Do Bats Roost and Forage in Shade Coffee Plantations? A Perspective from the Frugivorous Bat *Sturnira hondurensis*

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ABSTRACT

Shade coffee plantations are considered important habitats for frugivorous bats. However, it is not known if bats use this agricultural habitat for shelter, food resources, or both. This study addresses these questions using the highland yellow-shouldered bat (*Sturnira hondurensis*) as an example. Twenty-six adult individuals of *S. hondurensis* were captured, 50 percent in tropical montane cloud forest (TMCF) and 50 percent in shade coffee plantations (SCP) in Veracruz, Mexico, and each was fitted with a radio transmitter for locating roosts and feeding areas. Data were obtained from 24 of them. The fieldwork was conducted between October 2010 and October 2011 covering all seasons. Twenty-two day roosts were located in the cavities of twelve different species of tree. Roosts located in TMCF differed significantly from those in SCP, having a smaller crown area and a greater species richness and density of plants around the roost. In SCP, both the average home range and the average core use area were smaller than in TMCF, but the differences were not statistically significant. Distances travelled by bats were generally longer and more variable in the SCP; the distance between capture site and foraging site was significantly greater in SCP than in TMCF. In SCP, there were fewer understory chiropterochorous plants, which are the main item in the diet of this bat and many other sympatric species of frugivorous bats. Although *S. hondurensis* does use roosts and foraging sites in the SCP, it is important to note that this species and others with similar requirements primarily depend on the preservation of intact forest adjacent to modified landscapes, where roosts and fruit are constantly available in abundance. Management practices should guarantee a greater density and diverse of trees and the preservation of understory plants with fruits in the coffee plantations that allow a long-term survival of frugivorous bats populations.

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

Key words: foraging area; home range; Mexico; roost; shade coffee plantation; *Sturnira hondurensis*; tropical mountain cloud forest.

Tropical montane cloud forest (TMCF) is one of the most important tropical ecosystems in the world, not only because of the large number of plants and animals that inhabit it (Bubb *et al.* 2004) but also because of the environmental services it provides (Hamilton 1995). TMCF is also highly threatened. It is estimated that worldwide, TMCF represents 2.5 percent of the total area covered by tropical forest, and 1.2 percent of that is located in the Americas (Bubb *et al.* 2004). In Mexico, 50 percent of original TMCF cover has disappeared (Challenger 1998), mainly to make way for coffee and other crops and agricultural activities. Coffee is mainly grown between 600 and 1200 m asl, where its production is highest (Moguel & Toledo 1999), so many of the areas where coffee is currently grown were originally TMCF (Pineda *et al.* 2005). In terms of coffee production, Mexico holds eighth place among coffee-growing countries, with an area of over 812,000 ha—two-thirds of which is used to grow shade coffee (Moguel & Toledo 1999, SAGARPA 2007).

Studies in coffee plantations with traditional management have demonstrated the potential for this type of crop to conserve biodiversity (Perfecto *et al.* 1996, Manson *et al.* 2008). Among mammals, bats are one of the best represented groups in shade coffee plantations (SCP). Some studies have shown that the species richness of phyllostomid bats in SCP can be equal to or even greater than that of the forest (Pineda *et al.* 2005, García-Estrada *et al.* 2006, Sosa *et al.* 2008), whereas their abundance is much greater in the forest (Saldaña-Vásquez *et al.* 2010, Williams-Guillén & Perfecto 2010). These studies posit that the presence of bats in SCP may be due to the availability of some kind of resource in this habitat such as refuge or food.

Bats provide crucial environmental services such as dispersing seeds, pollinating a large number of plants, controlling the size of insect populations, and producing guano which is useful as a fertilizer (Kunz *et al.* 2011). As seed dispersers, frugivorous bats contribute significantly to forest regeneration in the Neotropics dispersing many species of trees and shrubs that have been identified as key elements in early successional stages (Muscarella & Fleming 2007). Given the importance of the environmental services provided by bats, it is essential to identify the role that agricultural land such as SCP plays in maintaining bat diversity and abundance.

Bat roosts are important sites for mating, resting, raising young, and facilitating social interactions; they also offer protection from the weather, allow for the conservation of metabolic energy and minimize the risk of predation (Kunz & Lumsden 2003). Therefore, knowledge of roosting requirements is a prerequisite for understanding the impact of anthropogenic disturbance on bat populations (Pierson 1998). Usually, coffee plantations have a lower density of trees compared to native forests

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(López-Gómez *et al.* 2008), and this could reduce roost availability for bats inhabiting these agroecosystems.

