BIOTROPICA 39(6): 737–746 2007 10.1111/j.1744-7429.2007.00322.x

Phyllostomid Bats of Lowland Amazonia: Effects of Habitat Alteration on Abundance

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ABSTRACT

Habitat fragmentation and conversion are among the human activities that pose the greatest threat to species persistence and conservation of biodiversity. This is particularly true in the Neotropics, where bats represent important components of biodiversity from taxonomic and functional perspectives, and provide critical ecosystem services (*e.g.*, seed dispersal and pollination). We assessed the degree to which conversion of lowland Amazonian rain forest to agriculture, and its subsequent abandonment and secondary succession, affect the abundances of populations of phyllostomid bats in the vicinity of Iquitos, Perú. During 90,720 net-m-h of sampling, we captured 3789 bats of five families; of these 3764 were phyllostomids representing 44 species, 23 genera, and three feeding guilds. We focus on the 24 most abundant species of phyllostomids. In terms of abundance, frugivores dominated assemblages in all habitat types and seasons. Eight species consistently responded to habitat conversion, two species consistently responded to season, two species responded consistently to both habitat and season, and five species responded to habitat conversion in a season-specific manner. Frugivores and nectarivores were abundant in areas that had been converted to agriculture, which suggests that these bats are resilient to extant levels of disturbance and may be important in promoting secondary succession. However, this result may be scale- or context-dependent. If habitat conversion continues and dramatically reduces the areal extent and increases fragmentation of mature forest, then a complex metacommunity dynamic may characterize the region and source populations of bats may become threatened or extirpated locally.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Amazonian rain forest; anthropogenic change; conservation; deforestation; habitat use; lowland; Neotropical bat biodiversity; population dynamics; seasonal dynamics.

AT A GLOBAL SCALE, HABITAT FRAGMENTATION AND CONVERSION TO AGRICULTURE are among the human activities that pose the greatest threat to species persistence and the conservation of biodiversity (Wilcox & Murphy 1985, Sala *et al.* 2000). The rate of habitat loss associated with anthropogenic activities is increasing (Vitousek *et al.* 1997; NRC 2001, 2003), especially in the Neotropics, which harbors a considerable proportion of the world's species (Heywood & Watson 1995). Fragmentation creates islands of habitat and subdivides or isolates populations (Hanski *et al.* 1995), thereby altering the behavior of species (Hargis *et al.* 1999), interspecific interactions (Aizen & Feisinger 1994), and ecosystem processes (Schowalter *et al.* 1981). In addition, loss of species diversity can enhance the emergence of vector-borne, zoonotic infectious diseases with consequences to human health (LoGuidice *et al.* 2003).

In the New World, species richness of bats rapidly increases toward the equator (Willig & Selcer 1989), thereby contributing significantly to increased mammalian species richness in tropical areas (Kaufman & Willig 1998). Moreover, tropical bats provide critical ecosystem services associated with pollination and seed dispersal (Fleming 1988, Patterson *et al.* 2003). In tropical forests, where bats may be the sole or primary agent of pollination and dispersal for some plants (Fleming & Heithaus 1981, 1986; Fleming 1988; Galindo-González *et al.* 2000), the Chiroptera may represent a keystone taxon. Indeed, some bat species, especially members of Phyllostomidae, promote secondary succession and regeneration of disturbed areas because they differentially disperse pioneer plants (Fleming 1988, Gorchov *et al.* 1993). Understanding the effects of habitat fragmentation and anthropogenic disturbance on bats is critical to designing a conservation program that maintains biotic composition and ecosystem functioning of lowland Amazonian rain forests.

Bats respond to habitat fragmentation in a species-specific manner. Abundances of some species increase, others decrease, and yet others are unaffected (Fenton *et al.* 1992, Estrada *et al.* 1993, de Jong 1995, Cosson *et al.* 1999, Medellín *et al.* 2000, Bernard *et al.* 2001, Aguirre *et al.* 2003, Gorresen & Willig 2004, Gorresen *et al.* 2005). Consequently, landscape heterogeneity resulting from

Received 5 May 2006; revision accepted 16 January 2007.

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deforestation and fragmentation affects bat communities in a complex manner (Gorresen & Willig 2004) and is dependent on the spatial scale of analysis (Gorresen *et al.* 2005). We used comparative observational studies (*i.e.*, nonmanipulative natural experiments) to evaluate the effects of habitat conversion (*i.e.*, mature forest converted to agriculture and subsequent abandonment to early successional forest) on populations of 24 phyllostomid bat taxa in the Peruvian Amazon. We expected frugivores (*e.g.*, *Carollia* spp. and *Sturnira* spp.) and nectarivores (*e.g.*, *Glossophaga soricina*) that primarily feed on fruits and flowers of successional species to exhibit higher abundance in disturbed areas, especially those areas undergoing secondary succession (Fenton *et al.* 1992). Elsewhere, we evaluate the effects of habitat conversion on bat biodiversity from the guild and community perspectives.

METHODS

STUDY AREA.—Research was conducted in lowland Amazonian forest in the environs of the city of Iquitos (3.74° S, 73.24° W), Loreto Province, northeastern Perú (Fig. 1). The climate of the area is tropical, with a mean annual temperature of 26°C. Rainfall is substantial (~2800 mm/yr), with a modest dry season (185 mm/mo) from June to October and a wet season (292 mm/mo) from January to May (Madigosky & Vatnick 2000). Based on the Holdridge System (Holdridge 1947, Holdridge *et al.* 1974), the region is in the Humid Tropical Forest Botanical Province (Tosi 1960). The terrain is rolling, dissected by numerous rivers and streams, and punctuated by low-lying moriche palm (*Mauritia flexuosa*) swamps (aguajales), ponds, and marshes (Vásquez 1997). Elevations range from 100 m to 220 m, flooded forest (igapo) characterizes low-lying areas, whereas white sand forest (varillal) or upland forest (monte alto) characterizes higher areas.

Iquitos is in the Inambari area of endemism, one of eight such recognized areas in Amazonia (da Silva *et al.* 2005). Inambari has lost less than 10 percent of its forest and is among the least threatened regions of the Amazon. Nonetheless, Inambari is a conservation priority because it has higher numbers of restricted-range endemic species than do other areas of endemism (da Silva *et al.* 2005). Over 28 percent of Inambari lands experience some form of protection; however, only 1.7 percent of those lands are protected strictly, with the rest subject to use by humans. Outside the city of Iquitos, human disturbance has primarily paralleled the banks of navigable rivers, and more recently, a network of highways and roads (Fig. 1). This project was conducted along the highway that connects the city of Iquitos with Nauta (4.53° S, 73.55° W), which is located 95 km to the SSW. A dirt road was present along the route from Iquitos to Nauta prior to paving, although the rate and extent of human disturbance along the road increased significantly as a consequence of paving (Mäki *et al.* 2001). Data were collected in two 5-mo periods: July–November 2002 and January–May 2003, corresponding to drier and wetter seasons of the year, respectively (Madigosky & Vatnick 2000). Additional details are available for the region (Vásquez 1997), local climate (Madigosky & Vatnick 2000), and Iquitos-Nauta highway (Mäki *et al.* 2001).

