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Bat Diversity and Movement in an Agricultural Landscape in Matiguás, Nicaragua

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ABSTRACT

Although agriculture dominates much of Central America, little is known about the bat assemblages that occur within agricultural landscapes and how bats use different types of tree cover within these landscapes. Using mist-nets and a mark-recapture protocol, we compared bat diversity and movement across six types of tree cover within an agricultural landscape in central Nicaragua. The tree cover types surveyed included secondary forests, riparian forests, forest fallows, live fences, pastures with high tree cover and pastures with low tree cover. We captured a total of 3084 bats of 39 species, including two new species records for the country (*Lonchorhina aurita* and *Molossops greenhalli*). Of these, 2970 bats and 27 species were in the Phyllostomidae family. There were significant differences in mean species density, abundance and evenness of phyllostomid bats across the different types of tree cover, but not in bat diversity. Riparian forests had the highest mean species density and bat abundance per plot. In contrast, mean bat abundance and species density were lowest in pastures with low tree cover. Of the 1947 phyllostomid bats marked, a total of 64 bats of eight species were recaptured. The average linear distance between extra-site recaptures was 2227 m (± 228 SE) and the maximum distance was 10.6 km. Bats were recorded moving between almost all types of tree cover, and especially to and from riparian forests. Our study suggests that agricultural landscapes retaining a heterogeneous tree cover may maintain a diverse bat assemblage, and that bats visit and use a variety of tree cover types within the agricultural matrix.

RESUMEN

Aunque la agricultura domina Centroamérica, se conoce poco sobre los ensamblajes de murciélagos que ocurren en los agropaisajes y cómo ellos utilizan los diferentes tipos de cobertura arbórea presente en estos paisajes. Utilizando redes de nieblas y un protocolo de mark-recapture, caracterizamos la diversidad y el movimiento de murciélagos en seis tipos de cobertura arbórea en un agropaisaje dominado por pasturas en Nicaragua. Los tipos de cobertura arbórea incluyeron bosques secundarios, bosques riparios, charrales, cercas vivas, y potreros con alta o baja cobertura arbórea. Capturamos un total de 3084 murciélagos de 39 especies, incluyendo dos nuevos registros para el país (*Lonchorhina aurita* y *Molossops greenhalli*). 2970 murcielagos de 27 especies fueron phyllostomidos. Hubo diferencias en la densidad promedia de especies, abundancia y equitividad de murciélagos phyllostómidos entre tipos de cobertura arbórea, pero no en la diversidad. Los bosques riparios tuvieron la mayor densidad de especies y abundancia por parcela. En cambio, la abundancia y densidad promedia de especies por parcela fueron las más bajas en potreros con poca cobertura arbórea. De los 2016 murciélagos marcados, un total de 64 individuos de ocho especies fueron recapturados. La distancia linear promedio entre sitios de recaptura fue 2227 m (± 228 SE) y la distancia máxima fue 10.6 km. Se registraron murciélagos en movimiento entre casi todos los tipos de cobertura arbórea, y especialmente desde y hacia bosques riparios. Nuestro estudio sugiere que los agropaisajes que retienen una cobertura arbórea heterogénea pueden mantener un ensamblaje diverso de murciélagos y que los murciélagos visitan y utilizan la cobertura arbórea presente en la matriz agropecuaria.

Key words: agroecosystems; conservation of biodiversity; live fences; mark-recapture; pastures; Phyllostomidae; riparian forests; rural landscapes; tropical moist forest.

AS AGRICULTURAL LANDSCAPES BECOME MORE PREVALENT WITHIN THE NEOTROPICS, it becomes increasingly important to understand what organisms can (or cannot) survive within these landscapes, and how agricultural mosaics can be designed and effectively managed for biodiversity conservation (Daily 2001, Daily *et al.* 2001, Daily *et al.* 2003, Lindell *et al.* 2004, Harvey *et al.* 2005a). This requires knowledge of which species still persist in agricultural landscapes, which land use types provide resources and habitats for different components of the flora and fauna, and how animals move across or within agricultural landscapes. However, with the exception of studies in Veracruz, Mexico (Estrada *et al.* 1993, 2000; Estrada & Coates-Estrada 2001a, 2001b, 2002; Galindo-González & Sosa 2003) and Coto Brus, Costa Rica (Daily *et al.* 2001, 2003; Ricketts *et al.* 2001), there is still only limited information on the distribution of organisms within neotropical agricultural landscapes and on the relative importance of different types of tree cover within agricultural matrices. There is also only scant information on the patterns of animal movement within such landscapes.