We compared the use of coffee plantations and TMCF fragments by the highland yellow-shouldered bat (*Sturnira hondurensis* Goodwin *sensu* Velazco and Patterson [2013]) as roosting and foraging sites in the mountainous central region of Veracruz (Sosa *et al.* 2008). *Sturnira hondurensis* mainly forages in the understory and prefers the fruit of plants in the family Solanaceae (Fleming 1986). Keeping in mind that the abundance of bat-fruit plants is greater in TMCF than in SCP (Saldaña-Vásquez *et al.* 2010), we expect frugivorous bats to forage more in the forest than in coffee plantations. This should be even more pronounced for bats that forage in the understory since plants in this vegetation layer are not common in coffee plantations.

Roost and foraging area use by *S. hondurensis* is not known, however there is some information from forested areas for *Sturnira parvidens* (before included in *S. lilium*), a slightly smaller species that is common in the lowlands. This species roosts mainly in tree cavities although it also uses cracks in river banks, the base of palm leaves and vines (Fenton *et al.* 2000, Evelyn & Stiles 2003). To date, there have been no studies of roost use or foraging areas in agroecosystems by frugivorous bats and their implications for conservation. Knowledge of the use these bats are making of the agricultural landscape would make it possible to define management strategies for improving habitat conditions and maintaining the elements of the landscape that are essential for bats, especially those such as *S. hondurensis* that forage in the understory. This is highly relevant considering the fast rate at which forest is being replaced by other types of vegetation cover.

METHODS

STUDY AREA.—We conducted the study in two areas in central Veracruz, Mexico: one in the surroundings of the municipalities of Xalapa and Coatepec and the other in the region of Huatusco and Totutla. In each region, we chose two landscapes: one primarily composed of TMCF, and the other composed of coffee plantations. The landscapes were selected via satellite images and field excursions. In the landscape dominated by coffee plantations, we selected a shade coffee plantation, while in that dominated by TMCF we chose a fragment of forest. The TMCF were largely surrounded by open areas with small forest remnants or isolated trees. The two TMCF fragments are known as Agüita Fría (19°31′19.76″ N, 96°59′30.43″ W) and Las Cañadas (19°11′23″ N, 96°59′11″ W); and the two coffee plantations as El Mirador (19°12′57″ N, 96°53′7″ W) and Finca Armand (19°26′1″ N 96°52′32″ W) (Fig. 1; Table 1). Sampling was initially done in the Cloud Forest Sanctuary at the Instituto de Ecología, A.C. (19°30′53″ N, 96°56′25″ W), where we captured and followed a bat, but we had to change to another site for logistical reasons.

We selected the coffee plantations in the study area, because they are managed in a traditional polyculture manner *sensu* Hérnandez-Martínez *et al.* (2009), which means the coffee plants replace those of the understory and the original tree cover of the

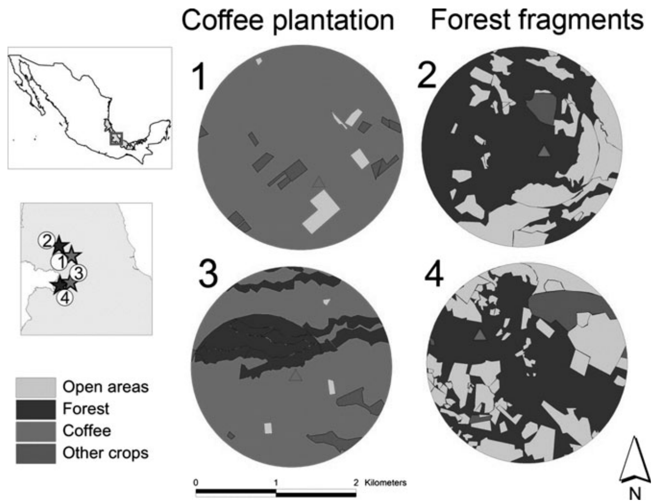

FIGURE 1. Central Veracruz, Mexico where the four study sites are located, and surrounding areas visited by the bats. The triangle indicates the place where the monitored bats were captured. 1 = Finca Armand, 2 = Agüita Fría forest, 3 = Finca El Mirador, 4 = Las Cañadas forest. (*Color version available online as part of Supporting Information*).

forest is kept or modified to obtain a mix of native sown trees (Table 1).

MONITORING BATS.—We captured bats using 3 m × 10 m mist nets, hung at each of the sampling sites. A total of 26 *S. hondurensis* were chosen to be monitored between October 2010 and October 2011, 50 percent in TMCF and 50 percent in SCP. We identified each bat caught, and determined its sex and reproductive status. For females, we chose those that were reproductively inactive and that showed no signs of pregnancy upon abdominal palpation. To determine habitat use and foraging activity, we used radiotelemetry. We used surgical adhesive to affix a radio transmitter (BD-2N or LB-2N Holohil Systems, Ltd., Carp, Ontario, Canada or Wildlife Materials Inc., Murphysboro, Illinois, U.S.A.) weighing 0.5 g (>5% of the bat's body mass) to the interscapular region of each bat. We held each bat in captivity for 30 min to make sure the radio transmitter was properly affixed and then released it at the site of capture. During each radio-tracking session, we followed a maximum of two bats, generally for eight consecutive days or until the radio transmitter fell off the bat. The battery of the radio transmitters lasted less than 2 wk.

