddling in groups, thus forcing them to roost in tent types with better heat retention provided by plants predominantly in forest understory.

Bats may build tents in habitats with high tree cover for increased protection from predators. In fact, roosting bats are at risk of predation from various monkey species, including *Saimiri oerstedii*, *Cebus capucinus* and *Harpagus bidentatus* that may more easily find tents in open habitats (Boinski and Timm, 1985). We observed both *S. oerstedii* and *C. capucinus* along transects.

To conclude, our results highlight the importance of conserving the riparian habitats and the natural forests that *A. watsoni* occupy at both micro and macro spatial scales. This is important given *A. watsoni*'s position as a key species in forest regeneration through seed dispersal. Further, *A. watsoni* is prone to losses in genetic diversity through low connectivity between habitats (Ripperger *et al.*, 2013). Because these habitats are under immense pressure from anthropogenic activities (Junk, 2013), there is an urgent need for further study of the roosting ecology of all tent-roosting bat species to ensure their long-term survival.

References

- ADAMS, R. A. and M. A. HAYES (2008) Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*. 77(6): 1115–1121.
- ALTRINGHAM, J. (2011) *Bats From Evolution to Conservation*. 2nd ed Oxfordshire, Oxford University Press.
- BOINSKI, S. and R. M. TIMM (1985) Predation by squirrel monkeys and double-toothed kites on tent-making bats. *American Journal of Primatology*. 9(2): 121–127.
- BROOKE, A. (1990) Tent selection, roosting ecology and social organization of the tent-making bat, *Ectophylla alba*, in Costa Rica. *Journal of Zoology*. 221(1): 11–19.

- CHAVERRI, G., M. GAMBA-RIOS and T. H. KUNZ (2007) Range overlap and association patterns in the tent-making bat *Artibeus watsoni*. *Animal Behaviour*. 73(1): 157–164.
- CHAVERRI, G. and T. H. KUNZ (2006a) Reproductive biology and postnatal development in the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae). *Journal of Zoology*. 270(4): 650–656.
- CHAVERRI, G. and T. H. KUNZ (2006b) Roosting ecology of the tent-roosting bat *Artibeus watsoni* (Chiroptera: Phyllostomidae) in southwestern Costa Rica. *Biotropica*. 38(1): 77–84.
- CHAVERRI, G., O. E. QUIRÓS, , M. GAMBA-RIOS and T. H. KUNZ (2007) Ecological correlates of roost fidelity in the tent-making bat *Artibeus watsoni*. *Ethology*. 113(6): 598–605.
- CHAVERRI, G., O. E. QUIRÓS and T. H. KUNZ (2007) Ecological Correlates of Range Size in the Tent-Making Bat *Artibeus watsoni*. *Journal of Mammalogy*. 88(2): 477–486.
- CHAVERRI, G., C. J. SCHNEIDER and T. H. KUNZ (2008) Mating system of the tent-making bat *Artibeus watsoni* (Chiroptera: Phyllostomidae). *Journal of Mammalogy*. 89(6): 1361–1371.
- CHOE, J. C. and R. M. TIMM (1985) Roosting site selection by *Artibeus watsoni* (Chiroptera: Phyllostomidae) on Roosting site selection by *Artibeus watsoni* (Chiroptera: Phyllostomidae) on *Anthurium ravenii* (Araceae) in Costa Rica. *Journal of Tropical Ecology*. 1(3): 241–247.
- CONDIT, R., R. PEREZ, and N. DAGUERRE (2011) *Trees of Panama and Costa Rica*. Oxfordshire, Princeton University Press.
- EVELYN, M. J., D. A. STILES and R. A. YOUNG (2004) Conservation of bats in suburban landscapes : roost selection by *Myotis yumanensis* in a residential area in California. *Biological Conservation*. 115(3): 463–473.
- FAO (2018) *State of the World's Forests 2018: Forest pathways to sustainable development*. [Online]. Rome Available at: <<http://www.fao.org/3/I9535EN/i9535en.pdf>>.
- GARGIULLO, M., L. KIMBALL and M. BARBARA (2008) *A Field Guide to Plants of Costa Rica*. Oxfordshire, Oxford University Press.
- GELUSO, KENNETH and KEITH GELUSO (2012) Effects of environmental factors on capture rates of insectivorous bats, 1975-2005. *Journal of Mammalogy*. 93(1): 161–169.
- GHAZOUL, J. and S. DOUGLAS (2010) *Tropical Rain Forest Ecology, Diversity, and Conservation*. Oxfordshire, UK, Oxford University Press.
- JENKINS, E. V, T. LAINE, , S. E. MORGAN, , K. R. COLE and J. R. SPEAKMAN (1998) Roost selection in the pipistrelle bat , *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. *Animal Behaviour*. 58(4): 909–917.
- JUNK, W. J. (2013) Current state of knowledge regarding South America wetlands and their future under global climate change. *Aquatic Science*. 75(1): 113–131.
- KORINE, C., R. ADAMS, , R. DANILO, , M. FISHER-PHELPS and D. JACOBS (2016) Bats and Water: Anthropogenic Alterations Threaten Global Bat Populations. Pp. 215-241, in *Bats in the Anthropocene : Conservation of Bats in a Changing World* (VOIGT, C. C. AND KINGSTON, T., eds.). Berlin, Germany, Springer.
- KORINE, C., S. DANIEL, and B. PINSHOW (2013) Roost selection by female Hemprich's Long-Eared Bats. *Behavioural Processes*. 100: 131–138.