In this study, we explore the value of different types of tree cover within a neotropical agricultural landscape for bat conservation. Bats are commonly used as indicators of forest fragmentation and forest condition as they are abundant, diverse, easy to sample, and exploit a wide variety of food resources within tropical forests (Bonaccorso 1979, Fenton *et al.* 1992, Medellín *et al.* 2000, Giannini & Kalko 2004). Bats are also widely studied because their ecological roles as pollinators, seed dispersal agents and predators make them key components of tropical ecosystems (Fleming *et al.* 1972, Fleming 1988, Charles-Dominique 1991, Stevens *et al.* 2003). In addition, neotropical bat assemblages are known to be sensitive to deforestation and fragmentation, with decreases in species diversity and population sizes due to changes in the availability of habitats and resources, as well as changes in landscape composition and structure which affect bat movement (Fenton *et al.* 1992, Brosset *et al.* 1996, Gorresen & Willig 2004, Quesada *et al.* 2004). Deforestation and forest fragmentation can also potentially change

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patterns of bat pollinator activity (Quesada *et al.* 2004) and seed dispersal (Medellín & Gaona 1999), with impacts on plant reproductive success. However, because bats are highly mobile and able to forage over large areas (including areas that constitute physical barriers for other species), they may be less affected by deforestation and habitat fragmentation than other animal groups and be able to take advantage of different habitats within agricultural landscapes (Estrada *et al.* 1993, Estrada & Coates-Estrada 2001a, Bernard & Fenton 2003, Estrada *et al.* 2004).

The objective of this study was to characterize the bat assemblage present in an agricultural landscape dominated by pastures in central Nicaragua, and evaluate the role of different types of tree cover within the agricultural matrix for bat conservation and movement. The specific objectives were: (1) to compare the abundance, species richness, diversity and composition of bat assemblages present within different types of tree cover in the agricultural matrix; and (2) to determine patterns of movement of bats across the agricultural landscape, using mark-recapture methods. We focus our analyses on bats in the Phyllostomidae family, as this family includes a high diversity of species and feeding ensembles, is easily sampled using ground nets, and contains species that are good indicators of deforestation and habitat alteration (Kunz & Kurta 1988, Kalko 1998, Fenton *et al.* 1992). In addition to exploring patterns of phyllostomid bat assemblages across a spectrum of tree cover types in an agricultural landscape, our study provides some of the first ecological information on bats within Nicaragua.

METHODS

STUDY AREA.—The study was conducted in an agricultural landscape (9200 ha) in the Bulbul watershed, municipality of Matiguás, department of Matagalpa, in north-central Nicaragua (85°27′ N, 12°50′ W), located 2 km southeast of the town of Matiguás. The life zone is locally classified as semi-deciduous forest (Salas 1993), and falls within Holdridge's Tropical Moist Forest life zone (Holdridge 1978). The annual temperature is 24°C, and annual rainfall ranges between 1200 and 1800 mm, with most rainfall occurring in the rainy season between May and December. Altitudes range from 200 to 900 m asl (Laurent *et al.* 2001).

The region is one of the main cattle production regions of Nicaragua and is typical of cattle-dominated landscapes throughout the Pacific and central regions of Central America. Most cattle production is dual-purpose (milk and meat), with large, extensively grazed pastures (primarily *Hyperrhenia rufa*, *Cynoden nlemfuensis* and to a lesser degree, *Brachiaria brizantha*) and little use of fertilizers and supplementary feed (Betancourt *et al.* 2003).

It is not clear when the region was first colonized; however, permanent settlements are known to be present from the 1920s onwards. The most recent period of deforestation occurred from the 1950s to present. However, some natural regeneration occurred in the region in the 1980s as the area was largely abandoned due to the Nicaraguan civil war. The current landscape is dominated by pastures, but retains a diverse and heterogeneous tree cover. According to a 2002 ICONOS image, pastures cover 68.2 percent of the landscape; other important land uses include arboreal plantations (including fruit trees and live fences; 8.5% of area), secondary forests (6.8%), forest fallows (6.8%), riparian forests (1.4%), crops (1.2%) and other land uses (7%; Harvey *et al.* in press).

We sampled bats in the six main types of tree cover present in the landscape: (1) secondary forests; (2) riparian forests; (3) forest fallows (young secondary regrowth on former pastures, locally known as "charrals"); (4) live fences dominated by *Bursera simaruba* trees; (5) pastures with high tree cover (consisting of scattered trees with crowns covering 16–25% of the pasture) and (6) pastures with low tree cover (*i.e.*, scattered trees covering 0–5%). We selected two types of pastures (with different levels of tree cover), because other studies have suggested a relationship between tree density and bat activity (*e.g.,* Estrada & Coates-Estrada 2001a, Lumsden & Bennett 2005). All tree cover types were open to entry by cattle and the forest habitats had been affected by firewood and timber extraction. No surveys were conducted in either continuous or fragmented primary forests, as these are not present in the agricultural landscape. The closest intact forest, Quiragua, is located 6 km to the northeast and occurs at a higher altitude, making comparisons inappropriate.