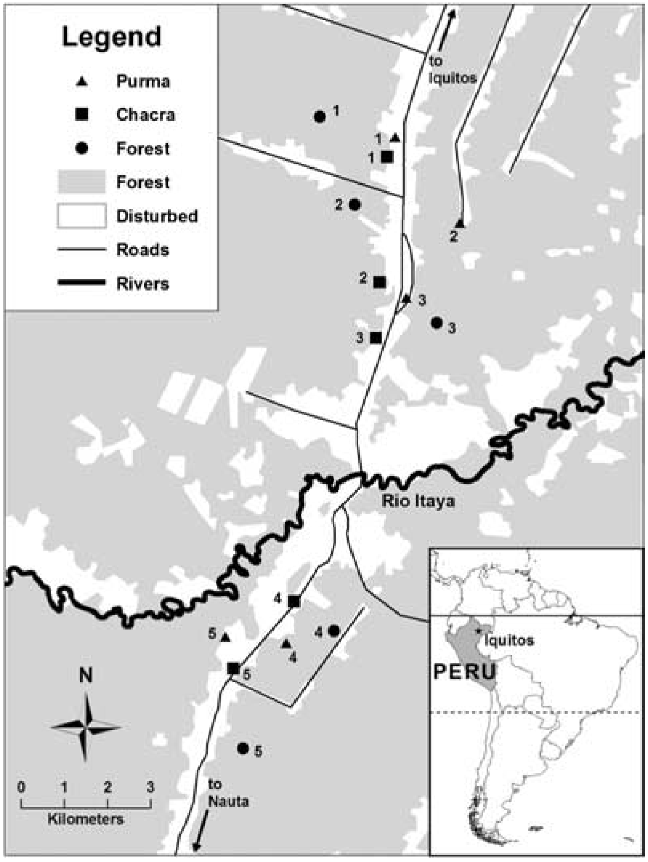

FIGURE 1. Map of environs south of Iquitos, Perú, illustrating the extent of deforestation and fragmentation along the Río Itaya and the Iquitos–Nauta Highway. Superimposed on this heterogeneous landscape are five replicate blocks (1–5), each comprises three plots (forest, purma, and chacra). The location of Iquitos in Perú, and its relationship to the rest of South America (Equator, solid horizontal line; Tropic of Capricorn, dashed horizontal line), appear in the insert.

Deforestation in the western Amazon, especially in the environs of Iquitos, typically proceeds over several days to weeks, during which the understory is removed and most of the trees are felled. The largest trees often are left where they fall (Fig. 2A, B). Burning is followed by 2–6 mo of cultivation that results in a plantation covering about 1 ha, which locally is called 'chacra' (Mäki *et al.* 2001; Fig. 2B). Chacras typically are planted with pineapple (*Ananas comosus*, Bromeliaceae), plantain (*Musa* spp., Musaceae), or manioc (*Manihot esculenta*, Euphorbiaceae) until the soil is no longer fertile. The influx of pioneer species into abandoned chacras during the subsequent 5–10 yr results in early successional forests that locally are called 'purma' (Mäki *et al.* 2001; Fig. 2C). Purma differs from mature forest in terms of species composition (*e.g.*, *Cecropia* spp. often dominate) and physical structure (< 10 m canopy, dense understory). Mature upland forest in the region is characterized by high tree diversity (Vásquez 1997) with a 30-m canopy punctuated by 50 m emergent trees (Fig. 2D). Chacra and purma typically

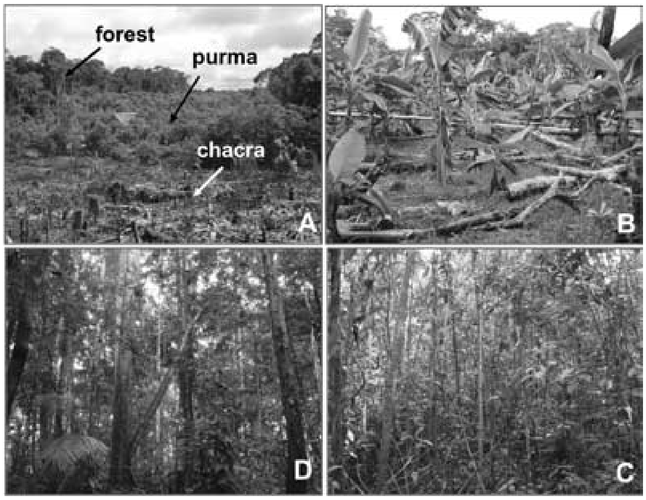

FIGURE 2. Aspect photos of the three habitat types from which bats were obtained in the vicinity of Iquitos, Perú. (A) Contrast of overall habitat stature, with a recently cleared and planted chacra in the foreground, adjacent purma (secondary growth) in the midground, and mature forest in the background. (B) Typical 3-yr-old chacra planted with a mixture of plantains, manioc, and pineapple. (C) Characteristic dense young growth of purma with most woody vegetation < 10 cm dbh and < 10-m tall. (D) Mature forest that generally has a more open and shaded understory than does purma, and a canopy of large trees, many of which are > 30-m tall.

have clearly defined boundaries and almost always occur adjacent to mature forest in the Iquitos region (Fig. 2A).

SAMPLING METHODS.—Five replicate blocks were located along the Iquitos–Nauta Highway between 40 and 70 km SSW of Iquitos, and within 3 km E or W of the road (Fig. 1). Each block contained three different plots: one in mature forest, one in agriculture (*i.e.*, chacra), and one in secondary forest (*i.e.*, purma). Because of the heterogeneous landscape and idiosyncratic availability of sites for use, the distances among plots within blocks were variable, as were the distances between plots in adjacent blocks (*i.e.*, average distance among plots within blocks was 1.5 km whereas the average interblock distance between plots of the same habitat type was 3.6 km). Each plot comprised 6.25 ha (250 × 250 m) and contained eight subplots. Four subplots (*i.e.*, interior subplots), each 75 × 75 m squares, were arranged as quadrants. The remaining subplots (*i.e.*, edge subplots) extended 50 m beyond the grid in each cardinal direction.

Each plot was sampled for two 3-night sessions, one during the dry season and one during the wet season. In the dry season, a different block was selected randomly for sampling each month; the order of sampling remained the same in the wet season to ensure that populations at each plot had the same number of months to recover from the removal of individuals in the preceding dry season. On the first night, two interior subplots and two edge subplots were chosen randomly. At selected locations within each of these subplots, three 12 × 3 m mist nets were erected, two at ground level and one in the upper understory, located directly above one of the ground nets. This design sampled bats flying up to 6 m above the ground. On the second night of sampling, the same number and configuration of nets were placed in the remaining four subplots. On the third night, two interior and two edge subplots were chosen randomly without regard to previous sampling.

