



## Reduced-impact logging and temporal activity of understory bats in lowland Amazonia

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### ABSTRACT

Because global timber demands continue to threaten tropical rain forests, identification of sustainable forest management protocols that meet human needs while preserving biodiversity is critical. Reduced-impact logging (RIL) protocols are increasingly common in the tropics and may be a viable option for sustainable forest use; however, few studies have documented faunal responses to RIL. Moreover, evaluations of abundance or diversity may not be sufficient for a comprehensive understanding of faunal responses to human activities, especially in the short-term. We assessed the effects of RIL on the temporal activity patterns of abundant bats in lowland Amazonian rain forest. More specifically, we characterized temporal patterns of activity, overlap of temporal activity, and dispersion of activity modes for seven abundant bat species and for four common bat guilds in RIL forest and in undisturbed forest in Tapajós National Forest, Pará, Brazil. Temporal activity of aerial insectivores, nectarivores, and gleaning animalivores did not change in response to RIL. In contrast, three of five species of frugivores and frugivores as a group changed their patterns of temporal activity in response to RIL. RIL had a greater effect on temporal activity of frugivores that foraged in the understory than on frugivores that foraged in multiple forest strata. Overlap of temporal activity of frugivores was greater than expected by chance in undisturbed forest, but was random in RIL forest. Changes in activity may be a response to a combination of increased predation risk and reduced distances of early evening flights between day roosts and feeding areas in RIL forest compared to undisturbed forest.

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### 1. Introduction

Human-induced habitat conversion and degradation are the most pervasive drivers of detrimental changes to biodiversity at a global scale (Sala et al., 2000; Lambin et al., 2003). Because tropical forests are hotspots of global biodiversity, loss of these habitats may have a disproportionate impact on global extinction rates (Pimm et al., 1995) and on the ability of these forests to provide critical ecosystem services to humans (Daily, 1997). Current networks of nature reserves do not provide adequate protection for biodiversity (Andelman and Willig, 2003; Rodrigues et al., 2004), with annual rates of habitat conversion exceeding the areal extent

of protected habitats (Hoekstra et al., 2005). In addition, demands for natural resources (e.g., timber) will likely increase in the future, further threatening tropical forests with inadequate protection or management plans (Laurence et al., 2001). In Amazonia, timber is an important resource that provides a substantial proportion of regional income (Uhl et al., 1997). Its exploitation must be reconciled with conservation of biodiversity and maintenance of ecosystem services via science-based management (Veríssimo et al., 2002; Nepstad et al., 2004). Timber harvest practices that minimize detrimental impacts on the environment are promoted as sustainable and profitable options for Amazonia (Putz et al., 2000; Holmes et al., 2002).

Reduced-impact logging (RIL) is a type of low-intensity logging that implements a series of measures to minimize damage to soils, to facilitate regeneration of trees (i.e., seedlings, saplings), and to maintain critical ecosystem processes (e.g., hydrological flow, nutrient cycling), which conveys long-term economic and environmental advantages over other logging practices (Johns et al., 1996; Barreto et al., 1998; Putz et al., 2000). Furthermore, RIL decreases the likelihood of post-logging fires, a common consequence of

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traditional selective logging in Amazonia (Nepstad et al., 1999). Importantly, the consequences of RIL on animal populations and communities have only been evaluated for selected groups of arachnids, beetles, birds, and mammals (Davis, 2000; Azevedo-Ramos et al., 2006; Wunderle et al., 2006; Castro-Arellano et al., 2007; Presley et al., 2008). The potential of RIL to meet conservation goals and to provide sustainable timber harvests needs to be evaluated with respect to a broad array of taxa, with emphasis on those that are crucial for maintaining ecosystem function (Mason and Putz, 2001).

In general, effects of deforestation, logging regimes, or habitat fragmentation on associated faunas have been addressed only with respect to changes in species diversity or abundance. However, anthropogenically-driven changes to habitat quality may have more subtle effects, influencing foraging efficiency, physiological stress, or sex ratios of bat species without greatly affecting abundances or presences of species (Henry et al., 2007), especially in the short-term. Temporal activity patterns of species are ecologically significant, and indicate the ways in which species exploit their environment (Pianka, 1973; Kronfeld-Schor and Dayan, 2003). Investigation of behavioural responses to logging, deforestation, or habitat fragmentation may provide a more complete understanding of the effects of these activities on the biota. For example, behavioural changes in response to logging may indicate stressors on populations that do not necessarily manifest as changes in abundance or diversity in the short-term, the most common time frame for such investigations. Short-term changes in behaviour may indicate which species are susceptible to longer-term effects or to slightly more intense or pervasive management plans. Moreover, behavioural changes evoked by habitat modification may indicate proximate causes (i.e., sources of stress) of species loss or reductions in abundance for ecologically similar species. For example, temporal shifts in activity can change the outcome of interspecific interactions that shape community composition (Morgan, 2004).

