

EFFECTS OF HABITAT CONVERSION ON TEMPORAL ACTIVITY PATTERNS OF PHYLLOSTOMID BATS IN LOWLAND AMAZONIAN RAIN FOREST

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Ecological assessments of the effects of anthropogenic change often focus on species richness or species abundances. Nonetheless, changes in behavior (e.g., activity patterns) may provide equally important insights into responses to disturbance that have conservation or management implications. Because many neotropical bats provide critical ecosystem services, their responses may be of particular conservation concern. We evaluated the effects of season and habitat conversion on temporal activity patterns of 8 abundant species of frugivorous bats in lowland tropical rain forest of Iquitos, Perú. Season had little effect on activity patterns of any species of bat. Five species exhibited different activity patterns in primary or secondary forest compared to agricultural habitats. No interspecific differences in activity patterns occurred in primary forest. In agricultural areas, the patterns of activity of *Carollia benkeithi* and *Rhinophylla pumilio* were distinct from those of other species. In secondary forest, activity patterns of *Artibeus lituratus* and *R. pumilio* were distinct from those of other species. Temporal activity patterns of common frugivores overlapped more than expected by chance, regardless of season or habitat. Neotropical frugivores avoid open areas during twilight to reduce risk of predation. Nonetheless, to meet their considerable minimum daily caloric intake requirements, frugivores forage throughout most of the night. Increased habitat fragmentation may effectively reduce foraging times and subject bats to increased risk from predators during twilight and periods of great lunar illumination, when bats avoid open areas.

Key words: anthropogenic change, behavior, competition, conservation, deforestation, habitat use, Perú, Phyllostomidae

Habitat conversion and resulting fragmentation are among the most pervasive human activities that threaten biodiversity and species persistence (Sala et al. 2000; Wilcox and Murphy 1985). Fragmentation isolates populations (Hanski et al. 1995), and may alter the behavior of species (Hargis et al. 1999), interactions among species (Aizen and Feinsinger 1994), and essential ecosystem processes (Schowalter et al. 1981). In Amazonia, much anthropogenically induced deforestation is associated with the opening of frontiers for the passage of people and commerce (Laurance et al. 2001). Habitat loss associated with human activities is increasing at an alarming rate, especially in the Neotropics (Vitousek et al. 1997), and forests likely will become increasingly degraded and fragmented as anthropogenic pressure on natural resources

accelerates in response to increases in human populations and per capita consumption.

Bats provide critical ecosystem services associated with pollination and seed dispersal (Fleming 1988). Indeed, bats are the sole or primary agents of pollination and dispersal for many species of tropical plants (Fleming 1988; Fleming and Heithaus 1981; Galindo-González et al. 2000). Neotropical phyllostomids may represent a keystone taxon, because many bat species differentially disperse pioneer species of plants, thereby promoting regeneration of disturbed areas (Fleming 1988; Gorchov et al. 1993). Consequently, understanding the effects of anthropogenic disturbance on bats is critical to designing a conservation program that maintains biotic composition and ecosystem functioning of lowland Amazonian rain forests.

Responses of bat species to habitat conversion and fragmentation are idiosyncratic: abundances of species may increase, decrease, or be unaffected by habitat degradation, loss, or fragmentation (Aguirre et al. 2003; Bernard et al. 2001; Castro-Arellano et al. 2007; Cosson et al. 1999; de Jong 1995; Estrada et al. 1993; Fenton et al. 1992; Gorresen and Willig

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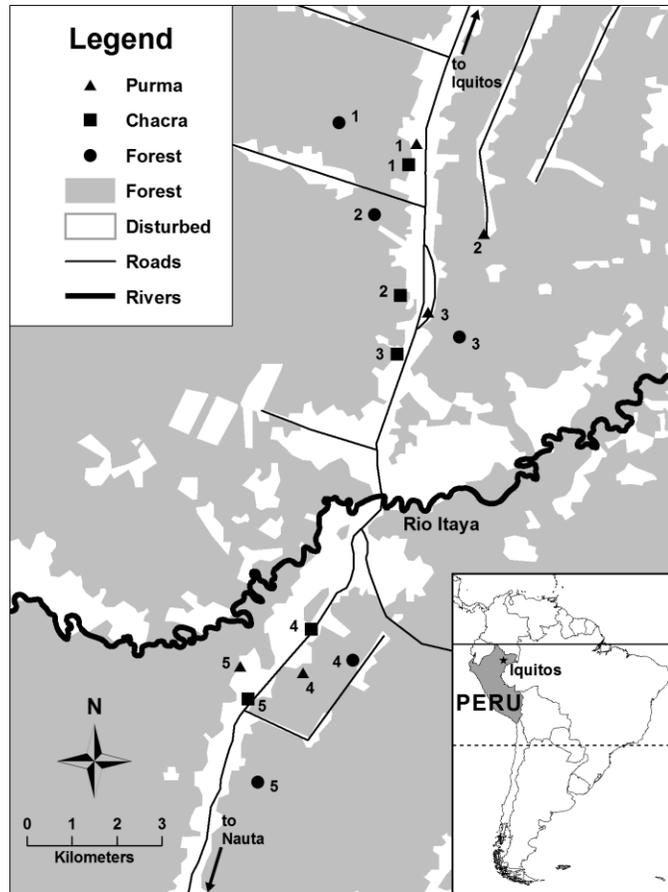


FIG. 1.—Map of the Iquitos region in northwestern Perú illustrating the extent of deforestation and fragmentation along the Río Itaya and the Iquitos–Nauta Highway. Five replicate blocks (1–5), each comprising 3 plots (forest, purma, and chacra), were located along the highway. The location of the city of Iquitos, and its relationship to the rest of Perú and South America (Equator, solid horizontal line; Tropic of Capricorn, dashed horizontal line), appear in the inset (after Willig et al. 2007).

2004; Medellín et al. 2000; Presley et al. 2008; Willig et al. 2007). In general, studies of the effects of anthropogenic disturbance on bats have evaluated responses in terms of species abundances or species richness. More subtle responses to deforestation, such as changes in temporal activity patterns, have been ignored for the most part. Compared to attributes of bat populations, species, or assemblages, temporal activity patterns may be quite responsive to deforestation or habitat conversion, and may be more sensitive to such perturbations. Few studies document (e.g., Brown 1968; Weinbeer and Meyer 2006) or compare (de Souza Aguiar and Marinho-Filho 2004; Marinho-Filho and Sazima 1989) temporal patterns of activity among species of neotropical bats. To our knowledge, no studies have documented changes in temporal activity of bats in response to deforestation, habitat conversion, or disturbance. As such, changes in activity in response to disturbance, seasonality, or habitat physiognomy, as well as the extent to which temporal niche overlap among species is nonrandom, remain poorly understood.