For each of the six land use types, we randomly chose eight replicates from the 2002 ICONOS image, resulting in a total of 48 sample plots. Each of these plots was visited in the field to ensure that it was of sufficient size for the monitoring protocol. This required a minimum of 1 ha for secondary forests, forest fallows, and pastures, a minimum length of 500 m for riparian forests and live fences, and a minimum width of 20 m for riparian forests. In addition secondary forests had to have a minimum canopy height of 15 m and a well developed understory, and forest fallows had to have a canopy height of between 3 and 10 m. Live fences had intact crowns (*i.e.*, unpollarded) and were not selected if they were next to a busy road. Plots that did not fulfill these criteria were replaced with another randomly chosen plot. Additional details on the vegetation structure and composition of each type of tree cover can be found in Sánchez Merlo *et al.* (2005). As plots were selected randomly from the satellite image, the distances between plots varied greatly, ranging from 151 m to 11,917 m, with a mean inter-plot distance of 3930 m (± 2142 m) across all pairs of plots.

Each of the 48 plots was sampled once, for two consecutive days, during the study period. Sampling excursions occurred approximately every 6 weeks between July 2003 and June 2004. In each sampling excursion, we sampled one plot of each habitat type, with plots being sampled in random order.

Bats were sampled using eight ground mist nets (each 12 × 2.5 m wide, and 1.5 cm mesh size). This method is considered the most effective and rapid sampling technique for phyllostomid bats (Fenton *et al.* 1992), but is biased against the capture of canopy bats or bats that typically fly at high levels (Kunz & Kurta 1988). In the secondary forests, forest fallows and pastures, mist nets were positioned in a circle, with a 55 m radius, with individual nets located roughly 50 m apart. Pilot studies showed this circular arrangement of mist nets to be an effective sampling strategy in the agricultural landscape. In contrast, in the linear habitats (riparian forests and live fences), mist nets were located along a transect, spaced 50 m apart. Mist nets were open from 1830 h to 0100 h during two consecutive nights in each plot, for a total of 104 mist net hours per plot and 832 hours per habitat. Mist-netting was not conducted on rainy days, or on days of full moon.

All captured bats were removed from the mist nets and identified using keys by Timm and Laval (1998), Timm *et al.* (1999), Laval and Rodríguez (2002), and Reid (1997), and the list of mammal species of Nicaragua (Martinez-Sanchez *et al.* 2000). Each bat species was classified by its feeding ensemble (frugivorous, insectivorous, nectarivorous, sanguinivorous, carnivorous, or omnivorous) using Laval and Rodríguez (2002) and Reid (1997).

All captured bats (of all species) were fitted with a plastic collar containing a numerical combination of colored beads on a plastic necklace (*sensu* Medellín *et al.* 2000), to allow the recognition of individuals and to prevent counting the same individual twice. However, due to problems in obtaining sufficient plastic collars, collars were only placed on the first 2015 bats (of which 1947 were phyllostomids). For bats that were recaptured, we noted the type of land use in which the bat was originally captured and the type in which it was recaptured, and calculated the linear distance (in km) between the two sites using ArcView v 3.3 (ESRI 2002). Bats that were recaptured in the same site during the 2 days of mist netting per site were only counted once and were not included in the recapture data. The number of recaptured bats therefore represents the number of bats that were recaptured in sites other than the original capture site.

DATA ANALYSIS.—In each of the 48 plots, the number of bats and the number of species captured on each of the two consecutive sampling days were combined (*i.e.*, one data point per plot) to obtain a total bat abundance and species richness per plot. We used four variables as indicators of phyllostomid bat diversity and abundance: the total number of bats, the total number of bat species, bat diversity as measured by the Shannon diversity index, and bat evenness (Magurran 1988). The Shannon diversity and the evenness index were calculated (for each of the 48 plots) based on the total bat abundance and species richness recorded in each plot over the 2 days. We also calculated the number of individuals and species of each feeding ensemble (frugivores, nectarivores, insectivores, sanguinivores, omnivores, and carnivores) present in each plot.