Neotropical bats are key elements of forest regeneration as they are important agents of pollination and seed dispersal for pioneer and successional plant species (Fleming, 1988; Gorchov et al., 1993). Because they are abundant, ecologically diverse, widespread, responsive to disturbance, and easy to sample, bats may be effective bioindicators (Fenton et al., 1992; Medellín et al., 2000; Jones et al., in press). Although Neotropical bats exhibit idiosyncratic responses to logging, two general trends are evident. Frugivorous and nectarivorous bats often show greater abundances in disturbed sites that harbor early successional plants (e.g., *Cecropia*, *Piper*, *Solanum*) that provide fruit and nectar on which these bats feed, whereas populations of gleaning animalivores (i.e., insectivorous and carnivorous phyllostomines) often respond negatively to any level of disturbance (Fenton et al., 1992; Brosset et al., 1996; Ochoa, 2000; Clarke et al., 2005a, b; Peters et al., 2006; Castro-Arellano et al., 2007; Presley et al., 2008). Timber harvest changes the physiognomy and microclimate of the forest; thereby, changing resource diversity, abundance, or predictability, which may affect temporal activity of species that exploit those resources. Changes in behaviour (e.g., temporal activity patterns) induced by anthropogenic disturbance have been rarely studied (but see Presley et al., 2009a, b). As such, quantification of bat activity patterns in natural and disturbed sites may enhance the understanding of the role of bats as pollinators or seed dispersers, as well as the potential effects of forest management protocols on these plant–animal interactions. RIL creates canopy gaps that directly affect the abundance and distribution of fruit on which species of *Carollia* rely, whereas RIL should have little effect on the abundance or distribution of canopy fruits (e.g., *Ficus*) on which species of *Artibeus* specialize. We hypothesized that RIL-generated changes in forest physiognomy and associated changes in resource abundance

and distribution (e.g., fruit, nectar, roosts) would influence patterns of temporal activity of bats. More specifically, we hypothesized that (1) because of differential effects of RIL on fruit resources, RIL would have a greater effect on temporal activity of species of *Carollia* than on species of *Artibeus*, (2) changes would be guild-specific because RIL does not affect the resources bases for each guild similarly, and (3) species may respond by decreasing early evening activity to avoid time of elevated predation risk associated with open area during times of greater ambient illumination (i.e., twilight).

## 2. Methods

### 2.1. Study area

Research was conducted in Tapajós National Forest (TNF), a 560 000 ha area of lowland rainforest in western Pará, Brazil (3°21'36" S, 54°57'0" W). The TNF is bounded by the Cupari River, Santarém-Cuiabá Highway (BR-163), and Tapajós River to the south, east, and west, respectively. Climate is tropical, with a considerable average rainfall (1920 mm/year) and a somewhat wetter season from December to May (Parrotta et al., 1995). *Terra firme* forest encompasses the entire study area and constitutes 33% of the forested lands of TNF. Canopy height ranges from 30 to 40 m, with emergent trees reaching 50 m. Typical tree species include *Bertholletia excelsa*, *Couratari* spp., *Dinizia excelsa*, *Hymenaea coubaril*, *Manilkara huberi*, *Parkia* spp., *Pithecellobium* spp., and *Tabebuia serratiolia* (Silva et al., 1985). Detailed descriptions of climate, soils, and vegetation appear in Silva et al. (1985), Daly and Prance (1989), and Parrotta et al. (1995), respectively.

