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INSIGHTS

Bats use live fences to move between tropical dry forest remnants

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Abstract

Linear features can benefit wildlife by assisting animal movement. We captured bats along barbed-wire and live-tree fences connecting Tropical Dry Forest patches in Nicaragua. Bat species richness and captures were higher along live fences but we noted differences in sex ratios, richness, and species composition compared to surrounding natural forests.

Key words: Connectivity; Chiroptera; forest patches; hedgerow; *Lophostoma brasiliensis*; Phyllostomidae

Palabras Clave: Conectividad; Chiroptera; parches de bosque; cercas vivas; *Lophostoma brasiliensis*; Phyllostomidae

RESUMEN

La degradación del hábitat y fragmentación del bosque son amenazas para la biodiversidad a nivel mundial. Estructuras lineales pueden beneficiar la vida silvestre, al asistir movimiento de animales entre parches de hábitat. Cercas definen cultivos o áreas de pastoreo usando alambre de púas y postes de madera, pero las cercas vivas reemplazan los postes de madera con árboles, creando corredores que animales pueden usar para moverse a través del paisaje fragmentado. Nosotros capturamos 279 murciélagos de 17 especies a lo largo de 27 sitios pareados de cercas tradicionales y cercas vivas conectando bosque seco tropical mesoamericano en el sudeste de Nicaragua. Riqueza y capturas de murciélagos fueron dos y cuatro veces más altas en cercas vivas. Sin embargo, diferencias en proporciones de sexo, riqueza y composición de las capturas indican que las cercas vivas no proveen los mismos beneficios de conectividad para todas las especies.

FRAGMENTATION AND LOSS OF HABITAT NEGATIVELY AFFECT ANIMAL POPULATIONS BY LIMITING access to resources, restricting demographic exchange, and impeding gene flow (Cosgrove, McWhorter, & Maron, 2018; Fahrig & Merriam, 1985; Hanski, 1991). Species have unique behavioral or morphological adaptations that influence their habitat requirements and affect dispersal through non-optimal environments (Bonaccorso, 1979; Cisneros, Fagan, & Willig, 2015a; Fleming, 1982; Fenton et al., 1992; Meyer & Kalko, 2008). In fragmented forests, even

small clearings can have a negative impact on many species, restricting movement across landscapes (Bierregaard, Lovejoy, Kapos, Dos Santos, & Hutchings, 1993; Davies, Margules, & Lawrence, 2000; Entwistle et al., 2001; Powell & Powell, 1987; Saunders & Ribeira, 1991). However, tree and fence lines, as linear landscape features, can be used as “spatial references” by bats to commute between roosts and feeding sites (Entwistle et al., 2001; Schnitzler, Moss, & Denzinger, 2003; Schaub & Schnitzler, 2007; Verboom & Huitema, 1997). Bat use of fences and hedgerows was described in Europe in mixed farmlands (e.g., Downs & Racey, 2006; Lacoëuilhe, Machon, Julien, & Kerbiriou, 2016; Toffoli, 2016). In Europe, the beneficial effects of linear structures on open landscape matrices are recognized and recommended for bat conservation (Entwistle et al., 2001).

In Latin America, standard fences typically consist of 3 to 6 lines of barbed wire supported by wooden posts spaced every 3 to 4 m. In Nicaragua, a single row of fast-growing trees (e.g., *Gliricidia sepium*, *Bursera simaruba*), spaced 1.5 to 4 m apart, often replaces posts as a common configuration for live fences (Albrecht & Kandji, 2003; Sauer, 1979; J. Martínez-Fonseca, pers. obs.). Some landowners prefer live fences because they provide a practical and permanent delimitation for properties, lower maintenance cost (live trees need less frequent replacement), shade and forage for livestock, and, eventually, production of fruit, firewood, and timber (Beer, 1987; Lagemann & Heuvelop, 1983; Sauer, 1979). Nevertheless, landowners recognize constraints to the establishment of live fences, making them less common than producers would desire in Nicaragua’s southwestern Tropical Dry Forest landscape (e.g., increased time and effort to establish; Dorgay, Muelle, & Klooster, 2016).

In the Neotropics, the use of fence lines by bats remains undocumented in many biomes. The ability of bats to use live fences and hedgerows was reported in Mexico in Tropical Rain Forest (Estrada, Coates-Estrada, & Meritt, 1993; Estrada & Coates-Estrada, 2001) and Tropical Moist Forest in Nicaragua (Medina, Harvey, Merlo, Vilchez, & Hernandez, 2007), although none of these studies explicitly compared live fences with standard fences.