- KUNZ, T. H. and M. B. FENTON, (2005) *Bat Ecology*. London, The University of Chicago Press.
- KUNZ, T. H. and L. F. LUMSDEN (2005) Ecology of Cavity and Foliage Roosting Bats. Pp. 3-89, in *Bat Ecology*. (T. H. KUNZ and M. B. FENTON, eds.) London, University of Chicago Press.
- LAVAL, R. K. and B. RODRÍGUEZ-HERRERA, (2002) *Murciélagos de Costa Rica*. Costa Rica. Instituto Nacional de Biodiversidad, Heredia (Costa Rica), INBio.
- MELO, F. P. L., B. RODRIGUEZ-HERRERA, R. L. CHAZDON, R. A. MEDELLIN and G. G. CEBALLOS (2009) Small Tent-Roosting Bats Promote Dispersal of Large-Seeded Plants in a Neotropical Forest. *Biotropica*. 41(6): 737–743.
- QGIS, D. T. (2019) QGIS Geographic Information System. [Online]. Open Source Geospatial Foundation Project Available at: <<http://qgis.osgeo.org>>.
- R CORE TEAM (2020) R: A language and environment for statistical computing. [Online]. Vienna, Austria, R Foundation for Statistical Computing Available at: <<https://www.r-project.org/>>.
- RAZGOUR, O. Ã., C. KORINE, , D. SALTZ, , R. S. CENTRE, and M. RAMON, (2010) Pond characteristics as determinants of species diversity and community composition in desert bats. *Animal Conservation*. 13(5): 505–513.
- REID, F. (2009) *A Field Guide To The Mammals of Central America & Southeast Mexico*. 2nd ed Oxfordshire, Oxford University Press.
- RIPPERGER, S. P., E. K. V. KALKO, B. RODRÍGUEZ-HERRERA, F. MAYER, and M. TSCHAPKA (2015) Frugivorous bats maintain functional habitat connectivity in agricultural landscapes but rely strongly on natural forest fragments. *PLoS ONE*. 10(4): 1–15.
- RIPPERGER, S. P., M. TSCHAPKA, E. K. V. KALKO, B. RODRIGUEZ-HERRERA, and F. MAYER (2013) Life in a mosaic landscape: Anthropogenic habitat fragmentation affects genetic population structure in a frugivorous bat species. *Conservation Genetics*. 14(5): 925–934.
- RODRÍGUEZ-HERRERA, B., R. A. MEDELLIN and M. GAMBA-RIOS (2005) Tent building by female *Ectophylla alba* (Chiroptera: Phyllostomidae) in Costa Rica. *Acta Chiropterologica*. 8(2): 557–560.
- RODRÍGUEZ-HERRERA, B., R. A. MEDELLÍN and R. M. TIMM (2007) *Murciélagos neotropicales que acampan en hojas (Neotropical tent-roosting bats)*. 1st ed INBio.
- RODRÍGUEZ-HERRERA, B., L. VÍQUEZ-R, , E. CORDERO-SCHMIDT, , J. M. SANDOVAL and A. RODRÍGUEZ-DURÁN (2016) Energetics of tent roosting in bats: The case of *Ectophylla alba* and *Uroderma bilobatum* (Chiroptera: Phyllostomidae). *Journal of Mammalogy*. 97(1): 246–252.
- SAGOT, M., B. RODRÍGUEZ-HERRERA, and R. D. STEVENS, (2013) Macro and Microhabitat Associations of the Peter’s Tent-Roosting Bat (*Uroderma bilobatum*): Human-Induced Selection and Colonization? *Biotropica*. 45(4): 511–519.
- SANCHEZ-AZOFEIFA, G. A., B. RIVARD, J. CALVO and I. MOORTH, (2002) Dynamics of Tropical Deforestation Around National Parks : Remote Sensing of Forest Change on the Osa Peninsula of Costa Rica. *Mountain Research Development*. 22(4): 352–358.