Experimental blocks were located within a 5000 ha grid (3°21'21" S, 54°56'58" W) that was established as a demonstration for logging practices near km 83 on the Santarém-Cuiabá Highway. Surveys were conducted in forests that represented two management types, with two experimental blocks (T18 and T2) established in RIL forest and two experimental blocks (C1 and C3) established in control forest. Each experimental block encompassed 100 ha (i.e., 1000 m by 1000 m). Control blocks were within a designated 500 ha control area and located 1–2 km from each of the RIL blocks. Control blocks were bounded by selectively logged (40 m<sup>3</sup>/ha) forest to the north and by undisturbed forest on the remaining sides. Half of the area of block C1 was 20-year-old secondary forest, whereas block C3 comprised only primary forest. RIL blocks were separated from each other by 2.5 km of selectively logged forest, and were bordered by undisturbed forest on one side and selectively logged forest on the other sides. Timber harvest in RIL blocks was completed 20 months before initiation of surveys, but continued in adjacent blocks throughout the study. In RIL blocks, trees larger than 45 cm dbh were harvested at low intensity (18.7 m<sup>3</sup>/ha). RIL uses several methods to reduce damage to the forest (e.g., soil compaction, collateral damage to non-harvested trees). Details about implementation of RIL techniques in Amazonia are described elsewhere (Veríssimo et al., 1992; Vidal et al., 1997). The most commonly harvested tree species via RIL in TNF were *M. huberi*, *M. paraensis*, *Protium pernevatum*, *D. excelsa*, and *Piptadenia suaveolens* (Keller et al., 2004). In total, 394 (1870.49 m<sup>3</sup>) and 379 (1872.708 m<sup>3</sup>) trees were removed from blocks T2 and T18, respectively.

### 2.2. Field methods

Surveys included three sessions of mist-netting: April–May 1999, November–December 1999, and April 2000 (Saldanha, 2000). Each block contained twelve sites, arranged in two parallel rows, each row containing six uniformly spaced (200 m) sites.

Each night, bats were sampled from four sites, with five 12-m nets deployed at ground level (0.5–2.5 m) at each site. Nets were opened before dusk (~1800 h) and checked at least once an hour until midnight. Each site was monitored once per session. To minimize effects of lunar phobia (Crespo et al., 1972) on sampling efficacy, netting was not conducted within two nights of a full moon. Taxonomic identifications (sensu Simmons, 2005) were aided by a reference collection that was amassed from nearby forest before initiation of the study. A set of voucher specimens was prepared for each species and deposited at the Museu Paraense Emílio Goeldi in Belém. Before release, species identity, sex, reproductive condition, age (adult or juvenile), and mass were ascertained for each captured individual. We followed published classifications (Wilson, 1973; Stevens and Willig, 1999) to assign bats to foraging guilds (frugivores, nectarivores, gleaning animalivores, aerial insectivores). Many species occurred in small number and did not allow for accurate estimates of activity patterns. Nonetheless, pooling captured individuals into broad guilds facilitated inferences that could be applied to groups of individuals with similar foraging strategies. Additional details about the experimental design appear elsewhere (Castro-Arellano et al., 2007).

Because the sampling protocol was limited to forest understorey, inferences about effect of RIL on temporal activity of bats are restricted to activity in the understorey. This limitation does not apply to specific taxa, per se, but to the part of the forest (understorey) about which we can confidently estimate the activity of bats. Analyses of temporal activity were based on the relative number of captures for each species in each time period and not on absolute numbers of captures. Assuming that biases in catchability associated with the use of ground-level mist nets is not contingent on time of day, the only potential effect of mist-net biases on analyses is that the smaller sample sizes resulting from missed captures reduced the accuracy of activity patterns estimates. Analyses of pair-wise comparisons of temporal activity (Kolmogorov–Smirnov two-sample tests) as well as of assemblage-wide temporal overlap (Rosario, see below) based on smaller sample sizes (i.e., those with less reliable estimates of activity patterns) have less power. Consequently, the primary effect of mist-netting on our results is to produce a more conservative test with an associated potential increase in Type II error rates.

### 2.3. Statistical analysis

Number of captures during each 1-h interval represented an estimate of activity by each species or guild, and was the basis of subsequent analyses. We restricted analyses of temporal activity patterns to seven abundant bat species and to four common guilds (Castro-Arellano et al., 2007). Although a comparison of activity patterns between management types was the primary goal, we also compared patterns of temporal activity between blocks within management types to evaluate spatial heterogeneity in activity within each treatment.

Pair-wise differences in temporal activity patterns were evaluated with Kolmogorov–Smirnov two-sample tests (Siegel, 1956) using SPSS version 11.0 for Windows. Intraspecific and intraguild differences in activity were evaluated for each of seven species and for each of four guilds, respectively. For each species or guild, analyses were conducted between blocks within each management type (RIL or control forest) and between management types with blocks combined.