To find and follow the bats, we used a TRX-1000 receiver from Wildlife Materials Inc. that was equipped with a three-element Yagi antenna. For each localization, we noted the time, position of the observer, signal pattern (slow or fast), signal strength, signal direction (with the help of a compass), and weather condition. When the bat was flying repeatedly over the same area, we assumed it was foraging. We made localizations every 5 min using the bearing together with distance, estimated according to signal strength and gain (variation in the sensitivity of the receiver to the signal; Winkelman *et al.* 2000). We calibrated the signal strength–distance relationship near the study

TABLE 1. *Sampling site descriptions.*

Site[a]	Region	Habitat type[b]	Elevation (m asl)	Management practices employed	Area (%)[c]			Structure
					Forest	Coffee plantation	Others	
AF	Xalapa-Coatepec	TMCF	1477	None	62.5	0	37.5	Forest
ARM		SCP	1056	Low hybrid	0	96	4	Polyculture
INECOL		TMCF	1460	None	39.8	3.5	56.7	Forest
CAÑ	Totutla-Huatusco	TMCF	1350	None	45.9	0.5	53.6	Forest
MIR		SCP	1070	Low	23.5	72.5	4	Traditional

[a]AF, Agüita Fría forest; ARM, Finca Armand; INE, INECOL Cloud Forest Sanctuary; CAÑ, Las Cañadas forest; MIR, Finca el Mirador.

[b]TMCF, tropical mountain cloud forest; SCP, shade coffee plantation.

[c]Calculated based on Figure 1. Each circle has an area of 492 ha.

area using standardized gain values and estimates to adjust to variations created by the topography or obstacles to signal reception (Bonaccorso *et al.* 2002). Using single-bearing telemetry, precision is 7.8° (±4.6°) and accuracy is 47 m according to our error estimate. Thus, many of the positions of the bats were calculated using single bearings and some positions when the bat was at a night roost were recorded using the triangulation method, when it was not possible to home in to find the roost.

O'Brien *et al.* (2000) compared triangulation data and single bearing data and found a good approximation of home range (95% MCP) for *Falco punctatus*. Some studies have used single-bearing telemetry to locate bats during foraging (Winkelman *et al.* 2000, Bonaccorso *et al.* 2002) or to complement triangulation data (Meyer *et al.* 2005).

Description of the trees used as roosts.—The day after the bat had been captured, we sought its roost using the receiver and the antenna. If we found the roost, we noted its coordinates using a global positioning device (Etrex model; Garmin, Ltd., Olathe, Kansas, U.S.A.) and we took the following data for the plant used as a roost: species, diameter at breast height (dbh), maximum height, canopy area, and degree of decay.

We laid out four 50 m × 2 m transects, extending outward from the roost tree in the four cardinal directions, to quantify the characteristics of the structure of the vegetation of the site where the tree was located. Along the first 25 m of each transect, we recorded the height of all the vegetation >50 cm tall and the dbh of all trees and shrubs with a diameter ≥5 cm; we also noted the species of each plant measured. We noted the percent cover of the vegetation for each transect by taking readings with a densiometer every 5 m. Along the remaining 25 m of each transect, we also measured the height and dbh of trees ≥20 cm in diameter. For these trees, and all those with dbh ≥20 cm observed in the first 25 m of each transect, we made note of which had hollows that bats might occupy to estimate the potential roosts at that site.

To identify characteristics that might result in the increased probability of a tree being selected as a roost, we selected a tree in a random direction (north, south, west, or east) and at a minimum distance of 100 m from each roost. The random tree was the first tree with dbh ≥20 cm that was visible 100 m or more away from the roost. Around this tree, four other transects extending outward from its trunk in the four cardinal directions were laid out to measure the corresponding vegetation. For these measurements around this randomly selected tree, we recorded only trees with a dbh ≥10 cm.

Measuring fruit availability.—We sampled the sites with the highest number of foraging records for each bat to estimate fruit availability in the foraging areas visited by bats in the SCP and TMCF based on field observations. In each site, we randomly laid out a 150 m × 6 m transect, along which the same person always recorded the abundance of fruit known or suspected to be eaten by bats according to the literature (Lobova *et al.* 2009). For this purpose, we measured trees and shrubs within the transect or those whose canopies extended over it. We assigned each of the plants to a relative fruit abundance category (1–25%, 26–50%, 51–75%, and 76–100%) according to the percentage of ripe fruit it had in its crown. In addition, we collected fecal samples from the monitored *S. hondurensis* and those caught in the mist nets, to get an idea of the composition of their diet. To do this, fecal samples were collected directly from bats when they were removed from the mist net and from the cloth bags where bats were held before processing.