To compare differences in phyllostomid bat abundance, species richness, diversity and evenness across the six land use types (as well as abundance and species richness of individual feeding ensembles), we used a one-way ANOVA (for normally distributed data, followed by Duncan pairwise tests) or Kruskal Wallis (for non-normally distributed data, followed by pairwise comparisons), with the type of tree cover as the main factor and eight replicates per tree cover type. As sampling effort was uniform both across plots and across the forms of tree cover, data were not transformed prior to analyses. All calculations of species diversity indices were conducted in Biodiversity Pro (McAleece 1997); all statistical analyses were performed using InfoStats Version 1.4 (2002). Rarefaction curves were also calculated in EcoSim v5 (EcoSim 2000) to compare phyllostomid bat species richness across tree cover types, due to differences in the number of bats captured in each site.

Data on bat recaptures were summarized in terms of the number of phyllostomid bats recaptured, and the linear distances between the sites at which individual bats were recaptured. For species with more than five recaptures, the mean linear distance between capture sites was also calculated.

RESULTS

GENERAL CHARACTERISTICS OF THE BAT ASSEMBLAGE IN AGRICULTURAL LANDSCAPES.—A total of 3084 bats of 39 species were captured in the Matiguás landscape (Table S1), with a total mist-netting effort of 4992 net hours (6.5 h/net × 8 nets × 2 nights/site × 48 plots). The bat assemblage was dominated by four species: *Sturnira lilium* (30.7% of all captures); *Artibeus jamaicensis* (24.6%); *Glossophaga soricina* (13.6%); and *Uroderma bilobatum* (6.0%), which together accounted for 74.9 percent of all captures. An additional eight species each accounted for between 1 and 4 percent of all bats captured, whereas the remaining 27 species were present in low abundances (each representing less than 1% of all captures). Nine species were represented by only a single individual. Two new bat species were reported for the first time in Nicaragua: *Molossops greenhalli* and *Lonchorhina aurita.* In addition, we registered three species that are on the IUCN Red List for Nicaragua: *Vampyrum spectrum* (one individual), *Diphylla ecaudata* (one individual), and *Choeroniscus godmani* (three individuals, IUCN 1999).

COMPARISON OF PHYLLOSTOMID BAT ASSEMBLAGES IN DIFFERENT TYPES OF TREE COVER.—Phyllostomid bats accounted for 2970 individuals and 27 species. The majority of these bats captured were frugivores, which were represented by 13 species and accounted for 78 percent of all phyllostomid captures (Table 1). The second most common ensemble were the nectarivorous bats, which accounted for 15.4 percent of captures (460 individuals of four species), with *Glossophaga soricina* accounting for 91 percent of this ensemble. The remaining ensembles each represented less than 5 percent of all captures. Three species of sanguinivorous bats were captured, of which the most common was *Desmodus rotundus.*

Total phyllostomid bat species richness varied from 15 to 19 per tree cover type, whereas the total number of bats caught ranged from 225 (in pastures with low tree cover) to 700 (in live fences). There were significant differences in the mean number of phyllostomid species ($F_{5,42} = 2.67$, $P = 0.03$), the mean number of individuals ($H = 13.47$, $P = 0.02$) and the mean evenness per plot ($F_{5,42} = 2.84$, $P = 0.03$) across the different types of tree cover, but not in bat diversity (Table 2). Mean bat species richness per plot was greater in riparian forests than in pastures with low tree cover; bat species richness per plot was intermediate in all other tree cover types. Bat abundance was higher in riparian forests and live fences than in either secondary forests or pastures with low tree cover. Phyllostomid bat evenness was greater in secondary forests, forest fallows, and pastures with low tree cover than in live fences.

TABLE 1. *Summary of phyllostomid bat species richness and abundance (by feeding ensembles) registered in six types of tree cover in an agricultural landscape in Matiguás, Nicaragua. All data represent summary statistics of eight plots/tree cover type, with a total effort of 832 mistnet hours per type of tree cover.*

Feeding ensembles	Secondary forests	Riparian forests	Forest fallows	Live fences	Pastures with high tree cover	Pastures with low tree cover	Total
Carnivorous spp.	1	0	0	0	1	0	2
Carnivorous bats	1	0	0	0	1	0	2
Frugivorous spp.	11	11	11	11	10	9	13
Frugivorous bats	224	558	300	445	610	197	2334
Sanguinivorous spp.	2	1	1	1	2	1	3
Sanguinivorous bats	29	44	14	13	15	2	117
Insectivorous spp.	2	2	0	0	0	1	3
Insectivorous bats	3	3	0	0	0	1	7
Nectarivorous spp.	2	3	3	2	2	2	4
Nectarivorous bats	48	54	84	229	23	22	460
Omnivorous spp.	1	1	2	1	1	2	2
Omnivorous bats	4	4	3	13	23	3	50
Total # spp.	19	18	17	15	16	15	27
Total # bats	309	663	401	700	672	225	2970