Nicaragua is a world biodiversity hotspot for bats (Hutson, Mickleburgh, & Racey, 2001) with 108 species of bats representing nine families (Reid, 2009; Medina-Fitoria, 2014; Medina-Fitoria et al., 2015). Three species are categorized as Near Threatened under the International Union for Conservation of Nature and Natural Resources (IUCN) because of habitat loss and fragmentation (Miller & Medina, 2008; Rodriguez & Pineda, 2015; Aguirre, Mantilla, Miller, &

Dávalos, 2008). This area also supports Tropical Dry Forest (TDF), one of the most threatened forest types in the tropics (Janzen, 1988; Miles et al., 2006).

High diversity and habitat loss of TDF accentuates the role of this region of Nicaragua for bat conservation. We selected an area with mixed human use in a populated region of Nicaragua that included farming, livestock ranching, and fragmented TDF. Based on activity of bats along live fences and hedgerows documented by other studies, we expected more bats and species to select live over standard fences. Our objective was to compare bat activity and diversity between live and standard fences simultaneously, and explicitly evaluate the utility of live fences as corridors for bats in this altered landscape.

METHODS

Our study area encompassed the Rivas Isthmus (11°12'33"N, 85°44'2"W), in southwestern Nicaragua, located between Lake Nicaragua and the Pacific Ocean (Figure S1), in forest recognized as TDF (Holdridge, 1967). At least 63 bat species occur in this area (Medina-Fitoria, 2014). Annual air temperature averaged 26.7 °C with annual precipitation of 1400-2000 mm; a well-defined dry season occurs from December to April (Sesnie, Hagell, Otterstrom, Chambers, & Dickson 2008).

We selected sites using four criteria: (1) the presence of two fences, one live and one standard, where each connected forest patches across open pastures or agricultural fields, (2) the pair of fences were ≤ 100 m apart to allow bats to be simultaneously monitored at both localities (Figure S2), (3) no other flyways, evident landforms or structures (e.g., creeks, buildings) intersected the fences across open areas, and (4) average distance between sites was > 10 km. We sampled from 29 May to 7 August 2015.

To capture bats, we used single mist nets (2.6 m x 6 to 18 m for bats, 38 mm mesh, Avinet, Inc., New York, USA; Kunz & Kurta, 1988) placed in similar configurations to maximize captures along both fence types. We opened nets simultaneously at dusk (~ 1800 h) for up to four hours per site (≥ 40 net h per site [one net h = one 6-m net open for one h], range 40 - 115 net h, mean and SE: 63.5 ± 3.6 net h).

Animals were captured under Nicaraguan Permit No. 015-122011, with the approval of the Northern Arizona University Institutional Animal Care and Use Committee (15-006) and following the guidelines of the American Society of Mammalogists (Sikes et al., 2016). For

species identification, we recorded morphometrical data and sex; nomenclature was adopted from Reid (2009) and Medina-Fitoria (2014).

We estimated species richness with EstimateS (Version 9.1.0, Colwell 2013) using the Abundance-based Coverage Estimator (ACE; Chao & Lee, 1992; Chazdon, Colwell, Denslow, & Guariguata, 1998; Chao, Hwang, Chen, & Kuo, 2000). We used these estimates to compare species richness between live and standard fences.

We modeled capture rate of bats using a generalized linear mixed model framework with a negative binomial (to test for overdispersion) or Poisson distribution and a logit link function (SAS 9.4 PROC GLIMMIX; SAS Institute, Cary, NC 2019). We assigned site as a random effect and adjusted count data for effort using net hours. We compared bat captures by contrasting individual species (if >50 individuals) with all other species combined (those with ≤ 50 individuals per species). We tested for effect of fence (live, standard), sex (female, male), moon phase (percent illumination since some bats are lunophobic and sampling nights were distributed across all lunar phases; e.g., Morrison, 1978; Thies, Kalko, & Schnitzler, 2006), and interactions for species, sex, and fence type. Because we did not observe overdispersion, we reported results using a Poisson distribution and applied the Laplace approximation for parameter estimation. We modeled species richness using the same procedures; however, we used only fence type and moon phase as parameters in the model. We set α at 0.05.

RESULTS

We found 27 sites that met our sampling criteria with a mean distance (\pm SD) of 13.0 ± 0.3 km between sites. We captured 279 individuals (225 along live fences and 54 along standard fences) during 1714 net hours (equally divided between live and standard fences). Bats represented 17 species, 11 genera, and four families (Table 1). Two species, *Artibeus jamaicensis* ($n = 147$) and *Carollia perspicillata* ($n = 58$) accounted for 73% of captures. We captured 15 and eight species along live and standard fences, respectively (Table 1). Per site, number of bats captured averaged 8.3 ± 0.9 for live and 2.0 ± 0.4 for standard fences. Predicted species richness was higher for live ($n = 24$) compared to standard fences ($n = 10$; Figure 1). Estimates of species richness were greater than our actual captures of species (Figure 1).