Nets remained open from 1800 to 0100 h, and were checked every 20–30 min. Nets were closed during heavy rain. If heavy rain occurred for more than 2 h of netting on any night, data from that night were excluded from analyses, and another night of netting was scheduled to replace the lost sampling effort. To minimize the effects of lunar phobia (Crespo *et al.* 1972; Morrison 1975, 1978) on sampling efficacy, no netting was conducted within two nights of a full moon. This sampling protocol and subsequent analyses assume that removal of bats during the first season has no effect on bat captures during the second season; that sampling bats on one portion of a plot did not affect bat captures on other portions of that plot within seasons; and that capture probabilities of species are independent of each other.

In terms of species richness and abundance, frugivores dominated captures at or near ground level in all habitat types in both seasons. The presence or abundance of some taxa, particularly species in the Emballonuridae, Molossidae, Thyropteridae, and Vespertilionidae, may be underestimated appreciably by mist netting, especially when restricted to ground or upper understory levels of rain forests (Handley 1967, Bernard 2001, Sampaio *et al.* 2003). We use the term 'abundance' to refer to the number of specimens captured by mist netting for each species because of its ease of exposition. Variation in the number of captured specimens at a site can be a consequence of the catchability of species or the behavior of species, as well as a change in true abundance. Our methodology cannot distinguish among these alternatives.

Up to 20 individuals of each species at each plot in each season were sacrificed and prepared as standard museum specimens. Individuals of abundant species (primarily *Carollia*) beyond the first 20 captures were released after identification to species, although all individuals for which identification to species was not certain in the field were collected; this included all individuals from several stenodermatine genera (*i.e.*, *Artibeus*, *Chiroderma*, *Platyrrhinus*, *Uroderma*, and *Vampyressa*). Before release, each individual was marked by fur trimming to prevent it from being counted more than once in estimates of abundance during a particular season. Although *Carollia perspicillata* and *C. brevicauda* are similar externally and difficult to distinguish in the field, identifications of collected *Carollia* were accurate for more than 96 percent of the individuals. Because all dubious individuals were collected, it is likely that overall accuracy of *Carollia* identifications exceeded 96 percent. Nonetheless, we chose to be conservative, and pooled captures of *C. perspicillata* and *C. brevicauda* into a category labeled *Carollia* spp. for all analyses. For convenience, we refer to *Carollia* spp. as a 'species.' Because *C. benkeithi* could be distinguished from *C. perspicillata* and *C. brevicauda* with confidence, it was not included in *Carollia* spp. Because we have at least one confirmed identification of *C. perspicillata* and *C. brevicauda* in each habitat in each season, we considered the composite taxon *Carollia* spp. to equal two species in all calculations of phyllostomid richness. We followed the systematic recommendations of Simmons (2005) for bat taxa in lowland Amazonia, except for recognizing *C. benkeithi* (Solari & Baker 2006) rather than *C. castanea*. We classified bats into broad foraging guilds based on published recommendations (Wilson 1973, Gardner 1977, Willig 1986, Willig & Moulton 1989). Research involving live animals followed the guidelines for the capture, handling, and care of mammals approved by the American Society of Mammalogists and was approved by the Animal Care and Use Committee of Texas Tech University (ACUC# 01084–03).

ANALYTICAL METHODS.—For each of the 24 most abundant species, a generalized linear mixed-effects model (GLMM; Venables & Ripley 2002) with the assumption of Poisson errors quantified the effects of habitat type (forest vs. chacra vs. purma), season (wet vs. dry), and their interaction on abundance (*i.e.*, total number of captures per session). *Phyllostomus discolor* was captured only in chacra, thus abundance data for this species lacked the necessary variation to execute a GLMM with habitat as a within-subject factor. Therefore, GLMM analysis was restricted to season for this species, with the assumption that habitat had a significant effect on abundance based on the restriction of this species to chacra. All GLMMs were conducted using the R programming environment (R Development Core Team 2005) and the MASS (Venables & Ripley 2002) and nlme (Pinheiro & Bates 2000) libraries. Habitat and season were modeled as fixed within-subject factors, whereas blocks were modeled as random effects. If a significant response to habitat or the season by habitat interaction occurred, *a posteriori* tests were performed to evaluate all possible pairwise comparisons. *A posteriori* tests were conducted using the R programming environment and the multcomp library (Westfall 1997). We were interested in the particular responses of each species to disturbance and season, rather than overall multivariate evidence of effects on the bat assemblage. As such, we report exact *P* values (Table S1) and discuss all responses that were significant (*i.e.*, $P \leq 0.05$) or approached significance *(i.e.*, $0.10 \geq P > 0.05$) without application of Bonferroni sequential adjustments (Rice 1989).

We employed a statistical metric of rarity (*e.g.*, Camargo 1992, 1993) to categorize species as rare or common (*i.e.*, not rare). Based on species richness, it considers a species to be rare if its relative abundance is less than the average relative abundance of species in a community or assemblage (*i.e.*, $< 1/S$, where $S =$ richness). Because our experimental design was based on equal sampling effort in each of three habitat types, we could assess the extent to which differences in rarity of phyllostomids among habitats were related to differences in the phyllostomid species abundance distribution in which a species occurs, differences in the capture frequency of a particular species among habitats, or both. Because the effects of forest conversion were the focus of the study, we considered a species to be rare if its abundance was less than or equal to the average abundance of phyllostomid species in forest ($n_{rare} = N_f/S_f$, where N_f is the total number of phyllostomid individuals captured from forest and S_f is the species richness of phyllostomids in forest). This definition of rarity accounts for the effects of unequal sample sizes (*i.e.*, number of captures) and variation in phyllostomid species richness among habitats despite equal sampling effort (*i.e.*, number of net-hours). Without this correction, a species could be captured more often in either of the two disturbed habitats than in forest, yet be considered rare in the habitat from which it is more abundant and common in the habitat from which it is less abundant. For phyllostomids in this study, $S_f = 37$ and $N_f = 725$; consequently, $n_{rare} = 19.59$.

RESULTS

The chiropteran fauna of Iquitos is taxonomically and ecologically diverse. During 90720 net-m-h of sampling, we captured 3789 bats representing 52 species, 30 genera, five families, and six feeding guilds. Of those, 3764 individuals, 44 species, 23 genera, and four guilds were phyllostomids (Table S2). Of the 11 bat species endemic to the Amazon (Marinho-Filho & Sazima 1998), two were captured in Iquitos (*Rhinophylla fischerae* and *Vampyressa brocki*), but each was rare in all habitats (Table S2).

Sixteen of 24 species, all phyllostomids, had at least one significant response to habitat, season, or their interaction (Table S1). In addition, *P. discolor* was restricted to Chacra. All five species of gleaning animalivore evinced at least one response, whereas only 63 percent of the nectarivores (1 of 2) and frugivores (11 of 17) responded significantly. Eight species (two gleaning animalivores, *P. discolor* and *Tonatia saurophila*; and six frugivores, *C. benkeithi*, *Carollia* spp., *Mesophylla macconnelli*, *Sturnira lilium*, *S. tildae*, and *Uroderma bilobatum*) responded consistently to habitat conversion (Table S1; Fig. 3). Five species (two gleaning animalivores, *Mimon crenulatum* and *P. hastatus*; and three frugivores, *Artibeus anderseni*, *A. planirostris*, and *S. magna*) responded to habitat conversion in a season-specific manner (Table S1; Fig. 4). Two species (one nectarivore, *G. soricina*; and one frugivore, *R. pumilio*) responded consistently to habitat and season (Table S1; Fig. 4). Two species (one gleaning animalivore, *Lophostoma silvicolum*; and one frugivore, *A. lituratus*) consistently responded to season, regardless of habitat (Table S1; Fig. 3).