Interspecific and interguild comparisons of temporal activity within each management type were restricted to frugivorous phyllostomids (five species) and to the four common guilds, respectively. Kolmogorov–Smirnov two-sample tests were used to evaluate differences in temporal activity between each pair of

species, or between each pair of guilds, within each management type. We did not implement a correction of  $p$ -values when performing multiple tests. Methods that maintain Type I error rates at prescribed  $\alpha$ -levels for a group of analyses are controversial in ecology (Hurlbert and Lombardi, 2003; Moran, 2003). In general, such corrections are not advised for exploratory analyses such as these (Roback and Askins, 2005).

Two aspects to temporal activity determine overlap: the co-location of activity peaks and the extent of temporal activity. To address overlap of peak activities, we examined their dispersion within a temporal domain using a mode clustering index (MC), in which  $MC < 1.0$  indicates evenly spaced modes,  $MC > 1.0$  indicates clustered modes, and  $MC \sim 1.0$  indicates randomly distributed modes (Poole and Rathcke, 1979). We executed this test for the five common frugivores and for the four phyllostomid feeding guilds, and did so separately for each management type.

We used Monte Carlo simulations to evaluate assemblage-wide temporal niche overlap among the five common species of frugivore, as well as among the four bat guilds, separately for each management type. The basis of an analysis was a species by time matrix or a guild by time matrix of the relative number of captures (i.e., activity) registered for each species or for each guild during each time interval. Relative number of captures (scaled to sum to 100) were used to remove effects of species-specific abundance on estimates of temporal overlap. Temporal overlap was quantified as the average of all pair-wise overlaps calculated with Pianka (Pianka, 1973) or Czechanowski (Feinsinger et al., 1981) indices. Null distributions of overlap values were generated using a randomization algorithm (Rosario) that was designed specifically for use with interval data (Presley et al., 2009a, b; Castro-Arellano et al., submitted for publication). Rosario maintains the shape of the empirical distribution of activity (i.e., temporal autocorrelation) of each species by shifting entire activity patterns a random number of intervals to create randomly generated amounts of temporal overlap. Alternative null models to evaluate niche overlap (e.g., randomization algorithm 3, randomization algorithm 4; Winemiller and Pianka, 1990) were designed for nominal data (e.g., categories of prey or microhabitat), and are not appropriate for ranked or interval data such as time, which are inherently ordered. Temporal overlap indices were calculated for each of 10,000 randomly generated sets of activity patterns, creating a null distribution of overlap values. Significance was determined by comparing each empirical index to its associated null distribution and all analyses were conducted as two-tailed tests. Temporal coincidence in activity (i.e., more overlap than expected by chance) was indicated by significantly more overlap (i.e.,  $P \leq \alpha/2$ ) than expected by chance. Temporal segregation (i.e., less overlap than expected by chance) was indicated by significantly less overlap (i.e.,  $P \leq \alpha/2$ ) than expected by chance. Simulations were conducted with the TimeOverlap program that runs in the Windows operating system (Castro-Arellano et al., submitted for publication; program available at [http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity\\_20%\\_pattern.html](http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity_20%_pattern.html)). For all analyses, we used an  $\alpha$  of 0.05.

### 3. Results

In general, activity patterns of species and guilds did not differ between blocks within management types (Table 1; Figs. 1 and 2). Nonetheless, the numbers of captures of the two species of *Artibeus* with block-specific activity patterns were sufficiently great so as to affect differences between blocks in activity patterns of frugivores in control forest. Differences in activity patterns between RIL and control forests occurred for three of five species of frugivore, contributing to guild-level differences for frugivores in temporal activity between management types.

**Table 1**  
Comparisons of bat activity patterns within and between (blocks pooled) management types sampled with understorey mist nets in the Tapajós National Forest, Brazil, based on the Kolmogorov–Smirnov two-sample tests.