Species richness was higher for live than standard fences ($df = 1, 26, F = 20.41, P = 0.0001$). We did not detect an effect of moon phase on richness ($df = 1, 26, F = 3.88, P = 0.06$). We found that the relative number of males and females captured depended on species ($df = 2,$

286, $F = 3.74$, $P = 0.02$) and captures by fence type also varied across species ($df = 2$, 286, $F = 3.64$, $P = 0.03$). Males dominated captures overall, although their representation varied across species (e.g., *Carollia perspicillata*; Table 1). Live fences benefitted some species (e.g., *Artibeus jamaicensis*) more than others (Table 1). We did not detect an effect of moon phase ($df = 1$, 286, $F = 2.83$, $P = 0.09$), Fence*Sex ($df = 1$, 286, $F = 0.02$, $P = 0.89$), or Fence*Sex*Species ($df = 2$, 286, $F = 2.45$, $P = 0.09$).

DISCUSSION

Our results show that use of live fences was four times greater than use of standard fences by bats. In addition, we captured twice as many species along live fences as standard fences; both richness estimates and species accumulation curves suggested our sampling underrepresented the richness of species using live fences. Our findings thus suggest that live fences favorably affect bats in the Tropical Dry Forest of Nicaragua. Phyllostomids dominated our captures (97%); these bats have special echolocation and morphological adaptations to fly in cluttered environments (Stockwell, 2001; Kalko, 2004), thus live fences may offer a familiar environment for leaf-nosed bats to move across disturbed areas. The most common Phyllostomids that we captured (*Carollia perspicillata*, *Artibeus jamaicensis*) can travel large distances and have low fidelity to local forest patches (Morrison, 1980; Bianconi, Mikich, & Pedro, 2006; Menezes Jr. et al., 2008) making them more adaptable to altered landscapes. However, *C. perspicillata* and *A. jamaicensis* benefitted from live fences. Given the important role of *Carollia* and *Artibeus* as seed dispersers of trees, live fences can increase gene flow across forest fragments and increase regeneration in open areas (Fleming, 2004; Hoffmaster, Vonk, & Mies, 2016).

We captured more males than females along both fence types. This contrasts with concurrent captures in nearby forested riparian sites, where sex ratios were equal ($n = 16$ sites, net $h = 891$, number of females = 480, number of males = 439, C. Chambers, unpubl. data). Sex ratio differences might be influenced by food availability, reproductive condition, or risk aversion (Rocha et al., 2017). Although we did not detect a significant effect of moon phase on captures or richness, we noted a trend towards an effect (more captures and higher richness on less bright nights), consistent with studies suggesting lunophobia in bats is species specific (Lang, Kalko, Romer, Bockholdt, & Dechman, 2006; Mello, Kalko, & Silva, 2013).

Live fences appeared to benefit species moving among forest patches in fragmented landscapes. However, the differences in abundance, species richness, and sex ratios in our captures compared to those found in adjacent mature forests suggest that live fences present constraints to movement and benefit species differently. Protecting natural corridors such as riverbeds and retaining forested strips across the landscape will better enhance survival for forest-associated species (Cisneros, Fagan, & Willig 2015b; Herrera, Duncan, Clare, Fenton, & Simmons, 2018; Naiman, 1993), particularly when coupled with protection of larger forested areas.

Our findings support the use of live fences to improve connectivity between forest patches in other parts of the TDF and likely other forest types in Mesoamerica. Our study also provides the first evidence that live fences are used by bats to move within a fragmented TDF landscape. Although we captured only one gleaning insectivore with specialized feeding habits and associated with less-disturbed forests (male *Lophostoma brasiliensis*; Bonaccorso, 1979; Fleming, 1982), it used a live fence. Chambers et al. (2016) found that *L. brasiliensis* was one of the most common Phyllostomine species in our study area, suggesting that some forest-associated bats might also benefit from live fences.

Future studies could use acoustic monitoring to assess selection of live fences by other bat families that are seldom caught in mist nets (Rodhouse, Vierling, & Irvine, 2011; Wilson, Cole, Nichols, Rudran, & Foster, 1996) and consider the effects of structural differences of live fences (e.g., density, height, and age of trees) on bats. Given the ecological importance of bats as pollinators, seed dispersers, and predators, we recommend that local entities support landowners in maintaining existing live fences and increasing their presence when possible in TDF in Latin America.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.00000> (Martínez-Fonseca, Chávez-Velásquez, Williams-Guillen, & Chambers. 2019).

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TABLE 1. Number of bats by sex (F = female, M = male) and species captured at sites with live (Live) and standard (Standard) fences between May and August 2015, Rivas, Nicaragua. Number of sites (# of Sites) represents the number of unique locations surveyed where the species was captured.