Temporal activity patterns indicate how species exploit the environment and generally are considered to represent an important niche dimension (Pianka 1973). Changes in resource diversity, abundance, or predictability may affect temporal activity of species that exploit those resources. Many plants that produce fruit on which bats feed are understory or successional species; therefore, habitat conversion likely affects the types, amounts, or predictability of fruit that is available to frugivorous bats. We hypothesized that temporal activity of frugivorous bats is habitat-specific and that differences in activity would be greatest for species of bats (e.g., *Carollia* and *Rhinophylla*) that specialize on fruit provided by successional plant species. As such, we evaluated effects of habitat conversion (i.e., mature forest converted to agriculture and subsequent abandonment) on temporal activity patterns of the 8 most abundant species of phyllostomid bats in the Iquitos area of the Peruvian Amazon lowlands.

MATERIALS AND METHODS

Study area.—Research was conducted in lowland Amazonia near the city of Iquitos (3.74°S, 73.24°W), Loreto Province, northeastern Perú (Fig. 1). Mean annual temperature is 26°C with little seasonal variation. Rainfall is substantial (~2,800 mm/year), with a modest drier season (185 mm/month) from June to October and a wetter season (292 mm/month) from January to May (Madigosky and Vatnick 2000). Iquitos is in the Inambari area of endemism (da Silva et al. 2005), which has lost <10% of its forest cover and is among the least-threatened regions of Amazonia. Nonetheless, this region is a conservation priority because it has greater numbers of restricted-range endemic species than do other areas of endemism (da Silva et al. 2005). In rural areas south of Iquitos, habitat conversion and fragmentation associated with anthropogenic activities primarily have paralleled the banks of navigable rivers, and more recently, a highway and associated logging roads. This project was conducted along a recently paved highway that connects the cities of Iquitos and Nauta (4.53°S, 73.55°W). A dirt road was present along this route before paving, but the rate and extent of human disturbance along it increased significantly as a consequence of improved travel conditions (Mäki et al. 2001). Data were collected in two 5-month periods: July–November 2002 and January–May 2003, corresponding to drier and wetter seasons of the year, respectively (Madigosky and Vatnick 2000).

The majority of deforestation in the Iquitos area results from establishment of small (~1-ha) agricultural fields called “chacras” (Mäki et al. 2001). Creation of a chacra takes several days to weeks, during which the understory is removed, most of the trees are felled, and the area is burned. The largest trees often are left where they fall. Chacras typically are planted with pineapple (*Ananas comosus*), plantain (*Musa*), or manioc (*Manihot esculenta*) until the soil is no longer fertile. During the subsequent 5–10 years, an influx of pioneer species into abandoned chacras results in early successional forest called “purma” (Mäki et al. 2001). Purma differs greatly from mature forest in terms of species composition (e.g., *Cecropia* often

dominate purma) and physical structure (<10-m canopy and dense understory in purma). 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. Chacras and purma typically have clearly defined boundaries and regularly occur adjacent to mature forest.

Sampling methods.—Five replicate blocks were located along the Iquitos–Nauta Highway between 40 and 70 km south-southwest of Iquitos, and within 3 km east or west of the road (Fig. 1). Each block contained 1 sample plot in each of 3 major habitats (i.e., mature forest, chacra, and purma). Each plot comprised 6.25 ha (250 × 250 m) and contained 8 subplots. Four 75 × 75-m interior subplots were arranged as quadrants. In each cardinal direction, an edge subplot extended 50 m beyond the interior subplots. Each night, each of 2 interior subplots and 2 edge subplots were sampled using 3 mist nets; 2 nets were erected at ground level and 1 was stacked directly above 1 of the ground nets. This design sampled bats flying up to 6 m above the ground. Each plot was sampled for 3 nights during the dry season and for 3 nights during the wet season; therefore, each season, one-half of the subplots in each plot were sampled for 2 nights and one-half were sampled for 1 night. A different replicate block was sampled each month during each season, replicate blocks were sampled in random order during the drier season, and replicate blocks were sampled in the same order during each season so that the same amount of time occurred between sampling periods in each block. Nets remained open from 1800 to 0100 h, and were checked every 20–30 min. Sex, mass, age (juvenile or adult), reproductive condition, and time of capture were recorded for each bat. 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. Each night, bats were released after sampling was concluded. 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 1978) on sampling efficacy, no netting was conducted within 2 nights of a full moon. We followed the systematic recommendations of Simmons (2005) for bat taxa in lowland Amazonia, except for recognizing *Carollia benkeithi* (Solari and Baker 2006) rather than *C. castanea*. Research involving live animals followed the guidelines for use of wild mammals in research approved by the American Society of Mammalogists (Gannon et al. 2007) and was approved by the Animal Care and Use Committee of Texas Tech University (ACUC #01084-03). Additional details about the study area and sampling methods are available in Willig et al. (2007).

Potential bias.—Because bats were not released until the end of sampling each night, the number of bats available for capture declined throughout the night. This could bias estimation of activity levels, and the magnitude of the bias would increase with each successive time interval. However, population densities of common neotropical frugivores are great; therefore, the proportion of the population of individuals that are removed

via sampling is small, as is the potential bias associated with our sampling protocol. Moreover, ensuring that each bat is counted only once avoids violation of the assumptions of independence of captures or allowing activity of a few individuals to dominate quantified patterns.

Analytical methods.—Analysis of activity patterns was restricted to the 8 most-abundant species of frugivorous phyllostomid bats for analytical and ecological reasons. Restriction of analyses to bats of a single guild should reduce inherent biases associated with use of ground-level mist nets (Voss and Emmons 1996). In addition, members of the same feeding guild should be more prone to interspecific competition than are species representing multiple feeding guilds. Because activity patterns may be molded by interspecific interactions (Halle and Stenseth 2000), comparison of species that occupy a similar trophic niche is more likely to provide results that are ecologically meaningful and interpretable. We restricted analyses to frugivores because they are species-rich and abundant, providing the necessary sample sizes to accurately estimate activity patterns. Captures were pooled into 1-h intervals (e.g., all captured from 1800 to 1859 h were pooled into a single time interval), which resulted in patterns of activity based on seven 1-h time intervals. Each time interval represents a “resource state” and the number of captures during each time interval is an estimate of the use of each resource state by each species.