Group	Between control blocks			Between RIL blocks			Control versus RIL		
	n	Z	P-value	n	Z	P-value	n	Z	P-value
<i>Species</i>									
<i>Artibeus jamaicensis</i> (FR)	24	0.939	0.341	33	0.792	0.558	57	1.073	0.200
<i>Artibeus lituratus</i> (FR)	162	1.612	<b>0.011</b>	223	0.882	0.509	385	1.382	<b>0.044</b>
<i>Artibeus obscurus</i> (FR)	44	1.358	<b>0.050</b>	53	0.292	1.000	97	0.267	1.000
<i>Carollia brevicauda</i> (FR)	38	0.643	0.476	19	0.433	0.992	57	1.780	<b>0.004</b>
<i>Carollia perspicillata</i> (FR)	678	1.315	0.063	351	0.481	0.975	1029	1.654	<b>0.008</b>
<i>Lonchophylla thomasi</i> (NE)	46	0.954	0.323	62	0.298	1.000	108	1.121	0.162
<i>Pteronotus parnelli</i> (AI)	65	1.067	0.205	32	0.713	0.690	97	0.748	0.630
<i>Guilds</i>									
Aerial insectivores	70	0.913	0.375	39	0.544	0.920	109	0.737	0.650
Frugivores	1021	2.978	<b>&lt;0.001</b>	738	1.193	0.116	1759	3.416	<b>&lt;0.001</b>
Gleaning animalivores	77	0.305	1.000	61	0.520	0.950	138	0.318	1.000
Nectarivores	61	1.132	0.154	89	1.132	1.000	150	0.585	0.883

Significant results in bold.

Degrees of freedom are 2 for all tests.

Abbreviations are: n, sample size; Z, Kolmogorov–Smirnov test statistic; AI, aerial insectivore; FR, frugivore; and NE, nectarivore.

Interspecific differences (Table 2) in temporal activity occurred for 5 of 10 comparisons in control forest, with most differences occurring between species of *Carollia* and species of *Artibeus*. Interspecific differences in temporal activity occurred in only 2 of 10 comparisons in RIL forest and always involved *C. perspicillata* and species of *Artibeus*. Differences in temporal activity between guilds (Table 3) were common in each management type, with each guild associated with at least one significant difference in each management type.

Regardless of index, temporal overlap among species of frugivore was greater than expected by chance in control forest, but not in RIL forest (Table 4; Fig. 3). Similarly, temporal overlap among guilds was greater than expected by chance in control forest, but not in RIL forest (Table 4; Fig. 4). Modes in temporal activity of species were significantly clustered in each management type. Similarly, modes in temporal activity of guilds approached significance ( $0.10 \geq P > 0.05$ ) in each management type.

#### 4. Discussion

Per unit distance, flight is an energetically more efficient method of travel than cursorial locomotion, which allows bats to avail themselves of resources (e.g., fruit, nectar) that are too patchy in distribution to support populations of less vagile homeotherms. Because such resources often occur in a sparse and scatter manner, bats are required to fly great distances each night, using large amounts of energy. As a result, the net energetic gain for foraging on scattered energy-rich resources such as fruit or nectar is small and energy turnover for bats can be exceptionally high. For example, nectarivorous bats use about 2/3 of the caloric content of their body mass each night (von Helversen and Winter, 2003), an exceptional amount of energy. Similarly, bats that feed on fruit may require consumption of up to twice their body mass in fruit nightly (Charles-Dominique, 1986). High energy demands associated with flight likely are a primary reason that bats developed torpor abilities to conserve energy that otherwise would be spent on maintenance of body temperature (Speakman and Thomaw, 2003). Despite spending the overwhelming majority of their active time foraging (Charles-Dominique, 1991), frugivorous and nectarivorous bats amass only enough body fat (10–15% of their body mass; von Helversen and Winter, 2003) to survive brief periods of resource shortage, suggesting that these resources are dependable in undisturbed forests. Changes to habitat quality that affect the

abundance or distribution of resources or the amount of time bats can effectively forage may be indicative of forest patches that are not capable of permanently sustaining populations of nectarivorous or frugivorous bats (i.e., sink habitats).

