Reduced-impact Logging has Little Effect on Temporal Activity of Frugivorous Bats (Chiroptera) in Lowland Amazonia

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ABSTRACT

Reduced-impact logging (RIL) represents a viable option for sustainable use of Neotropical lowland forests while minimizing negative effects on local biodiversity. Many Neotropical bats of the family Phyllostomidae provide ecosystem services associated with pollination and seed dispersal that promote the regeneration of disturbed areas; therefore, effects of RIL on these species is of particular concern. We determined patterns of temporal activity, degree of temporal overlap of activity, and dispersion in peaks of activity for seven abundant species of frugivorous bat in Tapajós National Forest, Pará, Brazil. In addition, we evaluated the effects of RIL at a harvest level of 18.7 m^3/ha and habitat physiognomy on temporal patterns of activity for these species. Bats were surveyed for four nights at each of 96 sites for a total sampling effort of 64,512 net-m-h. Sites were distributed among four experimental blocks, two blocks of unlogged forest and two blocks of forest subjected to RIL. Half of the sites in each management type were in forest gaps and half were in closed-canopy forest. In general, species exhibited similar patterns of activity, and greater than expected temporal overlap in activity among species. RIL and forest physiognomy had little effect on activity patterns of species. RIL in Amazonia removes fewer trees than do naturally occurring treefalls and such changes in habitat structure do not alter activity patterns of frugivorous bats. Evidence suggests that RIL does not have an appreciable adverse effect on frugivorous bats in Amazonia.

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

Key words: behavior; conservation; deforestation; habitat use; Phyllostomidae; sustainable use forest management; Tapajós, Brazil; temporal overlap.

RAPID GROWTH OF HUMAN POPULATIONS, coupled with land-use change and global climate change, is increasing pressure on natural ecosystems at an unprecedented rate (Vitousek *et al.* 1997, Mc-Kee *et al.* 2003). Indeed, the rate of habitat loss associated with anthropogenic activities is alarming (Soares-Filho *et al.* 2006), especially in tropical regions that harbor a large proportion of the world's species and play a critical role in regulating global climate (Heywood & Watson 1995). Logging pressure related to economic growth, as well as local and global timber needs, threatens pristine Neotropical forests throughout Amazonia (Veríssimo *et al.* 1992, 2002; Laurance *et al.* 2001; Fearnside 2005). Prior to completion of the Transamazônica Highway in 1970, the Amazon largely was intact; however, deforestation associated with agriculture, cattle, and logging industries increased rapidly with improved access to previously remote areas (Fearnside 2005). Considering increased global demand for food and fiber, and the prospect for economic benefits associated with timber harvest, much of the Brazilian Amazon undoubtedly will be subject to logging (Dickinson *et al.* 1996, Veríssimo *et al.* 2002). Importantly, the result of such use need not be devastating to the local biota or to ecosystem function if proper management and planning are enacted and enforced (Dickinson *et al.* 1996, Putz *et al.* 2000, Veríssimo *et al.* 2002). Recent advancements in understanding the effects of timber harvest regimes

on nontarget species indicate that environmentally sustainable and economically profitable use of tropical forests may be achieved with little impact on biodiversity or ecosystem processes (Putz *et al.* 2000, Holmes *et al.* 2002, Milner-Gulland 2008 and sources therein).

Since the 1980s, low-intensity logging practices (as opposed to conventional selective harvesting, timber liquidation, or clear cutting) that harvest 2–8 trees/ha have become increasingly common in the New World Tropics (Veríssimo *et al.* 1992, 2002; Clarke *et al.* 2005a; Fearnside 2005). Reduced-impact logging (RIL) is a type of low-intensity logging that implements pre- and postlogging guidelines to protect seedlings, saplings, and small trees from injury, minimizes soil damage, prevents substantial damage to nontarget plant species, and protects critical ecosystem processes (*e.g.*, hydrogeological flow, carbon sequestration; Dykstra & Heinrich 1996, Putz *et al.* 2000). Felling and skidding techniques used in conventional selective logging practices can kill an additional 27 trees ($\geq$ 10 cm dbh) for every harvested tree (Veríssimo *et al.* 1992). In contrast, implementation of RIL in the Brazilian Amazon reduces damage to surrounding forest while extracting a reduced number (2–4 trees/ha) and volume (5–19 m^3/ha) of commercially valuable trees (J. Zweede, pers. comm.). After logging, the forest is permitted to recover for several years before being eligible for reharvest (Fimbel *et al.* 2001). Compared to other logging techniques, RIL significantly decreases the likelihood of postlogging fires, which are a common and catastrophic consequence of traditional selective logging techniques in Amazonia (Nepstad *et al.* 1999). Moreover,

current patterns of climate change are causing stronger El Niño episodes that create drought conditions in Amazonia, increasing the frequency and intensity of postlogging fires (Nepstad *et al.* 2004). The cyclic nature and low impact of RIL harvests on the physical environment of the forest may reduce negative effects on biodiversity and sustain a renewable resource of economic value (Grieser Johns 1997). Moreover, RIL in the Amazon is less costly than conventional logging methods, with greater profits realized during first harvests and greater residual stand value after harvest, such that the profit advantage of RIL over conventional logging increases with time (Holmes *et al.* 2002).