For each of 8 abundant species of phyllostomids, intraspecific differences in temporal activity patterns were evaluated between seasons (wet versus dry) in each habitat, as well as between each pair of habitats (forest versus purma versus chacra) with Kolmogorov–Smirnov 2-sample tests (Seigel 1956) using SPSS version 11.0 for Windows (SPSS, Chicago, Illinois). Similarly, Kolmogorov–Smirnov 2-sample tests were used to evaluate interspecific differences in activity patterns between each pair of species for each of the 3 habitats, separately.

Amount of temporal overlap at the ensemble level (i.e., among the 8 common species of frugivores) was estimated via the Pianka (Pianka 1973) and Czechanowski (Feinsinger et al. 1981) indices. We used 3 simulation approaches to evaluate the amount of temporal niche overlap among the 8 species. Randomization algorithm 3 (RA3—Winemiller and Pianka 1990) retains the niche breadth of each species and randomly reshuffles the values for each time interval within each species. Randomization algorithm 4 (RA4—Winemiller and Pianka 1990) is similar to RA3, except that observed values of 0 are fixed (i.e., only nonzero values are shuffled randomly); this modification assumes that zeros represent resource states that cannot be used by a particular species. RA4 is conservative and can be prone to type II errors when zeros are common values for resource states, which was not a problem with our data. RA3 and RA4 destroy the shape of activity patterns, eliminate empirical temporal autocorrelation, and create inappropriately large null spaces that include biologically unrealistic activity patterns. In contrast, a new algorithm, Rosario (developed by I. Castro-Arellano et al.; available from the authors on request), maintains much of the temporal structure of activity patterns of each species, thereby restricting randomly generated patterns of

TABLE 1.—For each of 8 species of common frugivorous bats from Iquitos, results (P -values) of Kolmogorov–Smirnov 2-sample tests evaluating differences in temporal activity patterns between seasons (wet and dry) for each habitat, and between each pair of habitats with seasons combined. Significance ($P \leq 0.05$) is indicated by bold font. A dash indicates insufficient sample size to complete analysis.

Species (sample size)	Between seasons			Between habitats		
	Chacra	Forest	Purma	Chacra versus forest	Chacra versus purma	Forest versus purma
<i>Artibeus lituratus</i> (86)	0.359	1.000	0.970	0.081	< 0.001	0.073
<i>Artibeus obscurus</i> (184)	0.804	0.927	0.568	0.005	0.235	0.713
<i>Artibeus planirostris</i> (198)	0.279	1.000	0.929	0.014	0.888	0.262
<i>Carollia benkeithi</i> (102)	0.461	0.982	0.347	0.082	0.875	0.247
<i>Carollia brevicauda</i> (282)	0.439	0.979	0.831	0.380	0.275	0.907
<i>Carollia perspicillata</i> (1,576)	0.004	1.000	0.145	< 0.001	< 0.001	0.253
<i>Rhinophylla pumilio</i> (324)	0.401	0.932	0.384	0.001	0.108	0.091
<i>Sturnira lilium</i> (79)	0.468	—	0.784	0.246	0.422	0.747

activity to be biologically more realistic. In each iteration, Rosario shifts the entire activity pattern of each species a random number of time intervals and calculates the amount of overlap in the randomly generated set of activity patterns. In a broad suite of comparisons (I. Castro-Arellano et al., pers. obs.), Rosario performed similarly to RA3 and RA4 when the number of intervals was small (i.e., <12), but was less prone to type I errors than were RA3 and RA4 with increasing numbers of intervals. Each randomization procedure was iterated 10,000 times to create a distribution of randomly generated overlap values for each index against which corresponding empirical index values were compared. Thus, analyses were capable of detecting temporal coincidence in activity (i.e., more temporal overlap than expected by chance) or temporal segregation (i.e., less overlap than expected by chance). Analyses using RA3 and RA4 were conducted using EcoSim version 7.72 (Gotelli and Entsminger 2001). Analyses using Rosario were conducted using TimeOverlap (I. Castro-Arellano et al.; program available from the authors on request). Temporal overlap for the 8 most common frugivores was evaluated separately for each combination of habitat and season, for each season regardless of habitat, for each habitat regardless of season, and for all habitats and seasons combined.

Considerable debate surrounds the use of methods to maintain type I error rates at a predetermined α -level for suites of analyses (Hurlbert and Lombardi 2003; Moran 2003; Roback and Askins 2005). The Bonferroni sequential adjustment is a common method (Rice 1989) used to maintain experimentwise error rate at an a priori level; however, this method is extremely conservative and leads to elevated type II error rates (i.e., failure to reject a null hypothesis that is false). Indeed, by applying the Bonferroni sequential adjustment or similar methods to a suite of ecological analyses, the likelihood of committing a type II error may be greater than the likelihood of committing a type I error in the absence of any correction. As such, controlling false discovery rate may be preferred to controlling for experimentwise error rate (Roback and Askins 2005 and sources therein). Nonetheless, for exploratory analyses such as those conducted here, corrections for multiple tests are not recommended (Roback and Askins 2005). We were more concerned about the consequences of ignoring results that could have biological implications than about the

potential for type I errors, which generally are a minor concern for most ecological studies (Hurlbert and Lombardi 2003). As such, we interpreted results without a correction for multiple tests and present exact P -values for all analyses.

RESULTS

Pairwise intraspecific comparisons.—With the exception of *Carollia perspicillata*, intraspecific seasonal differences in activity patterns were indistinguishable from those produced by chance (Table 1). In contrast, intraspecific differences in activity patterns were common between primary forest and chacras (*Artibeus obscurus*, *Artibeus planirostris*, *C. perspicillata*, and *Rhinophylla pumilio*), were less frequent between chacras and purma (*Artibeus lituratus* and *C. perspicillata*), and were nonexistent between primary forest and purma (Table 1). When significant, greatest differences in activity intervals between habitats always involved much less activity during the 1st hour of night in chacras compared to either forested habitat (Fig. 2).