Data analysis.—We used a one-way analysis of variance to compare the structural characteristics of each tree used as a roost by *S. hondurensis* and those of the surrounding vegetation between both vegetation types (SCP and TMCF), and between the roost tree and the randomly selected tree (Tables 3 and 4). When the conditions of homogeneity of variance and normality were not met prior to analysis, the data were appropriately transformed. The data corresponding to movement and home range variables were transformed using logarithm, whereas only the variables crown area and vegetation cover from the roosts analysis were transformed with logarithm and arcsine of the square root respectively.

For vegetation variables recorded as counts, we made comparisons between vegetation types by means of a deviance analysis of a generalized linear model, initially assuming a Poisson distribution for the residuals. However, we refitted the model using quasi-likelihood estimates to control for a slight overdispersion revealed by the first fitting (Crawley 2005). We analyzed plant richness in two ways: the richness of all plants taller than 50 cm, and the richness of all plants with dbh ≥5 cm. We ran the analyses in R (R Development Core Team 2008).

We defined home range as the utilization distribution (UD) or probability bivariate distribution of an individual's relative use of space (Worton 1989). To estimate UD, we used the Kernel method implemented in the Animal Movement extension for ArcView GIS 3.2 (ESRI™, Redlands, California, U.S.A.), and to determine the smooth parameter we used the Least Square Cross Validation (LSCV) (Seaman & Powell 1996). For each individual, this produced a minimum area of 95 and 50 percent of its UD, the latter considered the area of intensive use or central area (Katajisto & Moilanen 2006). The home range described here for *S. hondurensis*, is—for most of the data—limited to the first part of the night, *i.e.*, from the time the bat emerges from its day roost until approximately 0100 h. We used a one-way analysis of variance to compare home range and foraging movements between vegetation types. An *F*-test of equality of variances was done to compare variances of home range and bat movements between TMCF and SCP.

We evaluated fruit availability in the foraging areas of each bat monitored using an *ad hoc* quantitative index, calculated as follows: for each plant species the proportion of mature fruit (per abundance category) was multiplied by the number of individuals of that species with mature fruit recorded in a given transect. This value was added to that of the other species of plants recorded in that sample to obtain an index that expresses the availability of fruit at each site. Using *t*-tests, we compared the fruit abundance index and the abundance of plants whose fruit is eaten by bats between SCP and TMCF. We verified homogeneity of variance and normality before the analysis.

RESULTS

We obtained data for 24 of the 26 *S. hondurensis* we monitored. We obtained data on both roost tree and foraging movement for 18 bats, whereas we identified only the roost locations for three bats and only the foraging areas for the other three bats. Bats were followed up for relatively short periods (8 d on average, range = 6 ± 12).

Roost use.—We detected 22 roosts on 12 different tree species (Table 2); all the trees were alive. This includes 18 roosts for 18 different bats, three roosts used by bat 144b and one roost used by two different bats on different occasions. The roosts that could be verified were in hollows. We determined the height to the roost cavities for six trees; the minimum height was 1.3 m, the maximum was 8 m, and the mean was 5.7 m. Of all the trees used as roosts, 12 (55%) were in SCP, nine (40%) were in TMCF, and one (5%) was in a pasture located 100 m from a TMCF fragment. One roost in TMCF was inaccessible and was not included in this calculation. Two of the roosts in SCP were used by bats initially captured in TMCF.

The tree species most used for roosting were: *Liquidambar styraciflua* ($N = 6$), *Quercus sartorii* (3), *Trema micrantha* (3), and *Enterolobium cyclocarpum* (2), which together represent 64 percent of the roosts (Table 2). The bats monitored used large trees; all their roosts were in trees with a dbh ≥25 cm. Roosts in TMCF were significantly different from those in SCP for six of the twelve characteristics evaluated (Table 3). Around the TMCF trees there was more shade from vegetation, which in turn is related to the greater density of plants in the understory and in the canopy compared to SCP. The crown area of the roost trees was smaller in TMCF, which can be explained by the smaller branching space relative to that of the more open environment of the SCP. Plant species richness around the roost was greater, by almost a factor of two, in TMCF relative to SCP.

Of the nine variables used to compare roosting trees with the randomly selected trees, only two were significantly different: plant species richness and the density of trees with dbh ≥20 cm, both of which were higher in the surveyed area surrounding the roosting trees (Table 4).

Foraging movement and home range.—Bats usually left their roosts approximately half an hour after sundown (mean emergence times were 1911 h during the winter and 2024 h during the summer). Home range varied widely among bats (observed range: 3.93–311.30 ha, average: 56.7 ha) (Fig. 2). According to the Kernel estimate, in the SCP both the average home range and core use area were generally larger than those of the TMCF, however the differences were not statistically significant (Table 5). For the majority of tracked bats (85%), foraging area was generally located in the same vegetation type where the bat had been captured.