From a conservation perspective, it is essential to determine consequences of RIL on the biota, especially for taxa that facilitate recovery from disturbance. Such logging regimes are increasingly common, widespread, and actively promoted as an environmentally sound and profitable harvest option (Holmes *et al.* 2002, Veríssimo *et al.* 2002) as well as a marketable carbon-offset method in the global economy (Putz & Pinard 1993). For example, general and detailed guidelines for the implementation of RIL to promote sustainable use of forests are available (Dykstra & Heinrich 1996) and have been modified for targeted application in particular parts of the world, including Indonesia (Sist *et al.* 1998) and Malaysia (Pinard *et al.* 1995). Despite the increasing prevalence of RIL regimes worldwide, effects of RIL on biota have been evaluated infrequently and for few faunal groups, including dung beetles (Davis 2000), ants, arachnids, birds, and large mammals (Azevedo-Ramos *et al.* 2006), birds (Wunderle *et al.* 2006), and bats (Castro-Arellano *et al.* 2007, Presley *et al.* 2008).

Neotropical bats are easy to sample, abundant, species rich, and functionally diverse. As a result, they are a useful indicator taxon for studying the effects of disturbance (Medellín *et al.* 2000). In addition, many common species of Neotropical bat are the sole or primary agents of pollination and seed dispersal for a variety of pioneer, early-successional, and understory plant species (Fleming & Heithaus 1981, Fleming 1988, Galindo-González *et al.* 2000). Consequently, bats in Neotropical forests may represent a keystone taxon, as they promote the regeneration of disturbed areas (Fleming 1988, Gorchov *et al.* 1993). Moreover, understanding the effects of anthropogenic disturbance on bats may be critical to designing a timber harvest regime that maintains a high degree of biodiversity and ecosystem function, while providing a valuable and sustainable natural resource.

Populations of bats respond to logging practices and associated habitat degradation, loss, or fragmentation in a species-specific manner: abundances of species may increase, decrease, or be 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, Castro-Arellano *et al.* 2007, Willig *et al.* 2007, Presley *et al.* 2008). Few studies have evaluated the effects of low-intensity logging on bats (Ochoa 2000; Clarke *et al.* 2005a, b; Peters *et al.* 2006) or RIL (Castro-Arellano *et al.* 2007, Presley *et al.* 2008). In general, the effects of anthropogenic disturbance on bats have been evaluated only in terms of species abundances or species richness; however, recent studies (*e.g.*, Henry *et al.* 2007) indicate that abundance may be a misleading indicator in evaluating effects

of habitat degradation on populations. More subtle responses to deforestation, such as changes in behavior or temporal patterns of activity have been ignored for the most part (but see Presley *et al.* 2009).

Temporal activity patterns indicate how species exploit the environment and generally are considered to reflect niche partitioning (Pianka 1973). Changes in resource abundance, diversity, or predictability may alter temporal activity of species that exploit those resources. Many Neotropical plants that produce fruit on which bats feed are understory or successional species; therefore, RIL likely affects the types, amounts, or predictability of fruit that are available to frugivorous bats in the family Phyllostomidae. Information about the temporal activity patterns of Neotropical bats and how their behavior changes in response to particular types of disturbance may improve understanding of bat–plant interactions, the effects of disturbance on the nature of these interactions, and how disturbance affects the ability of bats to continue to promote regeneration of disturbed areas. We investigated the effects of RIL and associated changes in forest physiognomy (*i.e.*, gaps created by individual tree harvest) on patterns of temporal activity of frugivorous bats. We expected that frugivorous bats that specialize on fruits of early-successional plants (*e.g.*, *Carollia*, *Rhinophylla*; Fleming & Heithaus 1981, Fleming 1988, Galindo-González *et al.* 2000) would be more active earlier in the night in RIL forest and in gap habitats than in undisturbed forest or closed-canopy habitats because: (1) fruits ripen during the day and fruit density or abundance is never greater than at dusk (Fleming 1988); and (2) because fruit densities are greater in gaps than under closed-canopy forest (Fleming 1988, Galindo-González *et al.* 2000) and RIL increases the density of forest gaps that promote the production of fruit. In contrast, we did not expect RIL or habitat physiognomy to affect the activity patterns of frugivorous bats (*e.g.*, *Artibeus* spp.; Charles-Dominique 1986, Kalko & Handley 2001) that specialize on canopy fruits. We documented patterns of temporal activity for seven common and abundant species of frugivorous bat in lowland Amazonia, and evaluated effects of RIL and habitat physiognomy on temporal activity patterns of those species.