There were also differences in the abundance and species richness of certain bat ensembles across tree cover types (Table 2). The mean number of frugivorous bat species per plot was greater in riparian forests than in secondary forests and pastures with low tree cover, with other habitats being intermediate ($F_{5,42} = 3.29$, $P = 0.014$). Frugivorous bat abundance was higher in riparian forests and live fences than in either secondary forests or pastures with low tree cover ($H = 14.11$, $P = 0.015$). The mean number of nectarivorous bat species was similar across different types of tree cover, but nectarivorous bats were more abundant in riparian forests, forest fallows and live fences than in either of the pasture types ($H = 12.17$, $P = 0.03$). No analyses of differences in insectivorous, sanguinivorous, omnivorous bats across land use types were conducted due to low sample sizes of these ensembles.

Rarefaction curves indicate that the number of phyllostomid bat species would increase in all habitats with increased sampling (Fig. 1). At $N = 225$, the secondary forests were the richest habitats in species, followed by the riparian forests and forest fallows.

The species composition was fairly similar across types of tree cover, with pairs of habitats sharing between 59 and 88 percent of the same species. Of the 27 phyllostomid bat species recorded, 13 were captured in all six land use types: *Artibeus jamaicensis, A. intermedius, A. lituratus, A. watsoni, Carollia perspicillata, C. subrufa, Desmodus rotundus, Glossophaga commissarisi, G. soricina, Phyllostomus discolor, Platyrrhinus helleri, Sturnira lilium*, and *Uroderma bilobatum.* In contrast, ten phyllostomid species were captured in only a single habitat type, but these species were each represented by less than three individuals.

TABLE 2. *Comparison of mean species richness, abundance, diversity and evenness of phyllostomid bats per plot (± SE) in six types of tree cover (*N = *eight replicate/tree cover type) in the agricultural landscape of Matiguás, Nicaragua.*

Variable	Secondary forests	Riparian forests	Forest fallows	Live fences	Pastures with high tree cover	Pastures with low tree cover
Total # species	8.25 ± 0.96 **ab**	10.50 ± 1.09 **a**	8.00 ± 0.60 **ab**	8.50 ± 0.98 **ab**	8.25 ± 0.94 **ab**	5.63 ± 1.05 **b**
Total # of individuals	38.63 ± 6.51 **bc**	82.88 ± 19.76 **a**	50.13 ± 8.56 **abc**	87.50 ± 34.44 **a**	84.00 ± 28.38 **ab**	28.13 ± 5.6 **c**
Shannon diversity index	0.71 ± 0.04	0.73 ± 0.05	0.70 ± 0.04	0.59 ± 0.04	0.63 ± 0.04	0.58 ± 0.08
Evenness index	0.80 ± 0.03 **a**	0.72 ± 0.02 **ab**	0.78 ± 0.04 **a**	0.66 ± 0.04 **b**	0.71 ± 0.04 **ab**	0.80 ± 0.04 **a**
# frugivorous species	5.13 ± 0.58 **bc**	7.38 ± 0.68 **a**	5.75 ± 0.45 **abc**	6.25 ± 0.7 **ab**	5.63 ± 0.68 **abc**	3.88 ± 0.72 **c**
# frugivorous bats	28.00 ± 5.16 **bc**	69.75 ± 17.07 **a**	37.50 ± 6.64 **abc**	55.63 ± 11.02 **a**	76.25 ± 27.91 **ab**	24.63 ± 5.04 **c**
# nectarivorous bat species	1.50 ± 0.27	1.75 ± 0.25	1.63 ± 0.18	1.50 ± 0.19	1.25 ± 0.16	1.00 ± 0.19
# nectarivorous bats	6.00 ± 1.79 **ab**	6.75 ± 1.77 **a**	10.50 ± 3.38 **a**	28.63 ± 22.66 **a**	2.88 ± 0.52 **b**	2.75 ± 0.7 **b**

Different letters within a row indicate statistical differences between habitats ($P < 0.05$).