Four (*P. discolor*, *S. lilium*, *S. tildae*, and *U. bilobatum*) of the eight species that responded consistently to habitat conversion attained highest abundances in chacra. Two species (*T. saurophila* and *Me. macconnelli*) attained highest abundances in mature forest. One species (*C. benkeithi*) attained highest abundances in purma. *Carollia* spp. attained higher abundances in purma and chacra than in mature forest (Table S2; Fig. 3). Each species (*G. soricina* and *R. pumilio*) that responded consistently to habitat and to season attained greatest abundances in chacra and during the dry season. Three (*Mim. crenulatum*, *P. hastatus*, and *S. magna*) of five species that evinced season-specific habitat use were most abundant in chacra during the dry season and most abundant in mature forest during the wet season (Fig. 4). In contrast, *A. lituratus* attained highest abundances in mature forest during the dry season and in chacra during the wet season. Of the species that exhibited seasonal differences in abundance regardless of habitat, *L. silvicolum* was more abundant during the wet season and *A. lituratus* was more abundant during the dry season (Fig. 4).

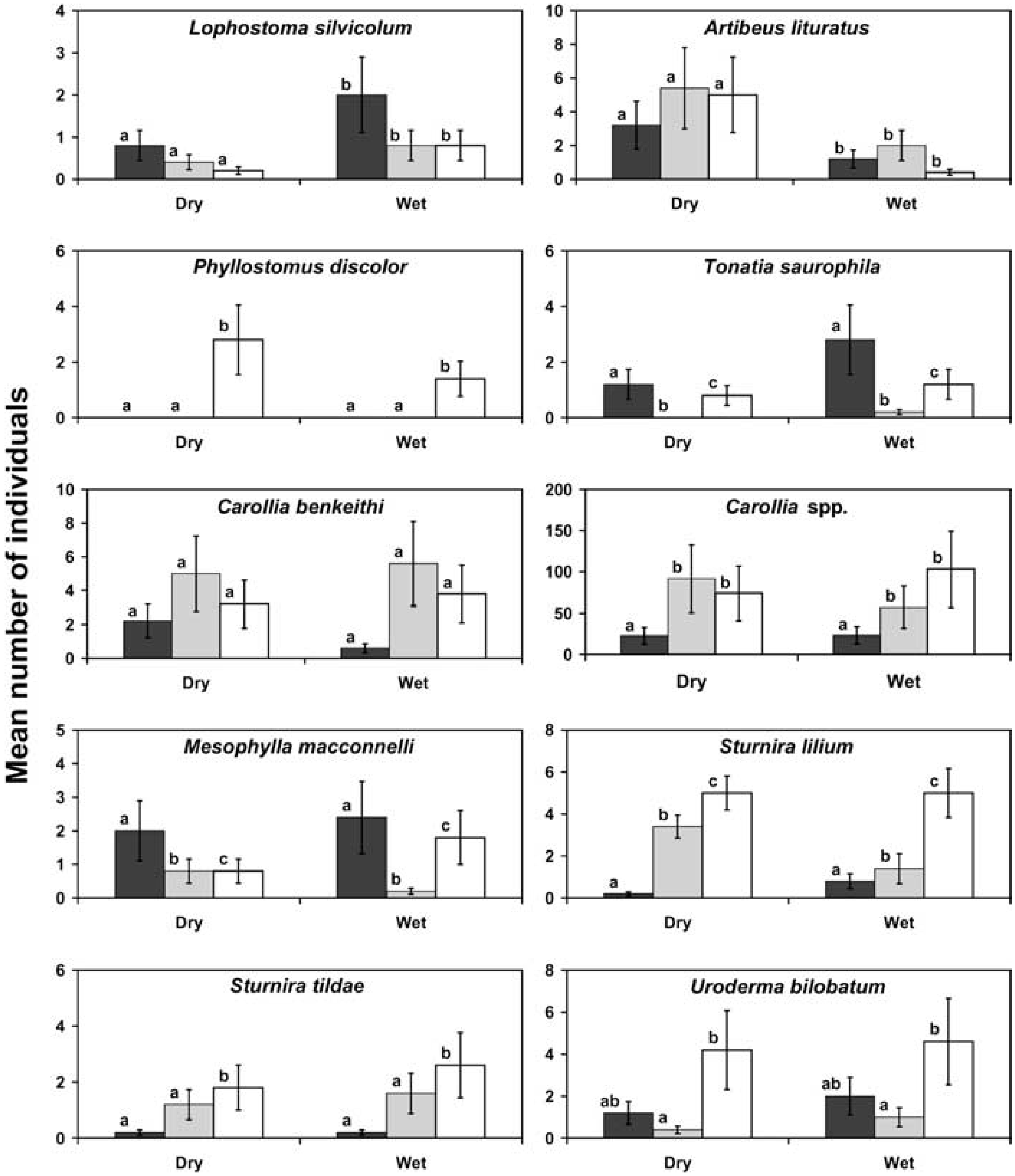

FIGURE 3. Graphical representation of the mean number of individuals captured in a plot for each combination of habitat (dark gray, mature forest; light gray, purma; white, chacra) and season for each species of phyllostomid bat that responded only to season (top row) or only to habitat type (bottom four rows). Abundances in combinations of habitat and season with the same alphabetic designation were indistinguishable in *a posteriori* analyses. Although vertical bars represent ± 1 SE of the mean, these statistics are not the basis of random error for statistical assessments of treatment effects in generalized linear mixed-effects models.

The majority of species consistently was rare in each habitat (77% in forest; 74% in purma; 69% in chacra). Moreover, most species that were common in forest (7 of 9) also were common in purma and chacra. Two species (*T. saurophila* and *Me. macconnelli*) were less abundant in disturbed habitats (*i.e.*, common in forest but rare in purma and chacra) and seven species were more abundant in disturbed habitats (Table S2).