Pairwise interspecific comparisons.—In chacras, 6 of the possible 28 pairwise comparisons of activity patterns between species were significant (Table 2). All significant differences for chacras involved *Carollia brevicauda* or *R. pumilio*, suggesting that these species had relatively distinctive activity patterns compared to other syntopic frugivores. In purma, 8 of the possible 28 pairwise comparisons of activity patterns between species were significant, and all involved *A. lituratus* or *R. pumilio*, suggesting that these species had distinctive activity patterns compared to other frugivores. No interspecific differences in activity pattern characterized any pair of species in primary forest (Table 2).

Ensemble-level overlap.—Results of analyses of temporal overlap were robust with respect to randomization algorithm and with respect to overlap metric (Table 3). Because of the consistent results and extremely low P -values, detected patterns likely are strong. Ensemble-level temporal overlap was greater than expected by chance in 10 of 12 instances when RA3 or Rosario was employed, and was greater than expected by chance in 11 of 12 instances when RA4 was employed (Table 3). In the instance (purma during the dry season) for which results depended on randomization approach, the

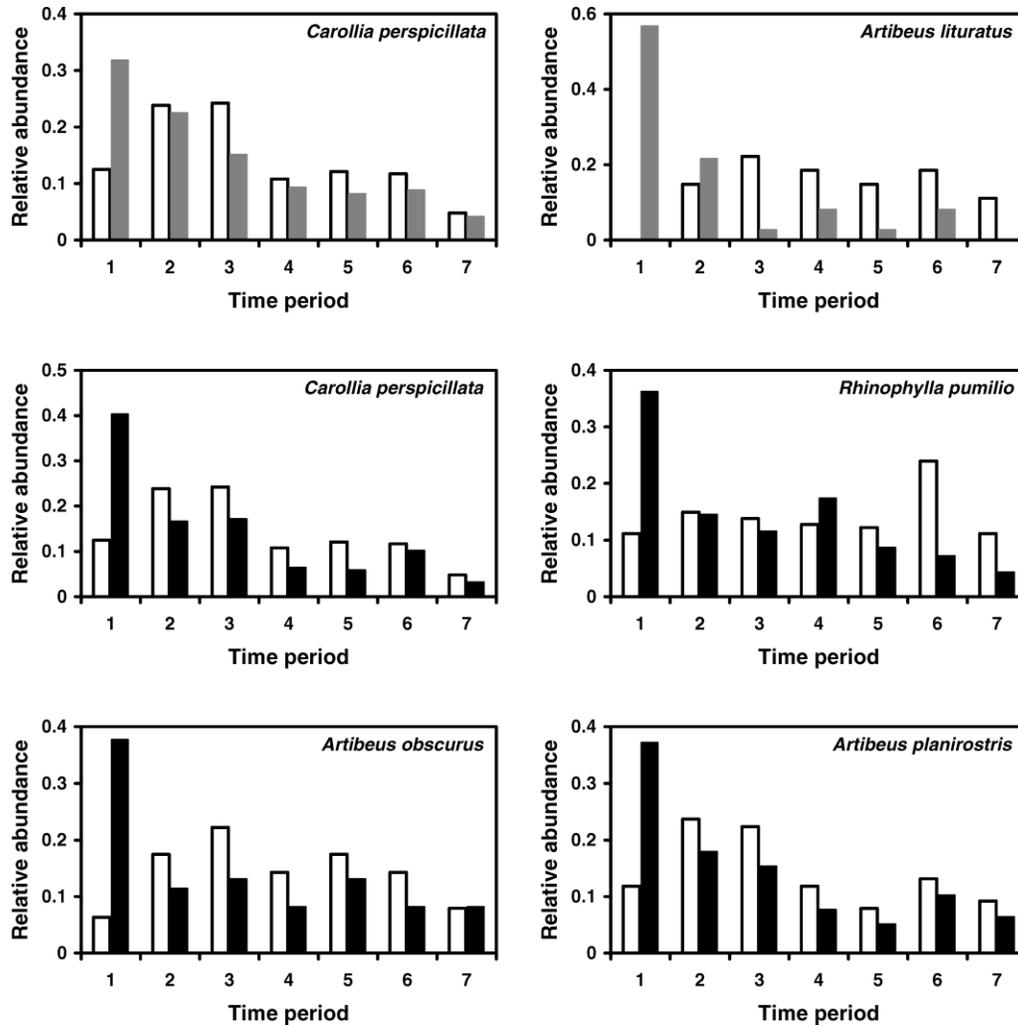


FIG. 2.—Temporal activity patterns for each species that exhibited significant differences in activity between chacras (white) and purma (gray) or between chacras and forest (black) based on Kolmogorov–Smirnov 2-sample tests (Table 1).

P-values did not differ dramatically (i.e., overlap approached significance for RA3 and Rosario algorithms, and was significant for RA4). In analyses within each habitat regardless of season and in analyses within each season regardless of habitat, all simulations indicated that niche overlap among species was greater than expected by chance alone.

DISCUSSION

Intraspecific variation in temporal activity.—In general, activity patterns of frugivorous bats did not differ between seasons, paralleling the general absence of seasonal differences in abundance for the same species at the same locations (Willig et al. 2007). These results indicate that seasonal variation in fruit availability is low compared to other neotropical areas. For example, abundances of frugivorous species in southeastern Brazil (de Souza Aguiar and Marinho-Filho 2004; Marinho-Filho and Sazima 1989) and in Paraguay (S. J. Presley, pers. obs.) can differ greatly with season. In those areas, many species are near the edges of their southern distribution and may not be permanent residents; their presence in those areas

may be restricted to particular seasons as they track changes in fruit availability.

No intraspecific differences in temporal activity patterns occurred between primary forest and secondary forest (purma). Nonetheless, the number of captures for 4 of the 8 analyzed species was significantly different between forest types (Willig et al. 2007); each species of *Carollia* was more abundant in purma than in primary forest, and *A. lituratus* was more abundant in primary forest than in purma. Taken together, these results suggest that each type of forest may provide similar resources but not in the same quantities. In contrast, 5 of 8 species differed in activity between agricultural (chacra) and forested (purma or primary forest) habitats. In these instances, the greatest difference in activity always was during the 1st hour of night (Fig. 2). Bats may avoid flying in chacras during twilight because its open physiognomy provides little physical cover and allows greater illumination, both of which may increase risk of predation (Crespo 1972; Kalko and Handley 2001; Morrison 1978).