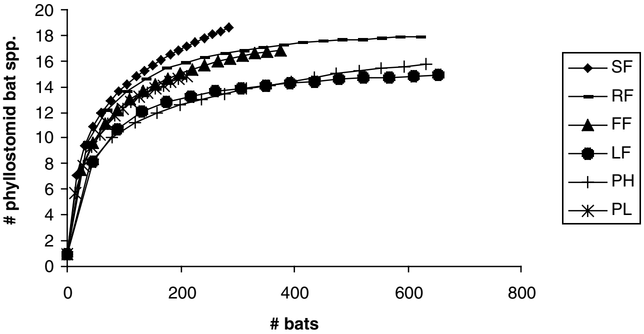

FIGURE 1. Rarefaction curves for phyllostomid bats in six types of tree cover (SF = secondary forests, RF = riparian forests, FF = forest fallows, LF = live fences, PH = pastures with high tree cover, PL = pastures with low tree cover) in the agricultural landscape of Matiguás, Nicaragua.

BAT MOVEMENT WITHIN THE AGRICULTURAL LANDSCAPE.—Of the 1947 phyllostomid bats marked with necklaces, 64 individuals (of eight species) were recaptured in a site other than the original capture site, for a recapture rate of 3.3 percent (Table 3). One individual (a male *Sturnira lilium*) was recaptured twice, so the total number of recaptures was 65. This individual was originally captured in a live fence habitat, then recaptured 137 days later in a pasture with high tree cover located 428 m away, and then recaptured the next day in a pasture with low tree cover located 2545 m away. Recaptures were obtained for eight bat species, of which *Artibeus jamaicensis* was the most common, accounting for 44 percent of the recaptures.

The patterns of recaptures showed that the eight recaptured bat species move readily amongst different types of tree cover (Table 4). Of the 65 recaptures, 15 individuals (or 23% of the recaptures) were recaptured in the same type of tree cover as the original site where they were tagged, with the greatest number of recaptures within the same type of tree cover occurring within riparian forests (seven individuals). The remainder of the individuals were originally captured in one type of tree cover and later recaptured in a distinct type of tree cover. Over 50 percent of the recaptures either originated or ended in riparian forests.

The mean linear distance between the original site where bats were marked and the recapture sites was 2227 m (SE = 228). The greatest distance between capture sites was 10,595 m, recorded by a female *Sturniria lilium*. The average interval between marking and recapture was 120.7 nights (SE = 12.2), and ranged from 4 to 325 nights. Recapture distances for individual species are shown in Table 5.

DISCUSSION

Our study suggests that Neotropical agricultural landscapes containing a heterogeneous on-farm tree cover may conserve a diverse bat fauna, as bats can readily move within the agricultural matrix and take advantage of the habitats and resources present. Despite the fact that Matiguás is dominated by pastures and retains less than 10 percent of its original forest cover, it has a high bat species richness (at least 39 species), comparable to that of intact Tropical Dry Forests and Tropical Moist Forests in the region (Fleming *et al.* 1972, Fenton *et al.* 1992, Schulze *et al.* 2000, Stoner 2001, Stoner & Timm 2004). It is likely that additional species could be found in the Matiguás landscape if complementary sampling methods (such as the use of canopy mist nets and ultrasonic bat detectors) were used to sample species that are adept at avoiding mist nets, or that forage and fly at high levels (Kalko & Handley 2001, Godoy Borgallo *et al.* 2003).

In addition to its high species richness, the Matiguás landscape contained several bat species of interest to conservation efforts, including *Vampyrum spectrum* (captured in pastures with high tree cover), a top predator that has previously been considered an indicator of intact forested landscapes (Estrada & Coates Estrada 2002), and two species (*Lonchorhina aurita* and *Molossops greenhalli*) that have been recorded for the first time in Nicaragua. These species had been expected to occur in Nicaragua and were included in the list of Nicaraguan mammals (Martinez Sanchez *et al.* 2000) but had not been reported previously. The agricultural landscape also contained three bat species that are listed as threatened by IUCN lists, albeit in very low abundances, indicating the potential value of this region for bat conservation.

Because there are no previous studies of bats in this area prior to its conversion to pasture, and not even any information on bat assemblages within forested landscapes in similar life zones in Nicaragua, it is difficult to determine how distinct the agricultural bat assemblage is from the original assemblage. On the one hand, the dominance of four phyllostomid bat species in Matiguás (*Sturnira lilium*, *Artibeus jamaicensis*, *Glossophaga soricina* and *Uroderma bilobatum*, which together represented 74.9% of the captures) is similar to that reported in undisturbed forests in Central America (*e.g.*, Carranza Almansa & Arias de Reyna Martinez 1984, Stoner 2001, Laval 2004). For example, *Artibeus jamaicensis*, *Carollia perspicillata*, and *Sturnira lilium* were the three most common bat species caught in ground mist nets in the Tropical Dry Forest of the Palo Verde National Park, Costa Rica (Stoner & Timm 2004), as well as in Tropical Moist Forests and Tropical Dry Forests in Panama (Fleming *et al.* 1972, Kalko *et al.* 1996). On the other hand, some