DISCUSSION

DISTURBANCE AND CONSERVATION.—During early stages of forest exploitation in the Neotropics, such as those in the vicinity of Iquitos, the effects of human activities manifest primarily as changes in bat abundance (*e.g.*, *Carollia* spp., *R. pumilio*, and *S. lilium*) rather than by alterations in the presence of species (Gorresen & Willig

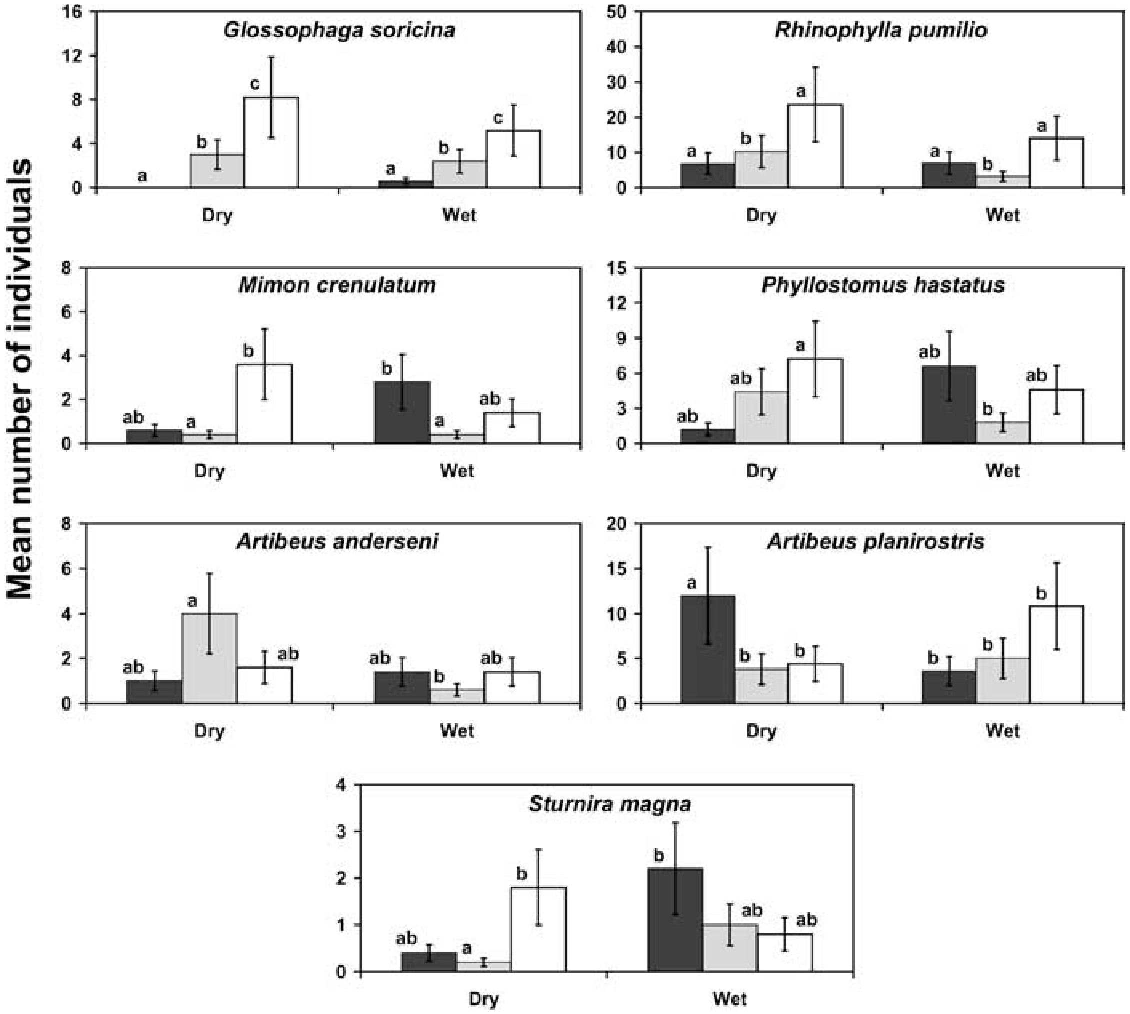

FIGURE 4. Graphical representation of the mean number of individuals captured at a plot for each combination of habitat (dark gray, mature forest; light gray, purma; white, chacra) and season for each species of phyllostomid bat that responded in a consistent manner to both habitat and season (*i.e.*, significant main effects with nonsignificant interactions; top row) or that responded in a season-specific fashion (bottom three rows) to habitat (*i.e.*, a significant interaction). Abundances in combinations of habitat and season with the same alphabetic designation were indistinguishable in *a posteriori* analyses. Although vertical bars represent ± 1 SE of the mean, these statistics are not the basis of random error for statistical assessments of treatment effects in generalized linear mixed-effects models.

2004; Clarke *et al.* 2005a, b; Gorresen *et al.* 2005). Indeed, every phyllostomid species that was captured in forest (37) was captured in purma or chacra, and 32 of those species were caught in both purma and chacra. In addition, some species (43%) evinced greater abundance (increase of $\geq$ 25% and more than five individuals) in disturbed habitats than in forest. Most of these species specialize on fruits and flowers of successional plants and their increase in abundance is expected. Nonetheless, these observations are consistent with a number of interpretations. The most optimistic scenario is that maintenance of large intact areas of forest with a mix of associated human-dominated land uses can sustain biodiversity with little negative impact on species richness, at least in the short term, as documented for bats in Trinidad (Clarke *et al.* 2005a, b) and Paraguay (Gorresen & Willig 2004). Alternatively, anthropogenic effects already may have altered the abundance of bat species in forested habitats that are in close proximity to chacra and purma in Iquitos, creating a biased view of the severity of anthropogenic effects. Comprehensive studies based on standardized protocols to estimate bat species abundances for a specified sampling effort are lacking for intact Amazonian forests that are not in proximity to disturbed areas (*i.e.*, logging, agricultural clearing, or urbanization), certainly for environs that are within close proximity to Iquitos. Therefore, it is difficult to know how bat species abundances in mature forest change in response to encroaching anthropogenic activity.

Any changes in abundance, increases or decreases, which are induced by anthropogenic disturbance signal concern from a conservation perspective. Reduced abundances in chacra and purma suggest concerns for long-term persistence, especially if the extent and frequency of disturbance in the area increase in the future. Higher abundances in purma or chacra may suggest that low levels of disturbance have positive effects on the demography of those bat species, and that recovering agricultural lands can play a pivotal role in designing landscapes to preserve some species. However, such positive responses could be transitory, a common feature characterizing initial responses to disturbance (Willig & McGinley 1999). If not temporary, such increases in abundance by some species would alter the biotic milieu in which other species interact, with possible indirect effects (*e.g.*, reduction in density of competing species) that subsequently are not conducive to conservation goals.