Because diurnal raptors are among the greatest predatory threats to bats (Baker 1962; Chacón-Madrigrá and Barrantes

TABLE 2.—For each of 3 habitats, results (*P*-values) of Kolmogorov–Smirnov 2-sample tests evaluating pairwise differences in temporal activity patterns between pairs of common species of frugivorous bats from Iquitos. Significance ($P \leq 0.05$) is indicated by bold font.

	<i>Artibeus obscurus</i>	<i>Artibeus planirostris</i>	<i>Carollia benkeithi</i>	<i>Carollia brevicauda</i>	<i>Carollia perspicillata</i>	<i>Rhinophylla pumilio</i>	<i>Sturnira lilium</i>
Chacra							
<i>Artibeus lituratus</i>	0.998	0.351	0.476	0.013	0.112	0.926	0.069
<i>Artibeus obscurus</i>	—	0.717	0.547	0.012	0.172	0.414	0.136
<i>Artibeus planirostris</i>	—	—	0.752	0.344	0.973	0.060	0.918
<i>Carollia benkeithi</i>	—	—	—	0.421	0.944	0.031	0.624
<i>Carollia brevicauda</i>	—	—	—	—	0.060	< 0.001	0.281
<i>Carollia perspicillata</i>	—	—	—	—	—	< 0.001	0.824
<i>Rhinophylla pumilio</i>	—	—	—	—	—	—	0.004
Purma							
<i>Artibeus lituratus</i>	0.002	0.005	0.029	0.283	0.026	< 0.001	0.005
<i>Artibeus obscurus</i>	—	0.770	0.924	0.084	0.203	0.895	0.783
<i>Artibeus planirostris</i>	—	—	0.776	0.138	0.428	0.109	0.239
<i>Carollia benkeithi</i>	—	—	—	0.317	0.239	0.337	0.208
<i>Carollia brevicauda</i>	—	—	—	—	0.751	0.001	0.120
<i>Carollia perspicillata</i>	—	—	—	—	—	0.001	0.122
<i>Rhinophylla pumilio</i>	—	—	—	—	—	—	0.506
Forest							
<i>Artibeus lituratus</i>	0.805	0.292	0.377	0.613	0.137	0.241	0.260
<i>Artibeus obscurus</i>	—	0.975	0.783	1.000	0.534	0.946	0.214
<i>Artibeus planirostris</i>	—	—	0.731	0.942	1.000	0.967	0.115
<i>Carollia benkeithi</i>	—	—	—	0.966	0.855	0.689	0.095
<i>Carollia brevicauda</i>	—	—	—	—	0.526	0.999	0.154
<i>Carollia perspicillata</i>	—	—	—	—	—	0.477	0.085
<i>Rhinophylla pumilio</i>	—	—	—	—	—	—	0.181

2004; Fenton et al. 1994), twilight hours (dawn and dusk) are a time of heightened predation risk. As such, twilight phobia exhibited in open areas may be similar to lunar phobia, which may not manifest in dense forests regardless of lunar

illumination (LaVal 1970). Undocumented historical claims that avian predation on bats likely was rare may have been based on the difficulty in observing these interactions; however, accumulated incidental accounts and specific studies

TABLE 3.—Indices of temporal overlap and associated *P*-values for the 8 most common species of frugivorous bats from Iquitos. *P*-values are reported for each of 3 algorithms: randomization algorithm 3 (RA3), randomization algorithm 4 (RA4), and Rosario (Winemiller and Pianka 1990; I. Castro-Arellano et al., in litt.). Separate analyses were conducted for each season within each habitat, for each habitat regardless of season, and for each season regardless of habitat. Significance ($P \leq 0.05$) is indicated by bold font. All significant results indicate more overlap than expected by chance.

Habitat and season	Pianka index				Czechanowski index			
	Mean overlap	<i>P</i> -RA3	<i>P</i> -RA4	<i>P</i> -Rosario	Mean overlap	<i>P</i> -RA3	<i>P</i> -RA4	<i>P</i> -Rosario
Chacra								
Dry	0.771	0.218	0.271	0.222	0.687	0.114	0.144	0.121
Wet	0.806	< 0.001	< 0.001	< 0.001	0.654	< 0.001	< 0.001	< 0.001
Combined	0.880	< 0.001	< 0.001	0.002	0.779	< 0.001	< 0.001	0.003
Purma								
Dry	0.827	< 0.001	< 0.001	< 0.001	0.696	< 0.001	< 0.001	< 0.001
Wet	0.717	0.087	0.041	0.093	0.624	0.067	0.020	0.068
Combined	0.857	< 0.001	< 0.001	< 0.001	0.738	< 0.001	< 0.001	< 0.001
Forest								
Dry	0.747	< 0.001	< 0.001	< 0.001	0.612	< 0.001	< 0.001	< 0.001
Wet	0.726	< 0.001	< 0.001	< 0.001	0.619	< 0.001	< 0.001	< 0.001
Combined	0.801	< 0.001	< 0.001	< 0.001	0.709	< 0.001	< 0.001	< 0.001
All								
Dry	0.918	< 0.001	< 0.001	< 0.001	0.806	< 0.001	< 0.001	< 0.001
Wet	0.818	0.002	0.001	0.005	0.735	< 0.001	< 0.001	0.002
Combined	0.918	< 0.001	< 0.001	< 0.001	0.823	< 0.001	< 0.001	< 0.001

demonstrate that predation risk from birds is significant. In Costa Rica, 14 species of birds, including 9 diurnal species and 5 species of owls, are documented to prey on bats (Chacón-Madrigal and Barrantes 2004). Moreover, during a 37-day period remains of 27 bats representing 14 species were taken from pellets of a single pair of black-and-white owls (*Ciccaba nigrolineata*—Ibañez et al. 1992). These owls preyed on molossid, vespertilionid, phyllostomid, and emballonurid representing several feeding guilds, and bats represented 71% of all vertebrates taken. Because the fastest of bats are relatively slow flying compared to birds (Baker 1962), avian predators can easily overtake a bat in open habitats. Indeed, a diurnal avian predator (merlin [*Falco columbarius*]) was more efficient at capturing bats in open areas than in cluttered areas; in response prey (*Pteronotus quadridens*) ceased to use open areas for movement from day roosts (Rodríguez-Durán and Lewis 1985). Species of bats that forage in the canopy use more open areas and exhibit stronger patterns of lunar phobia than do species of bats that forage in the understory (Kalko and Handley 2001). Many canopy frugivores feed on figs; predators cluster in and near fig trees when they have a great concentration of fruit that attracts many bats. In addition, bats do not exhibit lunar phobia in environs that lack visually oriented nocturnal predators (Gannon and Willig 1997). Similar to our results for chacras, *Macrophyllum macrophyllum*, a gleaning insectivore that feeds over water, exhibited twilight phobia and foraged under overhanging vegetation along shorelines during twilight hours (Weinbeer and Meyer 2006) to avoid predation from bat falcons (*Falco rufigularis*). In contrast, *M. macrophyllum* foraged over open water during full darkness. Although many successional species of plants on which bats feed may be concentrated along the interfaces between chacras and forest, bats appear to avoid these areas during times of increased illumination, regardless of the source of light. To summarize, diurnal and nocturnal avian carnivores are effective predators of bats, avian predators may change hunting strategy in response to localized activity by bats, lunar phobia is strongest in bats that forage in open areas, lunar phobia does not manifest in areas without visually oriented nocturnal predators, bats that forage in areas of high clutter and low light levels (i.e., forest understory) do not exhibit lunar phobia, and twilight phobia manifests only in open areas. As a result, predation is a likely explanation for photophobic responses in activity by bats.