TABLE 3. *Total number of bat species marked and recaptured in each types of tree cover in the Matiguás agricultural landscape, Nicaragua.*

Variable	Secondary forest	Riparian forests	Forest fallows	Live fences	Pastures with high tree cover	Pastures with low tree cover	Total
Bats marked	187	483	220	483	401	173	1947
Bats recaptured	6	26	9	14	7	2	64
Percent bats recaptured (per tree cover type)	3.2	5.4	4.1	2.9	1.7	1.2	3.3

TABLE 4. *Summary of the movement patterns of bats between their original capture habitats and the habitats where they were recaptured, in an agricultural landscape in Matiguás, Nicaragua. The numbers represent the number of bats that moved from an original habitat (where they were marked) to the recapture habitat.*

	Original capture habitat[a]						
Recapture habitat	SF	RF	FF	LF	PH	PL	Total
SF	1	2	2	0	1	0	6
RF	0	7	2	4	1	0	14
FF	1	3	1	0	1	0	6
LF	0	4	1	2	0	0	7
PH	2	5	0	5*	4	2	18
PL	2	5	3	3	0	0	13
Total	6	26	9	14	7	3	64*

Note: Bats recaptured within the same site during mist netting were not included in these data.

[a]SF = secondary forests, RF = riparian forests, FF = forest fallows, LF = live fences, PH = pastures with high tree cover, and PL = pastures with low tree cover.

*One individual was marked in a live fence, recaptured in a pasture with high tree cover, and then recaptured later in a pasture with low tree cover. The table only shows the first movement, from live fence to pastures with high tree cover.

TABLE 5. *Bat species recaptured in the agricultural landscape of Matiguás, Nicaragua, and the distances between the initial capture and recapture sites.*

Species	Number of individuals recaptured	Mean distance (m) between capture sites (± SE)	Range of distances (min–max) between capture sites (m)
Artibeus intermedius	2	2414 (± 1932)	482–4346
Artibeus jamaicensis	28	2307 (± 295)	287–5292
Artibeus lituratus	1	764	764
Artibeus phaeotis	1	1983	1983
Desmodus rotundus	2	2377 (± 2052)	325–4428
Glossophaga commissarisi	1	151	151
Glossophaga soricina	7	1081 (± 343)	271–2166
Sturnira lilium	22	2631 (± 472)	287–1095

species that are considered indicators of disturbed habitats, such as the common vampire bat *Desmodus rotundus* (Fenton *et al.* 1992, Medellín *et al.* 2000), are common in the landscape and have likely benefited from the conversion of forest to pasture and the availability of large numbers of cattle upon which they prey. Additional studies that compare the Matiguás bat assemblage to that of an intact forest in a similar life zone are therefore needed to better determine the effects of deforestation and fragmentation on bat assemblages.

Bat assemblages in different types of tree cover.—Although bats used all types of tree cover within the agricultural landscape, bat abundance and species richness were clearly associated with the different types of tree cover present. The high species density and abundance of bats (and particularly frugivorous bats) in riparian forests may reflect the fact the greater tree diversity and fruit availability in these habitats relative to other types of tree cover (Sanchez Merlo *et al.* 2005), which make these sites good foraging areas. In addition, riparian forests had large trees and exposed root systems on riverbanks that provide key roosting sites for bats (Bernard & Fenton 2003). Other studies have similarly reported bats using river systems and riparian forests as foraging sites, roosting sites, and sources of water, as well as corridors for bat movement between forest remnants, isolated trees and other tree cover within pastures (*e.g.*, Fleming *et al.* 1972, Estrada & Coates-Estrada 2002, Galindo-González & Sosa 2003).

In contrast to the riparian forests, the secondary forests registered intermediate numbers of bats, but had the greatest total number of bat species (19), suggesting that even though bats are less abundant, these forests are still important habitats. Studies of the vegetation within secondary forests in the region indicate that these habitats are less floristically and structurally diverse than the riparian forests (Sanchez Merlo *et al.* 2005), and this may account for the lower bat abundance observed in this tree cover type.

Bats were abundant in live fences, despite the narrowness of these habitats (most consist of only a single row of trees and have canopies less than 5 m wide), their limited tree species diversity (mainly *Bursera simaruba*) and their frequent disturbance by management (Harvey *et al.* 2005b). Bats appear to use live fences and other linear features to orientate their flights across agricultural landscapes and to cross open pasture areas (Limpens & Kapteyn 1989; Estrada *et al.* 1993; Estrada & Coates-Estrada 2001a, 2001b; Medellín *et al.* 2000; Medina *et al.* 2004). They also feed on fruiting trees within live fences (*e.g.*, planted species such as *Spondias mombin*, *Spondias purpurea, Byrsonima crassifolia* and naturally regenerated species, such as *Cecropia peltata* and *Ficus* spp.; Harvey *et al.* 2005b) and the insects that are deposited on the leeward side of live fences (Epila 1986).