METHODS

STUDY AREA.—Research was conducted in the Tapajós National Forest (TNF), a 560,000-ha area managed by the Instituto Brasileiro de Meio Ambiente e dos Recursos Naturais Renováveis. The TNF is located in western Pará, Brazil on the eastern bank of the Tapajós River in central Amazonia (Fig. 1). Climate is hot and humid, with mean monthly temperatures of 24.3–25.8°C, and mean annual rainfall of 1920 mm (Silva 1989). Our study area (3.05° S, 54.95° W) occurred in terra firme forest, the most prevalent of the moist and wet forest types in the TNF. It is characterized by gently rolling terrain on poor upland soils (dystrophic yellow latosol; Silva 1989) and has a canopy height ranging 30–40 m. The study area occurred within a 5000 ha demonstration forestry grid. Four 100-ha experimental blocks were established in the study area; two control blocks were located in undisturbed forest and two cut blocks were located in
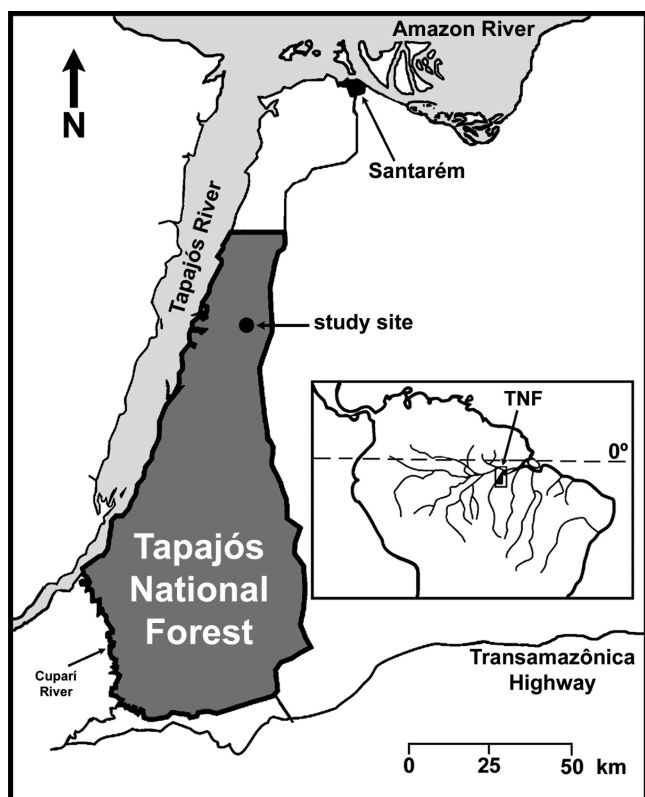
FIGURE 1.   Location of lowland Amazonia study site (3.05° S, 54.95° W) in Tapajós National Forest, Pará, Brazil. Modified from Wunderle *et al.* (2005).

forest subjected to RIL. Timber harvest in cut blocks was completed 20 mo before the initiation of the study. All harvested trees in RIL forest were > 45 cm dbh, with 3.94 (18.7 m^3) and 3.79 (18.7 m^3) trees/ha harvested from the two cut blocks. The most commonly harvested species were *Manilkara huberi*, *M. paraensis*, *Protium pernevatum*, *Dinizia excelsa*, and *Piptadenia suaveolens* (Keller *et al.* 2004).

FIELD AND LABORATORY METHODS.—Ninety-six sites were selected within the experimental blocks based on habitat physiognomy and logging treatment. Half of the sites were in treefall gaps and half were under closed canopy (henceforth gap and closed canopy, respectively). Sixteen gaps were formed by natural treefalls and 16 closed-canopy sites were selected in each control block; eight gaps resulting from RIL harvest of individual trees and eight closed-canopy sites were selected in each cut block. The mean size of gaps (219 m^2 ± 55 SE) in cut blocks that resulted from tree harvest was indistinguishable from the mean size of gaps (286 m^2 ± 37 SE) in undisturbed forest that were formed naturally (Wunderle *et al.* 2006). Each block was divided into four quadrats, and an equal number of gaps and closed-canopy sites were located in each quadrat to ensure dispersion of sites throughout each block. In addition, to enhance comparable sampling of variation within quadrats, each gap site was associated with a closed-canopy site. Location of a

closed-canopy site with respect to its associated gap site was random with respect to direction, and at a random distance between 25 and 50 m. Distance to the nearest nonassociated site was at least twice as great (*i.e.*, > 100 m) as the distance between associated sites.

Sampling was conducted during four time periods between June 1999 and April 2000, and each site was surveyed for one night during each time period (Saldanha 2000). Seasonal changes in abundances and behavior are minor for most species of frugivorous bat in lowland Amazonia (*e.g.*, Willig *et al.* 2007, Presley *et al.* 2009), therefore we combined data from all four sampling periods and resultant activity patterns represent the best estimate of average activity throughout the entire year. Depending on the size and shape of the gap, 24 m of net in various combinations and configurations of 6 m and 12 m segments were deployed in gaps. To account for possible effects of net configuration on sampling, matching net configurations were used in associated closed-canopy sites. Mist nets were erected at ground level and checked at least once an hour from 1800 h to 0100 h. To reduce possible effects of lunar phobia (Crespo *et al.* 1972) on sampling efficacy, netting was not conducted within two nights of a full moon. Additional details of field methods are available elsewhere (Presley *et al.* 2008).

Information recorded for each captured bat included species identity, sex, reproductive condition, age, mass, standard morphometric measurements, and time of capture. Accurate field identification of bats in TNF was facilitated by collecting a series of voucher specimens prior to the study, which was deposited in the Museu Paraense Emílio Goeldi/MCT Mammals Collection (Belém, Brazil). Voucher specimens were not collected from sites associated with this study (Saldanha 2000). We followed the systematic recommendations of Simmons (2005) for all bat taxa.

ANALYTICAL METHODS.—For analytical and ecological reasons, assessments of patterns of activity were restricted to the seven most commonly captured species of frugivorous bat of the family Phyllostomidae. Restriction of analyses to bats of a single guild reduced capture biases associated with use of ground level mist nets (Voss & Emmons 1996). In addition, greater capture rates of frugivores provided more accurate estimates of patterns of activity than was possible for other groups of bats, which generally had lower capture rates. Because activity patterns may be molded by interspecific interactions or by shared constraints (Halle & Stenseth 2000), comparison of species that occupy a similar trophic niche is more likely to provide results that are ecologically meaningful and interpretable. Moreover, we restricted analyses to frugivores because they are species rich and abundant, providing an appropriate group for intraspecific and interspecific comparisons. Captures were pooled into seven 1-h time intervals (*e.g.*, all bats captured at 1800–1859 h were pooled into a single time interval) from 1800 h to 0100 h. To facilitate comparisons based on unequal sample sizes, all analyses were conducted on relative number of captures, such that values for all seven time intervals for each activity pattern summed to 1.0.