The mean distance from the daytime roost to the foraging area was not statistically significant across the habitat types (Table 5). There was greater variation in the distances covered by bats in the SCP, specifically in the distance from roost to foraging site ($F = 5.67$; df = 10, 10; $P = 0.05$) and the maximum distance travelled ($F = 5.30$; df = 11, 12; $P = 0.05$). The maximum distance covered by *S. hondurensis, i.e.*, the distance between the roost and the furthest point of its home range, was not significantly different between vegetation types, although bats usually covered greater distances in the SCP (Table 5). One quarter of the bats that foraged in TMCF and 60 percent of the SCP covered distances greater than 1 km. Among vegetation types, the distance from the capture site to the foraging area was significantly greater in the SCP where the bats flew, on average, 802.5 m (Table 5).

Fruit availability.—The *S. hondurensis* from which fecal material was collected ($N = 38$) ate a total of 16 species of fruit, of which 47 percent belongs to the Solanaceae and 19 percent to Piperaceae (Table S1). In TMCF, seven of eight species consumed by bats belonged to the Solanaceae and Piperaceae, whereas in SCP, six of ten species belonged to these families. In the transects sampled in the foraging areas, we recorded a total of 30 plant species that were potentially used (Lobova *et al.* 2009) by *S. hondurensis*, with ripe or unripe fruit (Table S2 and S3). Although the

TABLE 2. *Trees used as roosts by* Sturnira hondurensis *in forest fragments and in coffee plantations in Veracruz.*

Land use	ID[a]	Sex[b]	Capture site[c]	Roost tree	dbh (cm)	Height (cm)	Crown area (m^2)
Coffee	098	F	ARM	*Enterolobium cyclocarpum*	101.5	24	352.49
Coffee	118	F	INE	*Inga jinicuil*	58.6	15	248.72
Coffee	139	F	MIR	*Quercus sartorii*	46.0	19	179.01
Coffee	198	F	CAÑ	*Trema micrantha*	41.38	15	95.00
Coffee	278	M	MIR	*Quercus sartorii*	89.1	21	152.68
Coffee	125	F	ARM	*Ficus crocata*	126.5	14	571.45
Coffee	105	M	MIR	*Quercus sartorii*	87.0	18	82.91
Coffee	185	M	MIR	*Inga paterno*	36.5	17	111.09
Coffee	377	M	ARM	*Enterolobium cyclocarpum*	103.8	15	240.33
Coffee	026	F	MIR	*Inga* aff. *spurio*	41.7	13	80.58
Coffee	417	M	MIR	*Trema micrantha*	54.0	21	90.71
Coffee	65	F	MIR	*Schizolobium parahyba*	73.9	16	240.00
Forest	159	M	AF	*Liquidambar styraciflua*	35.7	19	73.40
Forest	218	F	AF	*Cinnamomum effusum*	68.5	21	117.62
Forest	144b	M	AF	*Liquidambar styraciflua*	81.8	25	223.84
Forest	144b	M	AF	*Anonna cherimola*	57.8	9	44.98
Forest	144b	M	AF	*Liquidambar styraciflua*	38.9	20	34.16
Forest	170	F	CAÑ	*Alchornea latifolia*	149.1	16	131.95
Forest	337	F	AF	*Liquidambar styraciflua*	113.8	22	70.69
Forest	297	F	AF	*Liquidambar styraciflua*	97.5	17	193.60
Forest	186	F	CAÑ	*Trema micrantha*	25.0	15	4.12
Forest	47	M	AF	*Liquidambar styraciflua*	83.7	21	152.68

[a]Frequency numbers of the radio transmitters used to identify the bats.
[b]M, Male; F, Female.
[c]ARM, Finca Armand; INE, INECOL Cloud Forest Sanctuary; MIR, Finca el Mirador; AF, Agüita Fría forest; CAÑ, Las Cañadas forest.

index of ripe fruit availability was not statistically different between vegetation types ($t = -1.372$, $P = 0.19$), the mean was greater for TMCF ($\bar{x} = 10.98 \pm 6.43$) than for SCP ($\bar{x} = 2.99 \pm 1.19$). The number of species of plants potentially consumed by bats was similar among vegetation types, though the composition was not: there were more representatives of Piperaceae and Solanaceae species in the TMCF than in the SCP (Tables S2 and S3). The abundance of chiropterochorous plants was significantly higher in TMCF than in SCP ($t = -3.604$, $P = 0.002$).

DISCUSSION

ROOST USE.—*Sturnira hondurensis* used hollows in old live trees as roosting sites. Like other bat species, it used tall trees that have a large dbh (Evelyn & Stiles 2003) and little cover from the surrounding vegetation (Sedgeley & O'Donnell 1999, Psyllakis & Brigham 2006). This gives them greater maneuverability on the wing when entering and exiting the roost.