Bat abundance was notably greater in pastures having high tree densities (16–25%) than those with low tree cover (< 5%). Other studies have observed bats visiting scattered trees in pastures, while foraging, commuting or searching for perches (*e.g.*, Law & Lean 1999, Estrada & Coates-Estrada 2001a, Galindo-González & Sosa 2003, Lumsden & Bennett 2005), and have similarly reported higher abundance and activity of bats in pastures with high tree densities (Lumsden & Bennettt 2005), due to the greater abundance and variety of food resources, roosting sites, and the shelter from predation by nocturnal raptors (Estrada & Coates-Estrada 2001).

Bat movement across the agricultural landscape.—Bats are clearly able to move across the entire agricultural landscape, using all types of tree cover, and it is this ability to readily cross and utilize the entire landscape which is likely key to their persistence

(Estrada *et al.* 2004). The eight bat species that were recaptured in the study can readily move large distances, with an average distance between recaptures of 2227 m and with a maximum distance recorded of just over 10 km. It is possible that bats move even larger distances, but the small size of the study area (9200 ha), and the fact that the greatest distance between two plots within this study area was just over 11 km, limited our ability to record longer movements.

While high mobility of Neotropical bats has been recorded previously (*e.g.*, Heithaus & Fleming 1978, Fleming 1988, Fenton *et al.* 1992), our study is one of the first to show movement between different types of habitats within a human-dominated landscape. Bernard and Fenton (2003) reported that bats moved freely across a naturally fragmented landscape of primary forests, forest fragments and savannas in Alter do Chao, Brazil, crossing distances from 0.5 to 2.5 km and routinely flying across open savanna areas. Bats have also been reported to move between riparian forests and isolated trees in pastures in Veracruz, Mexico (Galindo-González & Sosa 2003). In our study, bats used multiple habitats within the agricultural landscape, moved freely between forested and non-forested habitats, and flew large distances (>10 km) within the landscape. While bats were recorded moving between all types of land uses, over 50 percent of the recaptures either originated or ended in riparian forests, suggesting that riparian forests may be preferred travel routes for crossing the agricultural landscape. Similar functions of riparian forests as corridors, travel paths, or flyways for bats have been reported elsewhere (Verboom & Huitema 1997, Law & Lean 1999, Galindo-González & Sosa 2003).

CONCLUSIONS AND CONSERVATION IMPLICATIONS.—Together with other studies (Estrada *et al.* 1993; Medillín *et al.* 2000; Estrada & Coates-Estrada 2001a, 2001b, 2002; Galindo-González & Sosa 2003; Estrada *et al.* 2004; Medina *et al.* 2004), our results suggest that Neotropical agricultural landscapes containing a heterogeneous and diverse tree cover can maintain diverse bat assemblages, and underscore the importance of conserving forest and tree cover within human-dominated landscapes. While efforts to conserve neotropical bats should focus foremost on the retention and protection of riparian forests and any remaining forest patches, our results indicate that integrating tree cover within pastures may also contribute to bat conservation. For example, planting additional live fences within pastures or diversifying live fences with species that serve as food for bats may be beneficial, as bats frequently visit and use live fences. Since the use of live fences is readily compatible with existing farming systems (Budowski & Russo 1988, Harvey *et al.* 2005b), it may therefore be possible to design and manage farming landscapes in ways which allow both productive and conservation goals to be achieved.

Although our study underscores the important role of on-farm tree cover for bat conservation, additional studies are needed to ascertain the exact status of the bat assemblages within agricultural landscapes and to obtain detailed information on the other bat species present in the landscape which were undetected by ground mist-netting. As the abundance of some tropical bat species is known to change both across seasons and years (Stoner 2001), it will be important to obtain additional information on the composition of bat assemblages over time, as well as long-term information on the demography of bat populations within agricultural landscapes to determine if they are viable over the long term. Although we now know that bats visit different parts of agricultural landscape and move frequently between different types of tree cover, it will also be critical to study how the bats use the different forms of tree cover. In addition, comparative studies should be conducted in landscapes that have different amounts of tree cover and/or different spatial arrangements, so that it is possible to determine whether there are thresholds of tree cover within agricultural landscapes below which bat conservation is compromised.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:
Table S1

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