Kolmogorov–Smirnov two-sample tests (Siegel 1956) were conducted to evaluate pairwise differences in temporal activity patterns within and between species (SPSS version 11.0 for Windows). For each of seven abundant species of frugivore, differences in

activity patterns were evaluated in a hierarchical fashion; differences were evaluated between RIL forest and primary forest separately for each physiognomy, and between gap and closed-canopy physiognomies (management types combined). Interspecific differences in activity patterns between each pair of species were evaluated separately for each physiognomy with management types combined and for each management type with physiognomies combined.

Temporal niche partitioning among species may manifest as hyperdispersed peaks of activity or as a reduction in the amount of temporal overlap in activity throughout the entire distribution of activity (*i.e.*, by changing the shape of the activity pattern). Each of these scenarios was evaluated for the group of seven abundant frugivores. The dispersion of peaks in activity was evaluated via a statistical assessment of a mode clustering (MC) index in which MC < 1.0 indicates evenly spaced modes, MC > 1.0 indicates clustered modes, and MC ~ 1.0 indicates randomly distributed modes (Poole & Rathcke 1979).

Amount of temporal overlap among all seven abundant species of frugivore was estimated as the mean Pianka (Pianka 1973) or mean Czechanowski (Feinsinger *et al.* 1981) index derived from all possible pairwise interspecific contrasts of temporal activity. We used a new randomization algorithm specifically designed for temporal data (Rosario; Presley *et al.* 2009; I. Castro-Arellano, *et al.*, pers. obs.) to evaluate if the amount of overlap was greater or less than expected by chance. Rosario maintains much of the temporal autocorrelation and empirical structure of activity patterns of each species, but shifts the entire activity pattern of each species a random number of time intervals to define stochastic outcomes (I. Castro-Arellano *et al.*, pers. obs.). For interval or rank data, Rosario creates a more biologically realistic null space and is less prone to Type I errors than are alternative null models (*e.g.*, randomization algorithm 3, randomization algorithm 4; Winemiller & Pianka 1990) that were designed specifically for analyses of nominal data. Each randomization was iterated 10,000 times, creating a null distribution of overlap values. Significance was determined by comparing each empirical index to the associated null distribution. Because analyses were conducted as two-tailed tests, temporal coincidence (*i.e.*, greater temporal overlap among species) in activity can be distinguished from temporal segregation (*i.e.*, less overlap among species). Temporal overlap for abundant frugivores was evaluated separately for each combination of physiognomy and management type, and for each management type regardless of physiognomy. Analyses that employed Rosario were conducted with program TimeOverlap (I. Castro-Arellano et al., pers. obs.; program available from the authors on request).

Considerable debate surrounds the use of methods to maintain Type I error rates at a predetermined α-level for suites of analyses (Hurlbert & Lombardi 2003, Moran 2003, Roback & Askins 2005). Methods for maintaining experiment-wise error rate at an *a priori* level are extremely conservative and application of such methods can inflate Type II error rates (*i.e.*, failure to reject a null hypothesis that is false) to levels that surpass Type I error rates in the absence of any correction for multiple tests. Consequently, for exploratory analyses such as those conducted herein, corrections for multiple tests are not recommended (Roback & Askins 2005). We were more concerned about the consequences of ignoring results that could have ecological and conservation implications than about the potential for Type I errors, which generally are a minor concern for most ecological studies (Hurlbert & Lombardi 2003). As such, we interpreted results without a correction for multiple tests and present exact *P*-values for all analyses. Results were considered significant if $P \leq 0.05$.

RESULTS

During 64,512 net-m-h of survey, 1468 bats representing 45 species, 29 genera, and four families were captured. Of those bats, phyllostomids represented 1379 captures, 39 species, 25 genera (Presley *et al.* 2008), with the Emballonuridae (11 captures, four species, two genera), Mormoopidae (76 captures, one species), and Thyropteridae (two captures, one species) represented by many fewer captures. Frugivores dominated captures (1169), with gleaning animalivores (121), aerial insectivores (89), nectarivores (85), and sanguinivores (four) being much less common. These data are the product of an exceptionally intensive study of the effects of logging on bats, with more sites, greater replication, and greater sampling effort at each site than that in similar contemporary studies (*e.g.*, Ochoa 2000; Clark *et al.* 2005a, b; Peters *et al.* 2006).

PAIRWISE COMPARISONS OF ACTIVITY PATTERNS.—RIL had little effect on patterns of activity for any of the seven most commonly captured species of frugivores in gaps or in sites with a closed canopy (Table 1). Only *Artibeus obscurus* exhibited differences in activity in response to RIL, and then only for gap sites (Fig. 2). Similarly, physiognomy had little effect on patterns of activity for most species; only *Carollia perspicillata* evinced differences in activity between physiognomies (Table 1; Fig. 2).