Family	Species	# of Sites	Standard		Live		Total bats
			F	M	F	M	
Noctilionidae	<i>Noctilio albiventris</i>	1	0	1	0	0	1
Phyllostomidae	<i>Artibeus jamaicensis</i> *	26	3	18	40	84	147
	<i>Carollia perspicillata</i>	22	9	6	16	27	58
	<i>Sturnira parvidens</i>	10	2	3	5	8	18
	<i>Glossophaga soricina</i>	13	2	0	7	7	16
	<i>Desmodus rotundus</i>	5	2	4	1	4	11
	<i>Artibeus lituratus</i>	7	0	2	1	7	10
	<i>Carollia subrufa</i>	5	0	0	3	3	6
	<i>Dermanura watsoni</i>	3	0	0	0	3	3
	<i>Artibeus intermedius</i>	1	0	0	0	1	1
	<i>Carollia castanea</i>	1	0	0	0	1	1
	<i>Glossophaga commissarisi</i>	1	0	0	0	1	1
	<i>Lophotostoma brasiliensis</i>	1	0	0	0	1	1
	Mormopidae	<i>Pteronotus mesoamericanus</i>	1	1	0	0	0
<i>Pteronotus personatus</i>		1	0	0	0	1	1
Noctilionidae	<i>Noctilio albiventris</i>	1	0	1	0	0	1
Vespertilionidae	<i>Myotis nigricans</i>	2	0	0	1	1	2

	<i>Eptesicus furinalis</i>	1	0	0	0	1	1
Total number of individuals			19	34	74	150	279
Total number of species			6	6	8	15	17

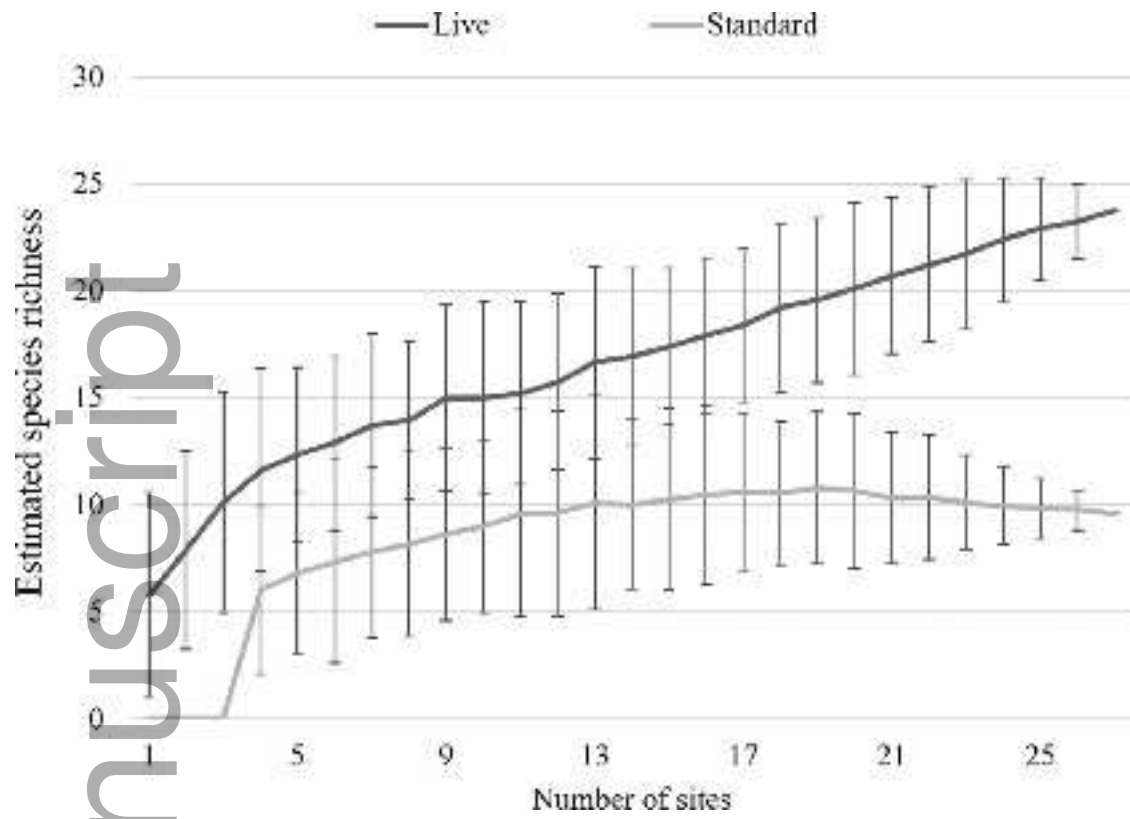
*Sex for 2 individuals, one from each fence type was not identified, total count includes those individuals.

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Figure legends

FIGURE 1. Estimated species richness (\pm SD) of bats using live and standard fences, May - Aug 2015, Rivas, Nicaragua.

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