The pattern of response by bat populations to anthropogenic disturbance and successional change is related to species-specific aspects of their foraging ecology (Schulze *et al.* 2000; Gorresen & Willig 2004; Clarke *et al.* 2005a, b). In general, frugivores and nectarivores exploit food resources after conversion to agriculture (*i.e.*, chacra). Moreover, many fruit-bearing plants (*e.g.*, *Cecropia*, *Piper*, and *Solanum*) on which bats feed are early or mid-successional species (Fleming 1988, Marinho-Filho 1991, Gorchov *et al.* 1993). This suggests that bats promote forest regeneration in lowland Amazonian rain forest. Indeed, six of the seven species that responded positively and significantly to disturbance were frugivores (*Carollia* spp., *S. lilium*, *S. tildae*, *U. bilobatum*, and *R. pumilio*) or nectarivores (*G. soricina*), an outcome consistent with predictions based on feeding ecology. Importantly, habitat conversion in the Iquitos region occurs at a relatively small scale (*i.e.*, 1- to 4-ha patches). Such small-scale deforestation may not diminish the tendency for bats to traverse open or disturbed areas (Gorchov *et al.* 1993). Indeed, many species of Neotropical bat will cross open areas of 0.5 km or greater (Bernard & Fenton 2003). Nonetheless, if the size of deforested areas becomes appreciably larger (*e.g.*, 5 km), frugivorous bats may not traverse them with the same frequency as they do small deforested areas. This would influence patterns of seed dispersal, and consequently influence the tempo and mode of succession and regeneration. Although birds disperse seeds within forests or along forest edges, bats disperse seeds more evenly across both of these landscape components, and disperse seeds to the interior of large clear-cut areas (Charles-Dominique 1986, Gorchov *et al.* 1993, Galindo-González *et al.* 2000). As the extent of deforestation increases, bats may become more important in the regeneration of forest because of their critical role in the dispersal of seeds of successional plants in tropical landscapes.

RARITY.—Most of the rare species in Iquitos were rare in all three habitats (Table S2). Similarly, most of the more common species in Iquitos were common in all three habitats. However, six species that were rare in disturbed habitats were not captured at all in forest, and nine species that were rare or absent from forest were common in disturbed areas. As a consequence, bat assemblages in disturbed areas have greater richness and evenness than do those from intact forest. In part, the higher richness of disturbed habitats that derives from the presence of rare species may be a consequence of mechanisms associated with the More Individuals Hypothesis (Srivastava & Lawton 1998, Scheiner & Willig 2005). Any attribute that increases the total abundance or catchability of species will enhance the likelihood of detecting or capturing rare species. This explanation may be most relevant for the rare species in disturbed habitat that were never captured from forest. Other explanations are necessary to account for the high abundance of species in disturbed habitats that were rare in forests.

Disturbed habitats may provide more or higher quality resources for some taxa (*e.g.*, *G. soricina*, *Carollia* spp, and *S. lilium*) that feed on fruits and flowers of early successional plants (Fleming 1988, Marinho-Filho 1991, Gorchov *et al.* 1993). These taxa often differentially exploit areas of natural disturbance, such as treefall gaps, landslides, and areas that recently have recovered from fire (Heithaus & Flemming 1978; Fleming & Heithaus 1981; Fleming 1988; Schulze *et al.* 2000; Clarke *et al.* 2005a, b). The openings caused by human activities in the environs of Iquitos may mimic the characteristics of such natural disturbances, enhancing the abundances of such species in purma and chacra. Consequently, a matrix of mature forest with patches of chacra and purma may provide a more desirable landscape for frugivores and nectarivores than do extensive, intact forests (Clarke *et al.* 2005a). A similar response to deforestation and fragmentation is documented for bats from the interior Atlantic rain forest of Paraguay (Gorresen & Willig 2004) and for birds from Tapajós, Brazil (Wunderle *et al.* 2005). In Paraguay, six of seven species of frugivorous bats attained higher abundances in moderately fragmented landscapes than in contiguous forest or in highly fragmented landscapes. In Brazil, frugivorous and nectarivorous birds were captured more often in gaps than in mature forest because the fruits and flowers they consume were more abundant in recently deforested areas than in forest. Neotropical bats roost in dense vegetation to avoid terrestrial predators (Kunz & Lumsden 2003), whereas some fruit resources are more abundant in disturbed areas (*i.e.*, chacras and purmas). In concert, this may increase carrying capacity and the number of viable niches available to bats in moderately disturbed landscapes. Moreover, capture of bats in any particular place may reflect use of habitats for roosting (Kalko *et al.* 1999, Bernard & Fenton 2003), foraging, or as a corridor for flight. That is, capture of a species in a habitat does not necessarily reflect a preference for that habitat and does not necessarily mean that the habitat contains all or even most of the vital resources needed by a species for persistence. Although chacras may not be critical to the survival of some species, they may exist between vital spaces (*i.e.*, intact forest) and thus appear to harbor various bat species. Although we captured more bat species and individuals in chacra than in mature forest, it is likely that mature forest is the habitat on which the long-term persistence of most species depends.

Vertical complexity and canopy height, which are markedly different in the chacra, purma, and forest (Fig. 1), may affect foraging or flight behavior of bats. Any effect of habitat structure on bat behavior could affect the ability to catch particular species and create a sampling bias. For example, bats in Iquitos do not fly far from foliage as often as they do within or near foliage. Capture rates in chacra were 35 percent lower in elevated nets, which were above the foliage, than in ground nets, which were within the foliage. In contrast, all nets in purma and mature forest were within the foliage, and capture rates in elevated nets were 25 percent and 65 percent greater in purma and mature forest, respectively, than in ground nets. Clearly, the presence of plant cover influences the use of space by bats. As vertical complexity of habitats increases, samples from mist netting may increasingly underestimate the number of individuals and presence of species, particularly rare species. Although bats in general use much of the vertical structure of forests and forage above the forest canopy as well (Voss & Emmons 1996, Simmons & Voss 1998, Giannini & Kalko 2004), phyllostomids generally stay within cover of foliage. Therefore, we expect to capture a higher percentage of the bats that fly through chacra than of those that fly through purmas or mature forest. Consequently, the relative quality of the faunal inventory should decrease as vertical structure increases. The degree to which our efforts encompassed the available vertical habitat may explain why more species and individuals were caught in areas with the least vertical structure (*i.e.*, chacra), and fewer species and individuals were caught in areas with the most vertical structure (*i.e.*, mature forest).

SEASONAL HABITAT USE.—The frequency with which species evinced season-specific differences in abundance among habitats has important ramifications in ecology and conservation biology. Even in tropical settings, which often are considered to be aseasonal, use of landscape components by bats differ between seasons. Views of habitat associations or assessments of habitat value for conservation must consequently be informed by data collected from more than a single time period to avoid misleading conclusions.

Many explanations for season-specific habitat associations of bats are plausible for the Iquitos region. Five species (*i.e.*, *Mim. crenulatum*, *P. hastatus*, *A. anderseni*, *A. planirostris*, and *S. magna*) responded to habitat in a season-specific fashion (Table S1; Fig. 4). For frugivorous species, fruiting phenology may influence changes in habitat associations in two ways. First, fruit productivity may differ with the relative position of plants within a habitat matrix (Thies & Kalko 2004). For example, the fruiting phenology of plants in disturbed (*i.e.*, chacra or purma) or edge areas may be different than that of plants under the canopy of a mature forest. Second, fruit abundance varies with season (Fleming 1988, Marinho-Filho 1991, Thies & Kalko 2004). Times of lower resource abundance require bats to spend more time assessing fruit availability and to change feeding grounds more often (Fleming 1988). This increase in activity could lead to more captures in open habitats (*e.g.*, chacras) because bats are using more open flight paths to search for fruit production in areas that are outside but near to their core home ranges (Fleming 1988, Kalko 1998).