TABLE 1. *For each of seven species of common frugivorous bat from lowland Amazonia (Tapajós, Brazil), results (P-values) of Kolmogorov–Smirnov two-sample tests evaluating differences in temporal activity patterns between management types separately for each physiognomy, and between physiognomies with management types combined. Significance (P ≤ 0.05) is indicated in bold.*

|	Between management types		
Species (sample size)	Gaps	Closed canopy	Between physiognomies
Artibeus concolor (46)	0.816	0.420	0.539
Artibeus lituratus (240)	0.961	1.000	0.986
Artibeus obscurus (109)	**0.035**	0.344	0.670
Carollia brevicauda (45)	0.805	0.668	0.996
Carollia perspicillata (533)	0.814	0.347	**0.003**
Rhinophylla fischerae (39)	0.993	0.548	0.707
Rhinophylla pumilio (35)	0.919	0.646	0.400
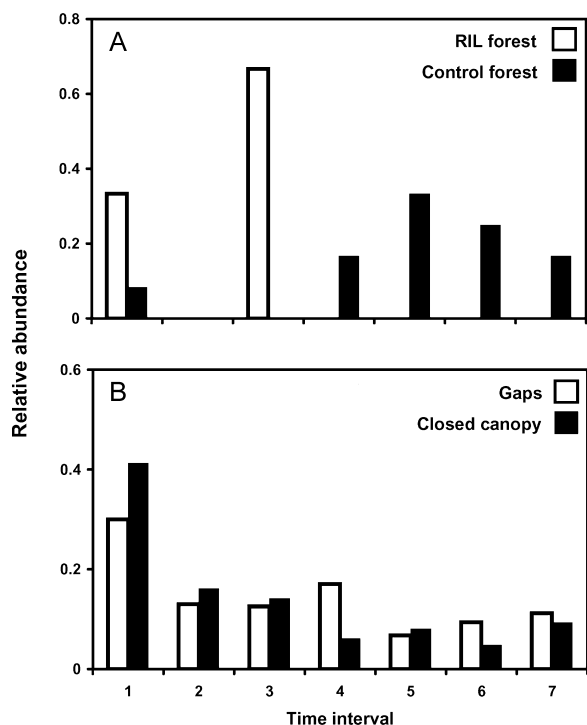
FIGURE 2. Temporal activity patterns for the species that exhibited significant differences in activity between (A) RIL-generated gaps and natural treefall gaps (*Artibeus lituratus*) and (B) gap sites and closed-canopy sites regardless of management types (*Carollia perspicillata*).

No interspecific differences in activity pattern were observed for gap sites with data combined for natural- and RIL-induced treefall gaps (Table S1). Three of 21 pairwise interspecific comparisons of activity patterns were significant in closed-canopy sites (Table S1; Fig. 3). All differences occurred between stenodermatine (*Artibeus lituratus* or *A. obscurus*) and carolliine (*C. perspicillata* or *Rhinophylla pumilio*) bats. With physiognomies combined, only two and three of 21 pairwise interspecific comparisons of activity patterns were significant in control forest and in RIL forest, respectively (Table S1). These differences were associated with *C. perspicillata* (Fig. 3). Activity patterns for *C. perspicillata* were significantly different from those of *A. lituratus* and *A. obscurus* in each management type. Patterns of activity for *Carollia brevicauda* and *C. perspicillata* were identical in control forest, but significantly different in RIL forest. This was the only congeneric difference in activity pattern (Table S1).

TEMPORAL OVERLAP AND CLUSTERING OF MODES.—For each analysis restricted to gap sites, amount of temporal overlap among species did not differ significantly from random (Table 2). In contrast, amount of temporal overlap among species was significantly greater than expected by chance for each analysis restricted to closed-canopy sites and for each analysis with physiognomies combined (Table 2). The amount of observed temporal overlap (Pianka index and Czechanowski index values) was always greater in control forest than

in RIL forest. Modes of activity were significantly clustered in four of six analyses and approached significance ($0.05 < P \leq 0.10$) in the remaining two cases (Table 2). Values for overlap indices and MC were not significantly correlated based on Pearson product moment or Spearman rank procedures, indicating that each of these methods measure unique aspects of coincidence of activity patterns.

DISCUSSION

EFFECTS OF RIL ON FAUNAL GROUPS.—In general, RIL does not negatively affect the abundances (Castro-Arellano *et al.* 2007, Presley *et al.* 2008) or alter the temporal behavior (this research) of common frugivorous bats in TNF. Similarly, abundances of nectarivorous bats that pollinate flowers of successional and understory plants were not affected negatively by RIL (Castro-Arellano *et al.* 2007, Presley *et al.* 2008). Results for bats from TNF are similar to those for forests subjected to low-impact logging in Trinidad (Clarke *et al.* 2005a) and southern Pará (Peters *et al.* 2006). As a result, no evidence suggests that timber harvest protocols such as RIL inhibit the ability of frugivorous or nectarivorous bats to provide important ecosystem services that promote forest regeneration in the Neotropics. RIL can change species composition (Ochoa 2000, Peters *et al.* 2006, Presley *et al.* 2008) of assemblages and relative abundances of species (Castro-Arellano *et al.* 2007); however, compared to other logging techniques, RIL and similar low-impact logging techniques have only small effects on Neotropical bat assemblages (Clarke *et al.* 2005a, b). Nonetheless, caution should be exercised when evaluating effects of RIL on species composition and rare species if sample sizes are small and result in the majority of species being represented by only a few individuals (*e.g.*, Peters *et al.* 2006).