A study of the tree diversity in SCP and TMCF in central Veracruz reports that *Inga jinicuil, I. latibracteata*, *Trema micrantha,* and *Enterolobium cyclocarpum* (species used by *S. hondurensis*) were among the most abundant trees in coffee plantations (López-Gómez *et al.* 2008). However, while species of the genus *Inga* are widely used as shade trees in the study area and in other coffee plantations of central Veracruz, their use by bats was low relative to their availability.

Trema micrantha, Enterolobium cyclocarpum, Quercus sartorii, and *Liquidambar styraciflua*, all species widely used by *S. hondurensis*, are timber species. This puts potential roosts at risk given that they are usually cut when their dbh is 20 cm or more (Bárcenas-Pazos & Ordoñez-Candelaria 2008); a size at which, according to our data, they can be used as roosts. In addition, the hollows may take a long time to form, even more than 100 yr (Psyllakis & Brigham 2006). Moreover, only very few cavities can be occupied by bats. For *Chalinolobus tuberculatus*, an insectivorous bat from New Zealand, only 1.3 percent of the cavities found in randomly selected trees met the characteristics required for them to be used as roosts (Sedgeley & O'Donnell 1999).

Although a little more than half of the roosts were in SCP, of these only 27 percent were in the landscape dominated by coffee plantations and with a scarcity of woody vegetation cover; that is, in the surroundings of, or within, Finca Armand. The remaining 73 percent were in coffee plantations that provide a better selection of food sources, especially from the understory plants, which could create a preference for these areas by the bats.

Considering that there are fewer large trees per unit area in the coffee plantations compared to TMCF, it is to be expected that roosts are a limited resource in coffee plantations. Perhaps in one of the coffee plantations, the same roost tree was used at

TABLE 3. *Comparison of the characteristics of the roosts of* Sturnira hondurensis *used in the coffee plantations and cloud forests studied (mean ± SE).*

	Coffee plantation	Forest	F	P
Roost tree	N = 12	N = 10		
dbh (cm)[a]	71.6 ± 8.6	75.18 ± 12.2	0.059	0.811
Height (m)[a]	17.33 ± 1.0	18.48 ± 1.4	0.474	0.498
Crown area[a]	200.4 ± 45.4	99.35 ± 24.6	4.611	0.045
Vegetation around the roost[a]	N = 11	N = 9		
Cover (%)[a]	78.93 ± 4.3	92.27 ± 2.5	6.176	0.023
Average dbh[a]	38.96 ± 4.9	31.01 ± 3.5	2.24	0.15
Average height[a]	05.36 ± 3.78	04.40 ± 1.31	0.14	0.711
Average height (≥10 cm dbh)[a]	11.62 ± 4.60	13.22 ± 2.79	1.157	0.295
Richness (plants ≥50 cm height)[b]	14.36 ± 2.7	35.55 ± 4.7	108.57	0.0004
Richness (plants ≥5 cm dbh)[b]	07.90 ± 1.20	15.11 ± 2.4	54.039	0.008
Tree density (≥20 cm dbh)[b]	08.45 ± 1.8	14.88 ± 1.5	57.845	0.022
Total density[b]	106.0 ± 16.2	236.1 ± 41.2	959.87	0.002
Trees with cavities[b]	01.18 ± 0.5	01.62 ± 0.40	33.477	0.762

[a]Results compared with an analysis of variance of a normal linear model.
[b]Results compared with an analysis of deviance of a generalized linear model.

TABLE 4. *Comparison of the characteristics of the trees used as roosts by* Sturnira hondurensis *and random trees within the same habitat (mean ± SE).*

	Roost tree	Random tree	F	P
dbh (cm)[a]	72.70 ± 7.8	68.05 ± 5.1	0.239	0.628
Height (m)[a]	17.79 ± 0.9	17.80 ± 0.7	0.0001	0.99
Crown area[a]	155.0 ± 26.8	194.4 ± 31.6	1.237	0.273
Vegetation around the roost				
Cover (%)[a]	83.01 ± 3.3	85.48 ± 2.6	0.184	0.67
Average dbh[a]	35.38 ± 3.2	30.34 ± 1.8	0.546	0.465
Average height (≥10 cm dbh)[a]	13.07 ± 0.9	11.67 ± 0.9	0.53	0.472
Richness (trees ≥10 cm dbh)[b]	12.75 ± 1.4	5.05 ± 0.6	77.558	0.003
Tree density (≥20 cm dbh)[b]	18.55 ± 2.7	6.22 ± 1.1	141.67	0.008
Trees with cavities[b]	1.3 ± 0.3	0.5 ± 0.2	57.93	0.06

[a]Results compared with an analysis of variance of a normal linear model.
[b]Results compared with an analysis of deviance of a generalized linear model.