Pairwise interspecific comparisons.—No difference in temporal activity occurred among frugivorous species of bats in primary forest, the most pervasive habitat in the region. For each species, 36–58% of captures occurred during the 1st hour after sunset, with dramatically fewer individuals captured during each of the 6 subsequent hours. These 2 characteristics likely reflect early evening travel to food patches by all species and subsequent decline in distance traveled once suitable feeding grounds are located by individuals.

Carollia brevicauda and *R. pumilio* displayed different patterns of temporal activity in chacras compared to other species of frugivores (Fig. 3). In general, bats in chacras were captured most frequently 2–3 h after dark, with a slow decline

in captures thereafter. In contrast, peaks in activity of *C. brevicauda* were within 1 h of sundown, with activity decreasing thereafter. Capture rates for *R. pumilio* were consistent throughout the night, with a slight peak in activity 6 h after sunset. In purma, *A. lituratus* and *R. pumilio* exhibited distinct activity patterns compared to other frugivores (Fig. 4). In purma, most species were slightly more active during the first 2 h of night than they were for the following 5 h. Most (57%) *A. lituratus* were captured during the 1st hour of darkness; no other species had >40% of their captures during that time interval. If capture rates reflect travel distance, these results may indicate that *A. lituratus* commutes longer distances to a food patch than do other species, but once individuals of *A. lituratus* arrive at a food patch, they travel little for the next several hours. This is consistent with radiotelemetry data for *A. lituratus* in French Guiana (de Foresta et al. 1984). Because this pattern only occurred in purma, it may indicate that *A. lituratus* prefers purma over other habitats for early evening commuting, perhaps to avoid predators in the dense understory of the purma. Activity levels of *R. pumilio* in purma changed little during the night, with little evidence of a peak in activity. *R. pumilio* is adapted to highly scattered food sources (Henry et al. 2007b), employs short search flights, and roosts close to resource patches. Consequently, travel by *R. pumilio* is relatively constant throughout the night (Henry and Kalko 2007), which is consistent with the absence of peaks in capture rates in purma or chacras. In forest, *R. pumilio* exhibited an activity pattern similar to those of other species (i.e., greatest amount of activity during the 1st hour of darkness, with dramatically reduced activity thereafter).

Ensemble-level overlap.—Patterns of temporal activity likely are molded by ecological attributes that are critical to survivorship and reproduction. For example, prey activity may be the most important determinant for predators. Alternatively, predation risk may shape activity patterns if food availability is relatively constant over time. In addition, species (or individuals) may reduce competition by partitioning the times during which they forage for common food resources (Halle and Stenseth 2000). Nonetheless, competition for fruit among frugivorous bats in the Neotropics does not appear to be strong. In many locations (e.g., Panamá; French Guiana; Suriname; Manaus, Brazil; and Cocha Cashu, Perú) fruit fall (i.e., overabundance of fruit that falls to the forest floor uneaten) is abundant for much or all of the year, although seasonal variation in precipitation may create occasional fruit shortages that intensify competition or lead to decreased body mass in bats (Charles-Dominique 1991; Smythe 1986). This implies that such resources may not be limiting for many frugivorous species, in particular in regions such as Iquitos that vary little in seasonal rainfall. In addition, multiple selection pressures may exist for bats to forage as early as possible, resulting in a convergence in activity times. Bats that do not begin to forage early have less time to meet their considerable nightly dietary requirements (Charles-Dominique 1986) as well as to devote to other vital activities. Consequently, the need to meet daily energetic requirements (see below) may be the primary force