Compared to other logging techniques, RIL better preserved primary forest assemblages with less species loss of ants, beetles, spiders, birds, or large mammals in Amazonia (Davis 2000, Azevedo-Ramos *et al.* 2006). For groups of animals that maintain small home ranges (*i.e.*, spiders, ants), RIL increased species richness as new species appeared in response to increased habitat heterogeneity created by logging (Azevedo-Ramos *et al.* 2006). Typically, these invaders were not associated with the extirpation of primary forest species, but represented native specialists from surrounding areas that were able to take advantage of newly created habitats.

The gleaning animalivores of the Phyllostominae are the only faunal group documented to respond negatively to low-impact logging techniques: they generally became rare or are locally extirpated after reduced- or low-impact harvests (Ochoa 2000; Clarke *et al.* 2005a, b; Presley *et al.* 2008). Nonetheless, gleaning animalivores increase in abundance and richness with time since logging (Clarke *et al.* 2005b), indicating that negative responses to RIL may be short term compared to responses to more destructive logging regimes. RIL removes only about 7 percent of large trees (dbh > 35 cm; Keller *et al.* 2001) from the forest, does not substantially modify habitat structure, or elicit negative responses by potential prey of gleaning animalivores (Azevedo-Ramos *et al.* 2006), indicating that lack of available roosting habitat and food availability likely do not
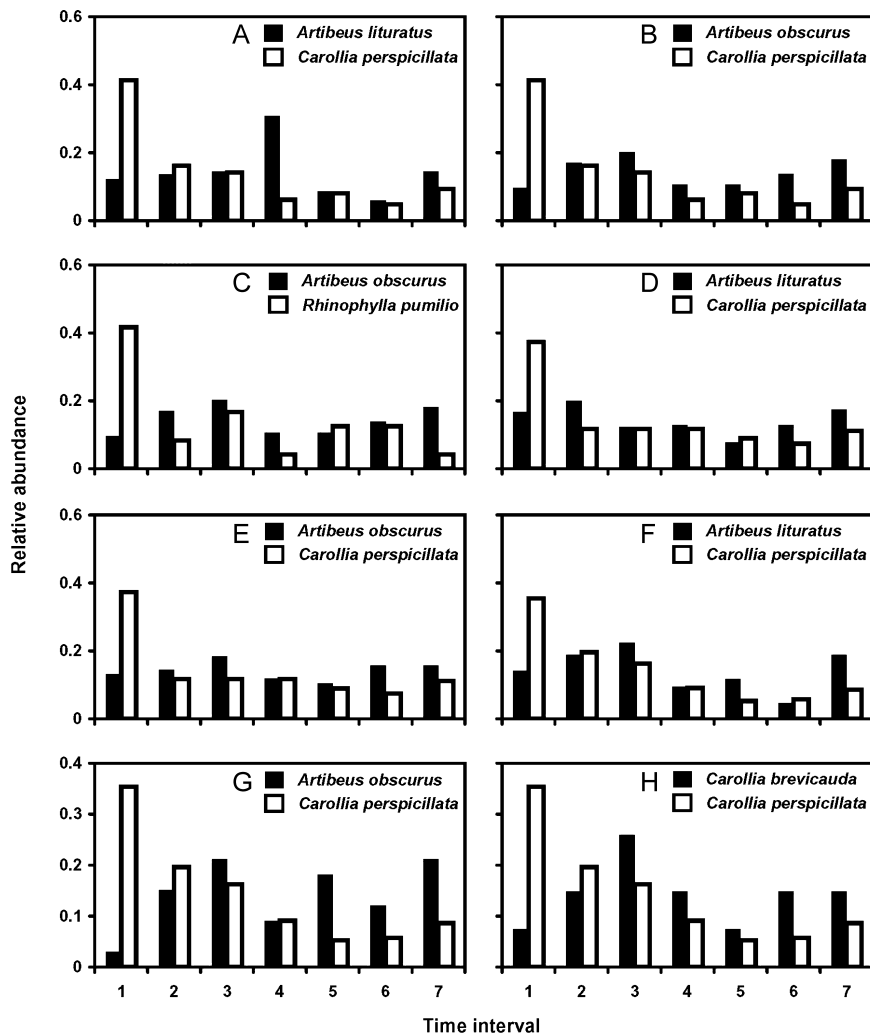
FIGURE 3.   Temporal activity patterns for each pair of species that exhibited significant differences in activity in closed-canopy sites (A–C), control forest (D–E), or RIL forest (F–H) based on Kolmogorov–Smirnov two-sample tests (Table S1).

explain local extirpations of gleaning animalivores after timber harvest. Predation can have a strong effect on the behavior of bats (Rodríguez-Duran & Lewis 1985, Presley *et al.* in press), especially in open areas where bats are particularly susceptible to predatory birds (Baker 1962, Rodríguez-Duran & Lewis 1985, Ibañez *et al.* 1992, Chacón-Madrigal & Barrantes 2004). Consequently, changes in forest physiognomy (*e.g.*, increased number of gaps, creation of skidder trails and logging roads) associated with logging activities may be sufficient to cause phyllostomines to leave an area for undisturbed forest, even if basic necessities such as prey and roosting habitat remain abundantly available.