different times by different bats reflects the scarcity of this resource in this site. These roosts can be reused over long periods of time, even over years (Willis *et al.* 2003), so it is important

TABLE 5. *Comparison of the characteristics of the movement and foraging activity of* Sturnira hondurensis *in coffee plantations and cloud forest fragments (mean ± SE).*

	Coffee plantation	Forest	P[a]
Home range size (ha)	89.82 ± 50.1	69.79 ± 32.8	0.945
Core use area (ha)	21.58 ± 11.8	17.74 ± 9.0	0.991
Distance from roost to foraging site (m)	822.71 ± 383.4	590.78 ± 161	0.237
Maximum distance travelled (m)	1466.73 ± 340	776.82 ± 141.4	0.494
Distance from capture site to foraging area (m)	802.49 ± 277	177.68 ± 51	0.008
Distance from capture site to roost (m)	610.91 ± 211.7	581.15 ± 178.3	0.962

[a]Probability of statistical difference in a one-way analysis of variance.

to conserve both the identified roosts and the trees that could potentially be used as roosts.

In contrast to the randomly selected trees, *S. hondurensis* selected roost sites where the surroundings had a greater density of large trees, and thus a higher number of hollows. Though marginally not significant ($P = 0.06$) there appears to be a tendency for the surroundings of the roost to have more trees with fissures than the randomly selected trees have. Proximity to other trees with cavities can provide energetic benefits to bats such as, the ability to find a roost nearby without having to expend much energy, in the event that there is a disturbance in the occupied roost tree (Vonhof & Gwilliam 2007).

FORAGING MOVEMENT.—Bats tended to cover greater distances in the coffee plantations and some of these distances were more variable than in TMCF. It may be that in SCP bats need to cover a larger area to find the resources they need to feed themselves. In Costa Rica *Artibeus watsoni,* another stenodermatine bat, covered a larger area when foraging in secondary forest with fewer resources (Chaverri & Kunz 2006).

The greater distances covered in the coffee plantations from the site of capture to the bat's usual foraging site may suggest that the bats visiting coffee plantations are often on their way to another site, or searching for a specific resource; it does not necessarily mean that they are always foraging in the SCP while they are en route. In fact, *S. hondurensis* were scarce at Finca Armand, which is immersed in a landscape dominated by coffee and sugar crops, and more than two nights of setting mist nets were necessary to capture the bats there. On one occasion, it was only after 10 d of sampling that it was possible to capture one of the bats for monitoring. One bat captured at this site was never detected again, and in spite of an exhaustive search was not found in the surrounding area either. In another study, bat recaptures were more frequent in the forest than in intensely managed coffee plantations (Williams-Guillén & Perfecto 2010), suggesting that

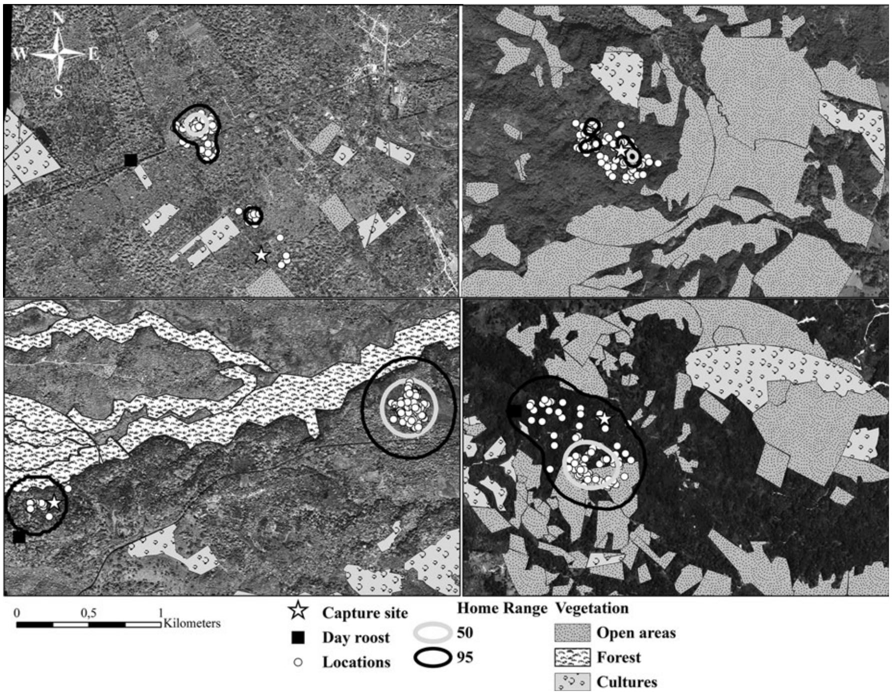

FIGURE 2. Examples of the home range (95) and the core use area (50) of *Sturnira hondurensis* in cloud forest fragments and shade coffee plantations in Veracruz, Mexico. The two coffee plantations are on the left: Finca Armand (on the top) and Finca El Mirador (on the bottom); and the two cloud forest fragments are on the right Agüita Fría (on the top) and Las Cañadas (on the bottom). The dominant coverage in each image corresponds to coffee plantations and cloud forest as each site. (*Color version available online as part of Supporting Information*).

coffee landscapes are visited less frequently owing to their limited resources.