PROSPECTUS.—The Iquitos area represents a natural laboratory in which to assess the effects of forest reduction and fragmentation on populations of wildlife, such as bats. The modest quantity and configuration of anthropogenic disturbance in Iquitos altered species abundance distributions and changed local species composition. As forest use continues, we expect more drastic alteration in the spatial distribution of species. Continued long-term research in areas like Iquitos could provide critical knowledge to land managers and policy makers that would guide sustainable use of tropical habitats. Understanding the extent and configuration of forest modification that will facilitate species persistence is a formidable challenge and requires various research approaches. First, comprehensive inventories are required throughout the Neotropics. These should be accomplished using mist nets at several levels aboveground in disturbed and undisturbed habitats, and augmented by equivalent acoustic monitoring. Second, it is necessary to know if thresholds exist beyond which additional modification of the landscape would incur substantial loss of species or drastic alterations in abundances, especially to keystone species. Third, experimental studies are needed to determine the nature of cause–effect relationships between disturbance and bat species abundances. Many studies support an association between the availability of fruit and flowers, and the presence or abundance of frugivores and nectarivores; however, factors that effect changes in abundance of predatory bats are poorly understood. Finally, long-term studies of bat populations are needed in the Neotropics so that short-term responses to disturbance can be distinguished from long-term trends, so that direct and indirect effects of habitat modification by humans can be distinguished with confidence.

ACKNOWLEDGMENTS

This research was supported by grant AI049725 from the National Institutes of Health through the joint National Science Foundation—National Institutes of Health Program on the Ecology of Infectious Disease. The offices of the Instituto Nacional de Recursos Naturales and CITES-Perú of the Ministerio de Agricultura provided administrative assistance. In addition, the Museo de Historia Natural and the Departamento de Mastozoología of the Universidad Nacional Mayor de San Marcos provided personnel and significant logistic support. The Department of Biological Sciences (M. San Francisco, J. Zak) and the Natural Science Research Laboratory (R. Baker, R. Monk) of Texas Tech University also provided assistance. For assistance in the field or laboratory, we thank J. Rios, W. Rojas, P. Velazco, U. Paredes, C. Chung, M. Villalobos, W. Chávez, A. Chávez, W. Sánchez, C. Dick, C. Valderrama, J. Amanzo, S. Solari, and B. Klingbeil. We are particularly grateful to S. Cox for his advice and guidance concerning generalized linear mixed-effects models and idiosyncrasies of the R programming environment. The exposition and focus of the manuscript was improved as a consequence of comments by I. Castro-Arellano, K. Stoner, and two anonymous reviewers.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online as: www.blackwell-synergy.com/toc/btp

Table S1 *Guild association and number of individuals captured in each habitat and season for each phyllostomid and* Carollia *spp. bat species in the environs of Iquitos, Peru.*

Table S2 *Results of generalized linear mixed-effects models (GLMM) that quantify the effects of habitat type, season, or their interaction on abundance for each of the species of phyllostomid bat.*

LITERATURE CITED

Aguirre, L. F., L. Lens, R. van Damme, and E. Matthysen. 2003. Consistency and variation in the bat assemblages inhabiting two forest islands within a tropical savanna in Bolivia. J. Trop. Ecol. 19: 367–374.

Aizen, M. A., and P. Feinsinger. 1994. Forest fragmentation, pollination and plant production in a Chaco dry forest, Argentina. Ecology 75: 330–351.

Bernard, E. 2001. Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. J. Trop. Ecol. 17: 115–126.

Bernard, E., and M. B. Fenton. 2003. Bat mobility and roosts in a fragmented landscape in central Amazonia, Brazil. Biotropica 35: 262–277.

Bernard, E., A. L. K. M. Albernaz, and W. E. Magnusson. 2001. Bat species composition in three localities in the Amazon Basin. Stud. Neotrop. Fauna Environ. 36: 177–184.

Camargo, J. A. 1992. Can dominance influence stability in competitive interactions? Oikos 64: 605–609.

Camargo, J. A. 1993. Must dominance increase with the number of subordinate species in competitive interactions? J. Theor. Biol. 161: 537–542.

Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana. *In* A. Estrada and T. H. Fleming (Eds.). Frugivores and seed dispersal, pp. 119–135. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Clarke, F. M., D. V. Pio, and P. A. Racey. 2005a. A comparison of logging systems and bat diversity in the Neotropics. Conserv. Biol. 19: 1194–1204.

Clarke, F. M., L. V. Rostant, and P. A. Racey. 2005b. Life after logging: Post-logging recovery of a Neotropical bat community. J. Appl. Ecol. 42: 409–420.

Cosson, J. F., J. M. Pons, and D. Masson. 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats in French Guiana. J. Trop. Ecol. 15: 515–534.

Crespo, R. F., S. B. Linhart, R. J. Burns, and G. C. Mitchell. 1972. Foraging behavior of the common vampire bat related to moonlight. J. Mammal. 53: 366–368.

da Silva, J. M. C., A. B. Rylands, and G. A. B. da Fonseca. 2005. The fate of the Amazonian areas of endemism. Conserv. Biol. 19: 689–694.

de Jong, J. 1995. Habitat use and species richness of bats in a patchy landscape. Acta Theriologica 40: 237–248.

Estrada, A., R. Coates-Estrada, and D. Meritt, Jr. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography 16: 309–318.

Fenton, M. B., L. Acharya, D. Audet, M. B. C. Hickey, C. Merriman, M. K. Obrist, and D. M. Syme. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. Biotropica 24: 440–446.

Fleming, T. H. 1988. The short-tailed fruit bat: A study in plant-animal interactions. University of Chicago Press, Chicago, Illinois.

Fleming, T. H., and E. R. Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. Biotropica (Reproductive Botany Supplement) 13: 45–53.

Fleming, T. H., and E. R. Heithaus. 1986. Seasonal foraging behavior of *Carollia perspicillata* (Chiroptera: Phyllostomidae). J. Mammal. 67: 660–671.

Galindo-González, J., S. Guevara, and V. J. Sosa. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rain forest. Conserv. Biol. 14: 1693–1703.

Gardner, A. L. 1977. Feeding habits. *In* R. J. Baker, J. K. Jones, Jr., and D. C. Carter (Eds.). Biology of bats of the New World family Phyllostomatidae. Part II, pp. 293–350. Special Publications, The Museum, Texas Tech University 13: 1–364.

Giannini, N. P., and E. K. V. Kalko. 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. Oikos 105: 209–220.

Gorchov, D. L., F. Cornejo, C. Ascorra, and M. Jamarillo. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Vegetatio 107/108: 339–349.

Gorresen, P. M., and M. R. Willig. 2004. Landscape responses of bats to habitat fragmentation in Atlantic Forest of Paraguay. J. Mammal. 85: 688–697.

Gorresen, P. M., M. R. Willig, and R. E. Strauss. 2005. Multivariate analysis of scale-dependent associations between bats and landscape structure. Ecol. Appl. 15: 2126–2136.

Handley, C. O., Jr. 1967. Bats of the canopy of an Amazonian forest. Atas do simposio sobre Biota Amazonica 5: 211–215.

Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72: 21–28.