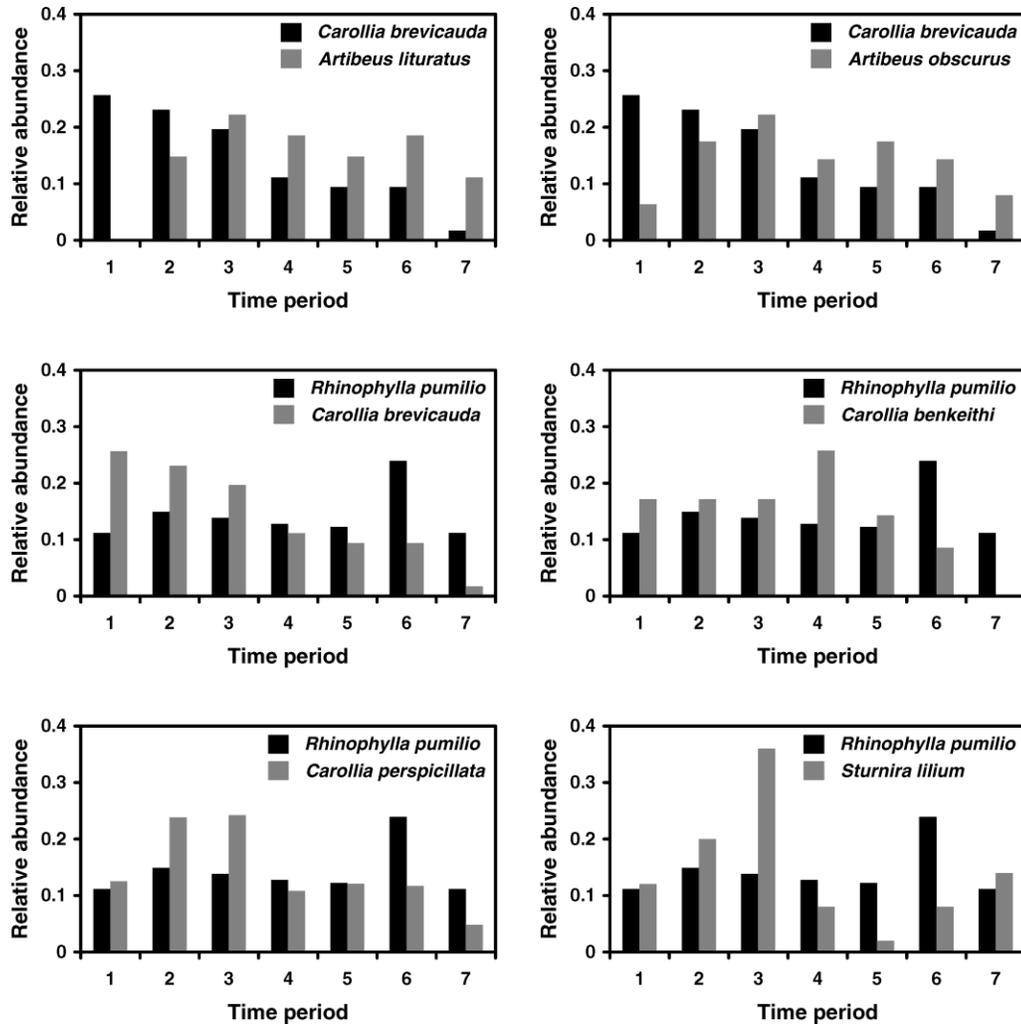


FIG. 3.—Temporal activity patterns for each pair of species that exhibited significant differences in activity in chacras based on Kolmogorov–Smirnov 2-sample tests (Table 2).

that structures patterns of activity for frugivorous bats, with seasonal interspecific or intraspecific competition of secondary import. Generally, frugivorous species of bats may need to emerge and forage as early as possible to meet energetic demands. In addition, for areas with habitat heterogeneity, the habitats in which bats forage may depend on the amount of ambient illumination at any given time of night and associated predation risk. If species exhibit similar photophobic responses, the combination of predator avoidance and energy requirements could lead to coincident patterns of temporal activity. This explanation is consistent with the observation that temporal niche overlap was greater than expected by chance in nearly all of the 12 combinations of habitat and season (Table 3), and that temporal overlap never was less than expected by chance. The only situation in which temporal overlap was not significantly positive, and in which early evening did not evince peaks in activity, was in chacras. Twilight phobia in chacras created flat patterns of activity. The randomization algorithms employed here are incapable of distinguishing flat distributions from random; such distributions lack the necessary variation to detect significant overlap.

Despite the general perception that frugivores are most active during the 1st few hours of darkness (e.g., de Souza Aguiar and Marinho-Filho 2004; Eckert 1982; LaVal 1970), *C. perspicillata* did not exhibit a significant decline in number of foraging flights throughout the night based on radiotelemetry surveys. Bats averaged 6 foraging flights during the 1st hour of night, and 4 or 5 flights each hour thereafter, until dawn (Charles-Dominique 1991). Similarly, the percent of time flying only decreased slightly after the 1st hour of night. Unfortunately, distance traveled each hour, which may affect mist-net capture rates, was unknown. Because fruit contains relatively little nutritive value, species of *Carollia* must consume 100–120% of their body mass in fruit pulp each night. Similarly, species of *Artibeus* must consume twice their body mass in fruit each night (Charles-Dominique 1986). Consequently, the apparent decline in activity recorded for frugivores using mist nets may not be reflective of activity budgets per se. Rather, patterns reflected in mist-net captures may indicate distance traveled during respective time intervals. For example, during the 1st hour of darkness bats may travel toward or in search of a suitable feeding area for the night, but