While we are not implying that the movement pattern recorded is representative of the *S. hondurensis* behavior in any year, the design of our study allows us to compare roost selection, foraging areas, and fruit resource used between coffee plantations and cloud forest. Differences in the mean values of several of the movements distances measured were not large enough between SCP and TMCF because of a great variability on these measurements, due likely to our relatively small sample size ($N = 12$ per vegetation type).

FRUIT AVAILABILITY.—The quantity of mature fruit available per transect did not differ between TMCF and SCP, although there was a tendency for there to be more fruit in the forest. However, the abundance of plants preferred by bats was much greater in the TMCF than in SCP. This may offer a more constant resource in the forest, in contrast to the coffee plantations where many plants with fruit consumed by bats are considered weeds and are constantly being removed from the understory (Garcia-Estrada *et al.* 2012). Of the fruit consumed in the forest, 85 percent belonged to the Piperaceae and Solanaceae families, and these same families accounted for 58 percent of the fecal material from bats captured in the coffee plantations. Bats that foraged in the SCP also visited canopy trees such as those of *Cecropia*, *Vismia,* and *Ficus*. Coffee plantations mainly offer bats the fruit of tree species that are used for shade. However, these resources are not part of the essential diet of understory frugivorous bats such as *S. hondurensis*, and instead are more suited to canopy frugivorous bats. The scarcity of food resources for understory frugivorous bats in the coffee plantations is most notable in the intensively managed coffee plantations, where the relicts of woody vegetation are scarce and weeds are commonly cut (Moguel & Toledo 1999).

Several studies have reported that frugivorous bats of the understory are poorly represented in coffee plantations and that their main response occurs not at the species richness level, but rather at that of abundance (Saldaña-Vásquez *et al.* 2010, Williams-Guillén & Perfecto 2010), with the abundance of *S. hondurensis* and other small frugivores decreasing in coffee plantations.

Sturnira hondurensis is an important seed disperser, in terms of both the quantity and the richness of the plants it disperses in TMCF and SCP (J.R. Hernández-Montero, unpubl. data). The composition of the species it disperses is different in the forest and in coffee plantations for the Solanaceae and Piperaceae families (J.R. Hernández-Montero, unpubl. data). This highlights the importance of having forest fragments near the coffee crops, and the importance of having frugivorous bats such as *S. hondurensis* present to contribute to the regeneration of plants originating in the forest in disturbed environments such as coffee plantations.

CONCLUSIONS

It is necessary to understand specific roost requirements of several species and to protect, in the coffee plantations, the trees, and other vegetation (*e.g.,* palms) that are known to be used as roosts by bats. Management practices that favor growing a single species of tree, the selective removal of dead and decaying trees, and short rotation periods all reduce the availability of roosts and should be avoided. In addition, to preserve the richness and abundance of bats, having a diversity of shade trees with fruit that might be eaten by bats in coffee plantations is not enough.

While understory-foraging species such as *S. hondurensis* can eat the fruit of tree species that are present in coffee plantations, their diet is made up primarily of Solanaceae and Piperaceae shrubs that are scarce in coffee plantations. Therefore, isolated coffee plantations would not be sufficient for conservation of frugivorous bats such as *S. hondurensis*. It is necessary to have more forest fragments in the landscape where plantations are located to successfully maintain bat populations, as well as other fauna and flora associated with forests. We propose that forest fragments in a coffee-dominated landscape should be assessed with respect to their potential high conservation value (HCV). Moreover, coffee plantations owners should allow the permanence of understory vegetation among coffee plants or in the surroundings as relicts of secondary vegetation that could offer constant food resource to frugivorous bats.

Further studies should examine the extent to which the behavior of organisms, such as birds, with similar requirements for food and shelter, is affected by the replacement of forest with agricultural areas and the resultant consequences for biodiversity management and conservation of the species. It is worthwhile remembering that simply comparing bat diversity between coffee plantations and forests is not sufficient to understand how these mammals are affected by and adapting to agrosystem-dominated landscapes. More behavioral studies are necessary to identify the patterns of their response to disturbance.

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SUPPORTING INFORMATION

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

TABLE S1. *A list of the species of the fruit eaten by S. hondurensis in the sampling sites.*

TABLE S2. *Plants with fruit potentially eaten by S. hondurensis and found in its foraging areas within cloud forest fragments.*

TABLE S3. *Plants with fruit potentially eaten by S. hondurensis found in the areas where it forages in the coffee plantations.*

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