Based on available evidence for multiple faunas, RIL has a small effect on biodiversity and may represent a viable option for long-term, sustainable use of forests. Considering the mounting pressure on natural resources and the near certainty that much of the Amazon will be subjected to some form of timber harvest, promoting RIL and providing incentives for land owners and timber companies to employ RIL techniques may represent an acceptable compromise between long-term conservation goals and short-term human needs. Nonetheless, care must be exercised when designing timber harvest schedules to ensure that sufficiently large tracts of primary forest (or forest that has not been logged for many years) are present to act as refugia as well as source populations for species that are sensitive to any amount of operation (*e.g.*, gleaning animalivorous bats).

RESPONSES OF BATS TO OPEN HABITATS.—In primary forests of lowland Amazonia, frugivores exhibit considerable temporal overlap in activity: most species exhibit peaks in activity during the first hour after sunset (Presley *et al.*, in press; Table 2; Fig. 4). Because primary forest is the dominant, naturally occurring habitat to which this assemblage of bats is adapted, patterns of activity in this habitat likely represent the 'natural state' for these bats. Species-specific responses to creation of forest gaps (whether naturally occurring or the result of RIL) decrease the amount of temporal overlap in activity (Table 2). Changes in activity could be a response to the redistribution of resources. Many species of fruiting plants (*Piper*, *Solanum*, *Cecropia*)

TABLE 2. *Indices of temporal overlap and mode clustering (MC), and associated P-values for analyses that include seven abundant species of frugivorous bat from lowland Amazonia (Tapajós, Brazil). Separate analyses were conducted for each combination of management and physiognomy as well as for each management type with physiognomies combined. Significance ($P \leq 0.05$) is indicated in bold. All significant results indicate more temporal overlap or greater MC than expected by chance.*

| Habitat | Temporal overlap | | | | Clustering of modes | |
| | Pianka index | | Czechanowski index | | | |
Season	Mean overlap	P-value	Mean overlap	P-value	MC	P-value
Control forest						
Gaps	0.699	0.417	0.612	0.323	**2.714**	**0.016**
Closed canopy	**0.773**	**0.003**	**0.645**	**0.004**	2.143	0.072
Combined	**0.880**	**< 0.001**	**0.775**	**< 0.001**	3.857	**< 0.001**
RIL forest						
Gaps	0.619	0.081	0.493	0.156	2.143	0.072
Closed canopy	**0.652**	**0.046**	**0.549**	**0.005**	4.429	**< 0.001**
Combined	**0.777**	**0.026**	**0.698**	**0.002**	4.429	**< 0.001**
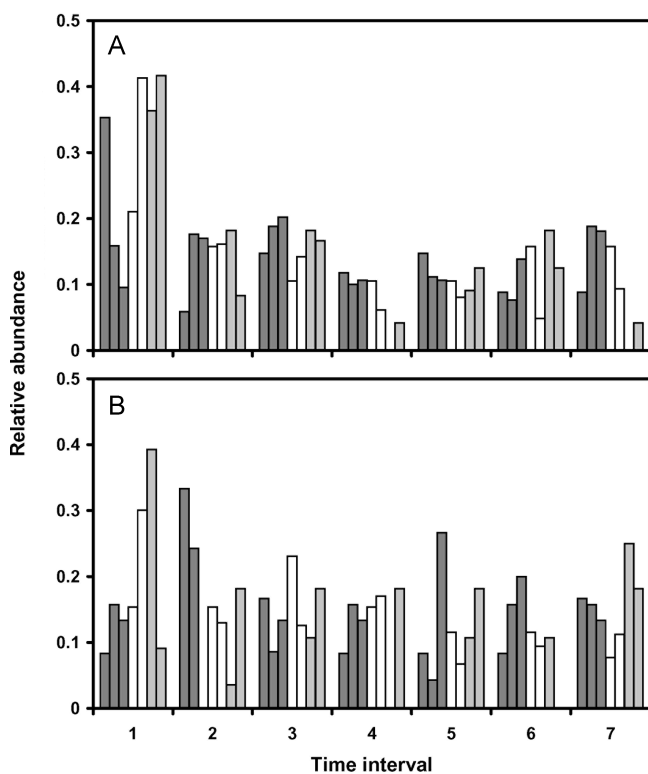
FIGURE 4. Patterns of temporal activity for seven abundant species of frugivorous phyllostomid separately for (A) gaps sites and (B) closed-canopy sites at Tapajós National Forest. Within each time interval, species are ordered alphabetically, with shading indicating common generic affiliations: *Artibeus concolor*, *A. lituratus*, *A. obscurus*, dark gray; *Carollia brevicauda*, *C. perspicillata*, white, *Rhinophylla fischerae*, *R. pumilio*, light gray.

on which these bats feed are successional and grow quickly in newly formed open areas (Fleming & Heithaus 1981, Fleming 1988, Gorchov *et al.* 1993). Their fruits typically ripen during the day so that abundance of ripe fruit is greatest at sunset. If bat responses are related to changes in resource availability, then bat activity should be greater in gaps than in closed-canopy forest, especially early in the night because of greater resource availability. Counter to expectations, activity was less in open areas early in the night. Consequently, redistribution of resources did not account for responses to changes in forest physiognomy.