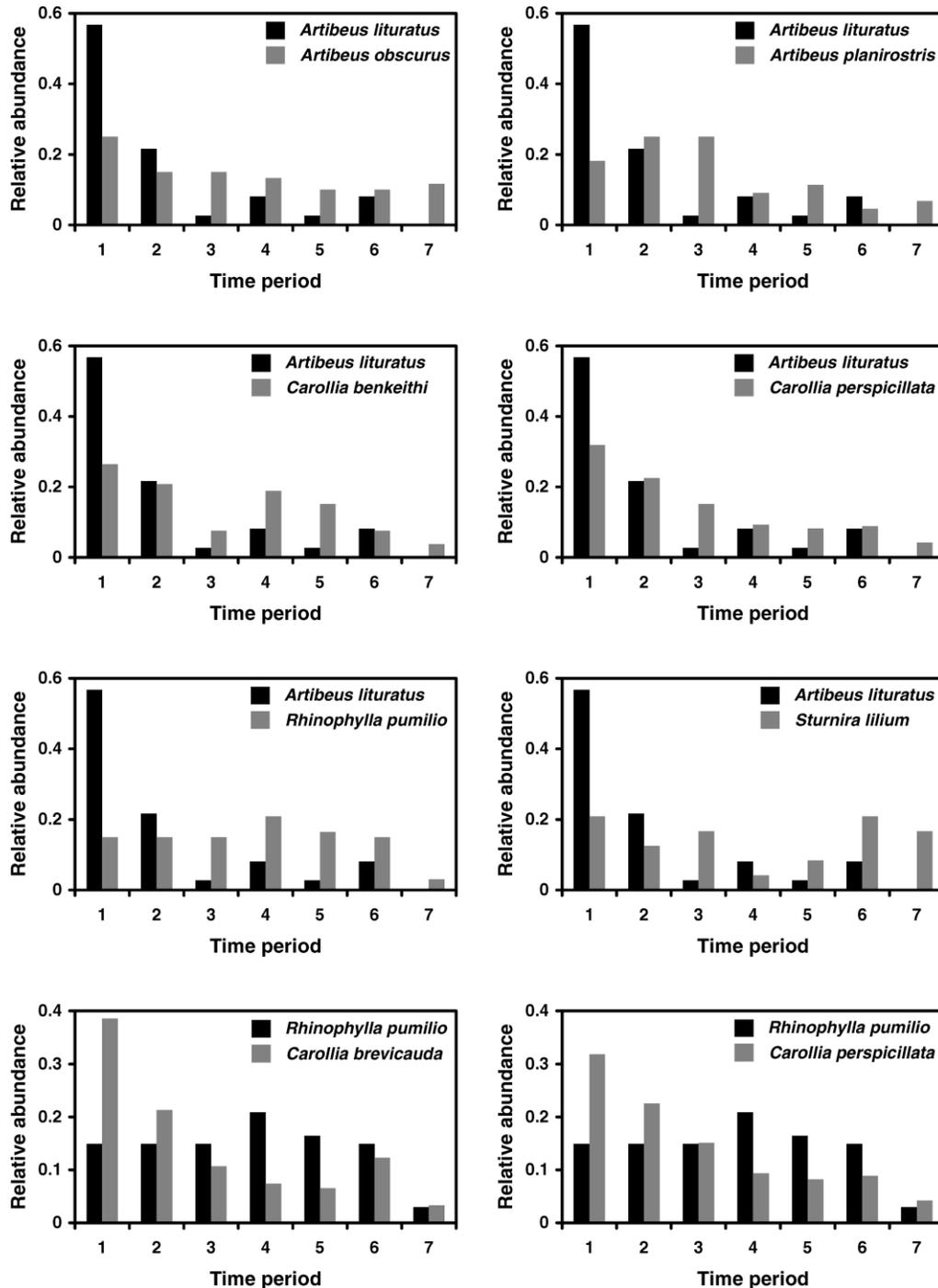


FIG. 4.—Temporal activity patterns for each pair of species that exhibited significant differences in activity in purma based on Kolmogorov–Smirnov 2-sample tests (Table 2).

once arriving at a foraging area, travel much less thereafter. This would result in a skewed distribution of captures, despite relatively constant activity throughout the night. A similar explanation (i.e., bats traveling from feeding areas to day roosts) has been invoked to account for predawn peaks in captures of bats (Marinho-Filho and Sazima 1989).

Conservation implications.—Changes in behavior may be more sensitive indicators of effects of habitat conversion, loss, or fragmentation than are commonly used indicators such as

species richness or abundance (e.g., Clarke et al. 2005; Estrada et al. 1993; Willig et al. 2007). Indeed, for some bat species, abundance may not be a suitable measure of sensitivity to disturbance, and other metrics may be required (Henry et al. 2007a). Behavioral changes in response to habitat degradation may be an indicator of more severe and impending negative consequences (e.g., decreases in abundance or local extirpation) for particular species if rates of habitat conversion, loss, and fragmentation do not abate. Because neotropical bats are

primary agents of seed dispersal or pollination for many species of successional plants, the ability to correctly anticipate responses of bats to disturbance may be imperative to effective management of neotropical forests.

As landscapes become increasingly fragmented and forests are replaced by open habitats (e.g., pastures and agricultural fields), bats may be subjected to 2 negative forces: increased risk of predation and reduced time for foraging that arises as a result of predator avoidance during times of greater illumination (i.e., twilight and full moon). As a result, dramatically fragmented habitats may no longer support viable populations of some species that are important dispersers of seeds or pollinators of flowers, altering the ability of disturbed areas to regenerate or for plant communities to develop species compositions that are similar to those in unfragmented communities.

The current level of habitat degradation in the Iquitos region is modest and has had only small effects on bat diversity or abundance, although assemblage composition is altered in disturbed areas (Willig et al. 2007). Nonetheless, bats fly through chacras and purma throughout the night, which suggests that seeds from fruits consumed earlier in the night can be deposited in those areas. Improved access for humans derived from the recent paving of the Iquitos–Nauta Highway likely will exacerbate habitat loss and fragmentation, with the potential to intensify negative effects of habitat conversion on bat populations and assemblages. Indeed, some species may cease to be effective seed dispersers at thresholds of abundances much greater than those considered to be rare (McConkey and Drake 2006). Species that do not commute long distances or that are averse to crossing open habitats may be most affected by modest levels of habitat fragmentation. *R. pumilio* is 1 such species (Henry et al. 2007b). It exhibited significantly different patterns of activity in disturbed habitats than in primary forest, and exhibited unique activity patterns compared to other frugivores in each disturbed habitat, but not in primary forest. Such responses in activity may be a precursor to more dramatic responses (e.g., decreases in abundance and loss of species) associated with more-extensive habitat loss. Studying changes in animal behavior in addition to population- and community-level characteristics (e.g., richness, abundance, and composition) may uncover mechanistic bases for how habitat loss and fragmentation translate into loss of species and altered ecosystem function.

RESUMEN

Estudios ecológicos acerca de los efectos antropogénicos usualmente se han concentrado en analizar cambios en la riqueza o abundancia de especies. Sin embargo, cambios en el comportamiento (e.g., patrones de actividad) pueden proveer un entendimiento igualmente importante de las respuestas a disturbios, con implicaciones de conservación o manejo. Debido a que numerosos murciélagos neotropicales proveen de servicios cruciales en los ecosistemas, sus respuestas a disturbios pueden ser de alta importancia para conservación. En nuestro estudio evaluamos los efectos de estacionalidad y

conversión de hábitat en los patrones de actividad de 8 especies abundantes de murciélagos frugívoros en el bosque tropical de Iquitos, Perú. La estacionalidad tuvo un efecto mínimo en los patrones de actividad de los murciélagos. Cinco especies mostraron diferentes patrones de actividad en bosque primario o secundario comparados con áreas agrícolas. No existieron diferencias interespecíficas en los patrones de actividad dentro del bosque primario. En áreas agrícolas los patrones de actividad de *Carollia benkeithi* y *Rhinophylla pumilio* fueron distintas al resto de las especies. En el bosque secundario, los patrones de actividad de *Artibeus lituratus* y *R. pumilio* fueron distintas al resto de las especies. Los patrones de actividad de los murciélagos frugívoros se traslapan más de lo esperado por procesos aleatorios, independientemente de la estación o hábitat. Los murciélagos frugívoros neotropicales evaden áreas abiertas durante el crepúsculo para reducir el riesgo de depredación. Sin embargo, para poder alcanzar sus considerables requerimientos calóricos diarios, los murciélagos frugívoros requieren de forrajear a lo largo de la mayoría de la noche. Un incremento en la fragmentación del hábitat puede reducir substancialmente los tiempos de forrajeo y someter a los murciélagos a un mayor riesgo de depredación durante el crepúsculo y periodos de luna llena, periodos en los que los murciélagos evaden las áreas abiertas.

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