Hargis, C. D., J. A. Bissonette, and D. L. Turner. 1999. The influence of forest fragmentation and landscape pattern on American martens. J. Appl. Ecol. 36: 157–172.

Heithaus, E. R., and T. H. Fleming. 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Chiroptera: Phyllostomidae). Ecol. Monogr. 48: 127–143.

Heywood, V. H., and R. T. Watson (Eds.). 1995. Global biodiversity assessment. Cambridge University Press, New York, New York.

Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105: 367–368.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi, Jr. 1974. Forest environments in tropical life zones: A pilot study. Pergamon Press, New York, New York.

Kalko, E. K. V. 1998. Organisation and diversity of tropical bat communities through space and time. Zoology 101: 281–297.

Kalko, E. K. V., D. Friemel, C. O. Handley, Jr., and H.-U. Schnitzler. 1999. Roosting and foraging behavior of two Neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). Biotropica 31: 344–353.

Kaufman, D. M., and M. R. Willig. 1998. Latitudinal patterns of mammalian species richness in the New World: The effects of sampling method and faunal group. J. Biogeogr. 25: 795–805.

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. *In* T. H. Kunz and M. B. Fenton (Eds.). Bat ecology, pp. 3–89. University of Chicago Press, Chicago, Illinois.

LoGiudice, K., R. S. Ostfeld, K. A. Schmidt, and F. Keesing. 2003. The ecology of infectious disease: Effects of host diversity and community composition on Lyme disease risk. Proc. Natl. Acad. Sci. USA 100: 567–571.

Madigosky, S. R., and I. Vatnick. 2000. Microclimatic characteristics of a primary tropical Amazonian rain forest, ACEER, Iquitos, Perú. Selbyana 21: 165–172.

Mäki, S., R. Kalliola, and K. Vuorinen. 2001. Road construction in the Peruvian Amazon: Causes and consequences. Environ. Conserv. 28: 199–214.

Marinho-Filho, J. S. 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. J. Trop. Ecol. 7: 59–67.

Marinho-Filho, J. S., and I. Sazima. 1998. Brazilian bats and conservation biology: A first survey. *In* T. Kunz and P. Racy (Eds.). Bat biology and conservation, pp. 282–294. Smithsonian Institution Press, Washington, DC.

Medellin, R. A., M. Equihua, and M. A. Amin. 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rain forests. Conserv. Biol. 14: 1666–1675.

Morrison, D. W. 1975. The foraging behavior and feeding ecology of a Neotropical fruit bat, *Artibeus jamaicensis*. Ph.D. dissertation, Cornell University, Ithaca, New York.

Morrison, D. W. 1978. Lunar phobia in a Neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Anim. Behav. 26: 852–855.

NRC (National Research Council). 2001. Grand challenges in environmental sciences. National Academy Press, Washington, DC.

NRC (National Research Council). 2003. NEON: Addressing the nation's environmental challenges. National Academy Press, Washington, DC.

Patterson, B. D., M. R. Willig, and R. D. Stevens. 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. *In* T. H.

Kunz and M. B. Fenton (Eds.). Bat ecology, pp. 536–579. University of Chicago Press, Chicago, Illinois.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S and S-plus. Springer Verlag, New York, New York.

R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3–900051-07–0, URL http://www.R-project.org.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Sala, O. E., *et al.* 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Sampaio, E. M., E. K. V. Kalko, E. Bernard, B. Rodríguez-Herrera, and C. O. Handley, Jr. 2003. A biodiversity assessment of bats (Chiroptera) in a tropical lowland rain forest of central Amazonia, including methodological and conservation considerations. Stud. Neotrop. Fauna Environ. 38: 17–31.

Scheiner, S. M., and M. R. Willig. 2005. Developing unified theories in ecology as exemplified by diversity gradients. Am. Nat. 166: 458–469.

Schowalter, T. D., J. W. Webb, and D. A. Crossley. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology 62: 1010–1019.

Schulze, M. D., N. E. Seavy, and D. F. Whitacre. 2000. A comparison of the phyllostomid bat assemblages in undisturbed Neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Petén, Guatemala. Biotropica 32: 174–184.

Simmons, N. B. 2005. Order Chiroptera. *In* D. E. Wilson and D. M. Reeder (Eds.). Mammal species of the world: A taxonomic and geographic reference. pp. 312–529. 3rd edition, vol. 1. John Hopkins University Press, Baltimore, Maryland.

Simmons, N. B., and R. S. Voss. 1998. The mammals of Paracou, French Guiana: A Neotropical lowland rain forest fauna. Part 1. Bats. Bull. Am. Mus. Nat. Hist. N. Y. 237: 1–219.

Solari, S., and R. J. Baker. 2006. Mitochondrial DNA sequence, karyotipic, and morphological variation in the *Carollia castanea* species complex (Chiroptera: Phyllostomidae) with description of a new species. Occ. Pap. Mus. Tex. Tech Univ. 254:1–16.

Srivastava, D. S., and J. H. Lawton. 1998. Why more productive sites have more species: An experimental test of theory using tree-hole communities. Am. Nat. 152: 510–529.

Thies, W., and E. K. V. Kalko. 2004. Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Oikos 104: 362–376.

Tosi, J. A., Jr. 1960. Zonas de vida natural en el Perú. Instituto Interamericano de Ciencias Agrícolas de la O. E. A. Boletín Técnico 5: 1–271.

Vasquez, R. V. 1997. Flórula de las reservas biológicas de Iquitos, Perú. Monographs in systematic botany, Vol. 63. Missouri Botanical Garden, Saint Louis, Missouri.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer Verlag, New York, New York.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277: 494–99.

Voss, R. S., and L. H. Emmons. 1996. Mammalian diversity in Neotropical lowland rain forests: A preliminary assessment. Bull. Am. Mus. Nat. Hist. N. Y. 230: 1–115.

Westfall, P. 1997. Multiple testing of general contrasts using logical constraints and correlations. J. Am. Stat. Assoc. 92: 299–306.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: The effects of fragmentation on extinction. Am. Nat. 125: 879–887.

Willig, M. R. 1986. Bat community structure in South America: A tenacious chimera. Rev. Chil. Hist. Nat. 59: 151–168.

Willig, M. R., and M. A. McGinley. 1999. Animal responses to natural disturbance and roles as patch generating phenomena. *In* L. R. Walker (Ed.). Ecosystems of disturbed ground, pp. 633–657. Elsevier Science, Amsterdam, The Netherlands.

Willig, M. R., and M. P. Moulton. 1989. The role of stochastic and deterministic processes in structuring Neotropical bat communities. J. Mammal. 70: 323–329.

Willig, M. R., and K. W. Selcer. 1989. Bat species density gradients in the New World: A statistical assessment. J. Biogeogr. 16: 189–195.

Wilson, D. E. 1973. Bat faunas: A trophic comparison. Syst. Zool. 22: 14–29.

Wunderle, J. M., M. R. Willig, and L. M. P. Henriques. 2005. Avian distribution in treefall gaps and understorey of *terra firme* forest in the lowland Amazon. Ibis 147: 109–129.