Many species of frugivorous bats in the Neotropics are less active in open habitats early in the night (Presley *et al.*, in press; Fig. 4). Although a few species (two of seven) in TNF exhibited significant differences in activity between gaps and closed-canopy sites throughout the night, more species had peaks of activity during the first hour of night in closed-canopy forest (five) than in gaps (two). Moreover, peaks of activity were more distinct in closed-canopy forest than in gaps (Fig. 4). At another lowland Amazonian site (Iquitos, Perú), deforestation primarily is associated with subsistence farming that creates agricultural plots adjacent to and often surrounded by primary forest. These agricultural areas are large (*ca* 4 ha) compared to gaps (0.2 ha) created by RIL. Nonetheless, bat species exhibited similar reductions in crepuscular activity in large agriculture-generated gaps and in small RIL-generated gaps compared to associated closed-canopy forest. Reduction of activity by bats in open habitats during twilight (Weinbeer & Meyer 2006, Presley *et al.*, in press) and times of high lunar illumination (Crespo *et al.* 1972, Morrison 1978, Kalko & Handley 2001) likely is a response to greater risk of predation by birds (LaVal 1970, Rodriguez-Duran & Lewis 1985, Ibañez *et al.* 1992, Chacón-Madrigal & Barrantes 2004). Responses by bats to predation risk associated with increases in exposure and illumination are similar to those observed for desert rodents (Kotler 1984,

Brown *et al.* 1988). Because increased predation risk may cause bats to avoid open areas, improved survival and persistence of bats in forests subjected to RIL compared to forests subjected to other logging techniques may be a result of greater canopy preservation associated with RIL protocols. Fruit is a nutrient- and energy-poor resource that requires bats to consume as much as twice their body weight in fruit each night (Charles-Dominique 1986); therefore, foraging likely occupies a large portion of bats' nocturnal activities. Consequently, environmental changes that negatively affect foraging time may have a significant effect on the ability of bats to meet daily dietary requirements. Indirect (*e.g.*, reduction in activity to avoid predation) and direct (*e.g.*, loss of roosting habitat) negative effects on bat populations associated with logging may be synergistic. Consequently, as the proportion of open habitat increases in the landscape, associated negative responses by bats may increase in a nonlinear fashion.

An alternative view point could invoke competition to explain observed changes in activity patterns. Gap creation increases the abundance of fruit on which bats feed. Such an increase in fruit abundance could reduce competition in RIL forest compared to control forest and relax the need for bats to be highly active early in the night. Although this explanation is consistent with observed activity patterns (*i.e.*, less distinct modes of activity and a shift in modes of activity to later times in RIL forest compared to control forest), fruit does not appear to be a limiting resource throughout much of Amazonia or for much of the year (*e.g.*, Smythe 1986, Charles-Dominique 1991); therefore, competition among bats for fruit likely does not strongly influence behavioral patterns in these species. Moreover, because dietary demands require frugivorous bats to forage throughout the night (see below), competition for food likely has little ability to structure patterns of activity.

NICHE-SPECIFIC ACTIVITY PATTERNS IN FRUGIVOROUS BATS.—Species of *Artibeus* and *Carollia* often differ in temporal activity pattern (Presley *et al.* 2009; analyses herein). In general, *Artibeus* are classified as canopy frugivores, specialize on figs, may commute relatively long distances to feeding areas, and commonly forage at multiple vertical strata of the forest. In contrast, *Carollia* are understory frugivores, specialize on fruits of *Piper* and *Solanum*, do not commute particularly long distances to feeding areas, and the majority of their activity occurs in the understory (*e.g.*, Fleming 1988, Charles-Dominique 1991, Kalko & Handley 2001). Because our surveys were conducted with mist nets erected at ground level, and because mist-net capture rates likely reflect distance traveled, apparent interspecific differences in patterns of activity between species of these genera likely do not reflect differences in activity *per se*, but differences in temporal use of the forest understory. As a result, differences in foraging ecology, spatial distribution of fruits on which particular bats specialize, and avoidance of predation risk associated with open areas during times of increased illumination likely contribute to shapes of patterns of activity as well as interspecific differences in activity.

METHODOLOGICAL CONSIDERATIONS AND BIASES.—Statistical power of Kolmogorov–Smirnov two-sample tests, such as those employed herein, is a function of the size of each sample (Siegel 1956). Within the context of our analyses, tests involving species with smaller sample sizes potentially could lack sufficient power to detect ecologically meaningful differences in intraspecific (Table 1) or interspecific (Table S1) patterns of temporal activity. Conversely, exceedingly large sample sizes could result in analyses with sufficient power to detect differences in activity that are smaller than would be ecologically meaningful. As a result, researchers must carefully consider the implications of both nonsignificant and significant results within the context of the research question of interest. To evaluate the role of sample size in our results, as well as to determine the robustness of the analyses to changes in sample size, we doubled the number of captures for all species and conducted analyses corresponding to those in Tables 1 and S1. Of the 36 analyses involving only species with relatively small sample sizes (*i.e.*, *A. concolor*, *C. brevicauda*, *R. pumilio*, *R. fischerae*), only a single result was significant with doubled sample size, indicating that results were relatively robust with respect to number of captures and that nonsignificance generally was a function of similarity of activity and not a lack of statistical power *per se*.

In addition to affecting statistical power, small samples may not accurately characterize patterns of activity or accurately identify activity modes potentially compromising the accuracy of such analyses. Nonetheless, inaccurately identified peaks in activity that result from small sample sizes likely would be distributed randomly among time intervals; therefore, small sample sizes likely reduce analytical power, making it more difficult to detect evenly spaced or clustered modes. Such a reduction in power is not evident in our analyses (Table 2).

SUPPORTING INFORMATION

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

TABLE S1. *Differences for each physiognomy and for each management type in temporal activity patterns between pairs of common species of frugivorous bat from lowland Amazonia.*

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