SIMMONS, N. B. and A. L. CIRRANELLO (2020) Bat Species of the World: A taxonomic and geographic database. [Online]. [Accessed 8 June 2020]. Available at: <<https://batnames.org/>>.

SINAC (2018a) Corcovado National Park. [Online]. Available at: <<http://www.sinac.go.cr/EN-US/ac/acosa/pnc/Pages/default.aspx>>.

SINAC (2018b) Costa Rica National Parks - Carate Wildlife Reguge. [Online]. Available at: <<http://www.costarica-nationalparks.com/caratewildliferefuge.html>>.

STONER, K. E. (2000) Leaf selection by the tent-making bat *Artibeus watsoni* in *Asterogyne martiana* palms in southwestern Costa Rica. *Journal of Tropical Ecology*. 16(1): 151–157.

TIMM, R. M. (1987) Tent construction by bats of the Genera *Artibeus* and *Uroderma*. *Studies in Neotropical mammalogy: Essays in honor of Philip Hershkovitz*. 39(January 1987): 187–212.

TIMM, R. M. and R. K. LAVAL (1998) A Field Key to the Bats of Costa Rica. Occasional Publication Series, Center of Latin American Studies. [Online]. 22: 1–30. Available at: <<http://kuscholarworks.ku.edu/dspace/handle/1808/4524>>.

VILLALOBOS-CHAVES, D., G. BARRANTES, E. J. FUCHS, and B. RODRÍGUEZ-HERRERA (2013) Canines as a Measuring Tool for Leaf Tent Construction in *Dermanura watsoni*. *Acta Chiropterologica*. 15(2): 441–449.

VILLALOBOS-CHAVES, D., M. SPÍNOLA-PARALLADA, K. HEER, E. K. V KALKO and B. RODRÍGUEZ-HERRERA, (2017) Implications of a specialized diet for the foraging behavior of the Honduran white bat, *Ectophylla alba* (Chiroptera: Phyllostomidae). *Journal of Mammalogy*. 98(4): 1193–1201.

VILLALOBOS-CHAVES, D., J. VARGAS-MURILLO, E. ROJAS-VALERIO, B. W. KEELEY and B. RODRÍGUEZ-HERRERA, (2016) Understory bat roosts, availability and occupation patterns in a Neotropical rainforest of Costa Rica. *Revista de Biología Tropical*. 64(3): 1333–1343.

ZUUR, A. F., J. HILBE and E. N. LENO, (2013) A Beginner’s Guide to GLM and GLMM with R: A Frequentist and Bayesian Perspective for Ecologists. Newburgh, Highland Statistics Ltd.

Table 5 Number of bats and tents along three habitat types in the Carate Wildlife Refuge.

(Percentage occupancy calculated as number of bats per tent.)

Transect	Tents	Bats	% of Occupancy
Secondary	40	5	12.5%
Primary	32	1	3.1%
Highly Disturbed	39	6	15.4%
Average			12.12%

Table 6 Results of the GLM to assess the effect of micro-habitat variables on number of tents. Significant predictor is indicated in bold.

Predictors	Estimate	SE	z-value	p-value
(Intercept)	-0.05	0.61	-0.08	0.933
Tree height	0.00	0.00	0.63	0.529
Distance from nearest fresh water source	0.00	0.00	-1.18	0.238
Cover abundance of bushes	-0.01	0.00	-1.52	0.128
Cover abundance of trees	0.01	0.01	1.97	0.049
Cover abundance of canopy cover	0.00	0.01	0.75	0.451
Cover abundance of water	0.02	0.02	1.61	0.107

Table 7 Results of Spearman's rank correlation analysis to assess the effects of macro habitat characteristics on number of plants hosting tents. Significant predictor is indicated in bold.

Predictors	rs	p-value
Distance to Sea	(10) = -0.08	0.827
Distance to Fresh Water	(10) = -0.69	0.013
Altitude	(9) = -0.47	0.140

Table 8 Results of Spearman's rank correlation analysis to assess the effects of micro habitat characteristics on number of plants hosting tents.

Predictors	rs	p-value
Aspect	(8) = 0.15	0.674
Blade width	(8) = -0.04	0.939
Rachis diameter	(10) = -0.56	0.088
Tent height	(12) = -0.53	0.051