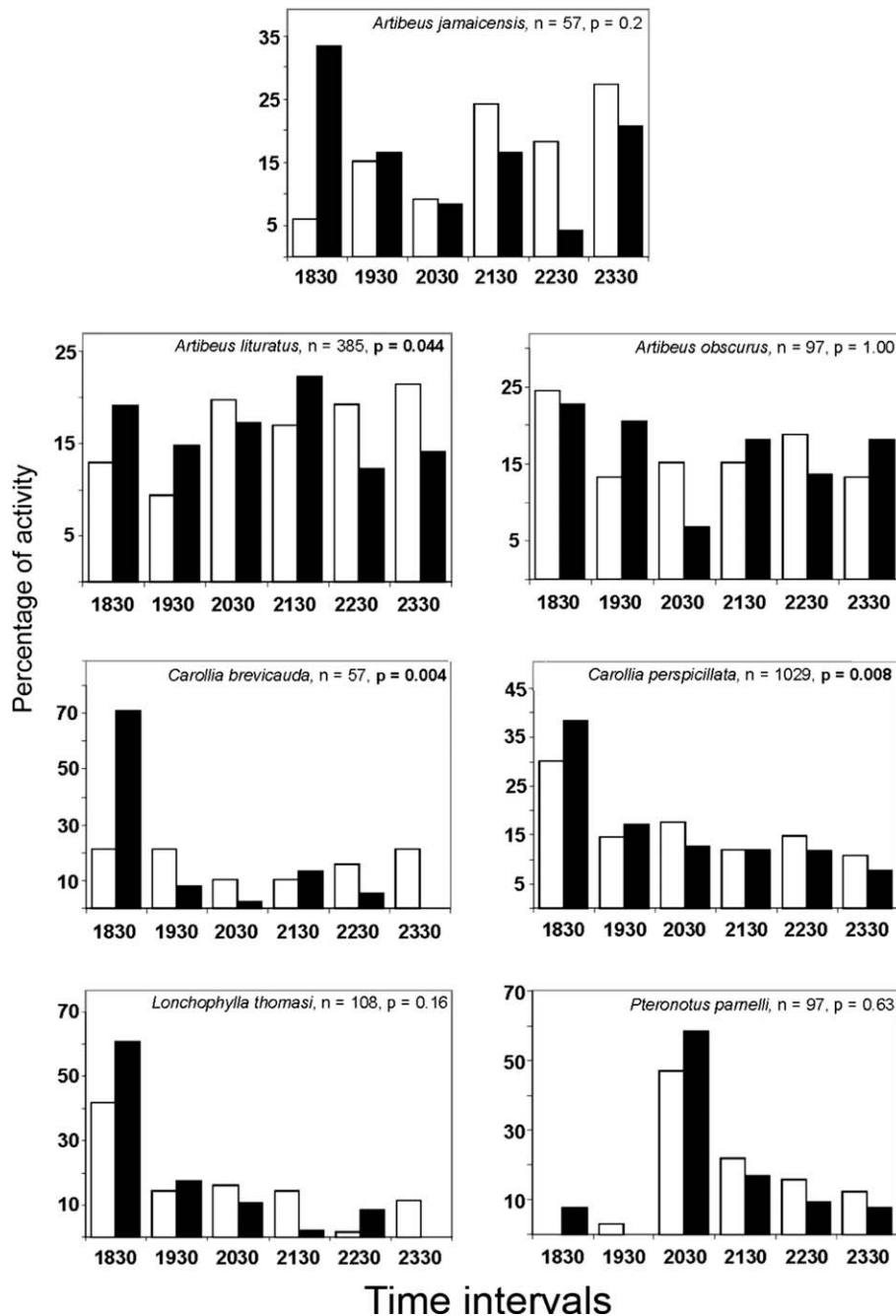
##### 4.1. Guild-specific responses to RIL

RIL affected temporal activity patterns of bats, but did so in a species-specific or guild-specific manner. More specifically, RIL did not affect abundances or the temporal activity of nectarivorous or gleaning animalivorous bats, whereas, abundances and temporal activity of frugivorous bats were affected by RIL (Castro-Arellano et al., 2007; present study). Moreover, responses to RIL were contingent on foraging ecology of species of frugivore. Temporal activity patterns of species that specialize on the understorey fruits (*Carollia brevicauda* and *C. perspicillata*) were affected more greatly by RIL than were those of species that specialize on the canopy fruits (*Artibeus jamaicensis* and *A. obscurus*), which were unaffected by RIL.

In general, species of *Carollia* are understorey foragers, commute relatively short distances to feeding areas, and specialize on fruits of *Piper* and *Solanum*, whereas species of *Artibeus* forage in multiple forest strata, may move considerable distances to feeding areas, and specialize on *Ficus* and *Cecropia* fruits (Gardner, 1977; Fleming, 1988; Charles-Dominique, 1991; Kalko and Handley, 2001). Because surveys were conducted with mist nets erected at ground level, capture rates reflect temporal use of the forest understorey rather than use of all forest strata; therefore, our data may provide better estimates of effects of RIL on overall temporal activity patterns of understorey foragers (e.g., *Carollia*) than for multi-strata foragers (e.g., *Artibeus*). Consequently, non-significant results for species of *Artibeus* indicate that temporal activity of these species is unaffected in the understorey, but can not directly address activity for other strata.

##### 4.2. Twilight avoidance in RIL forest

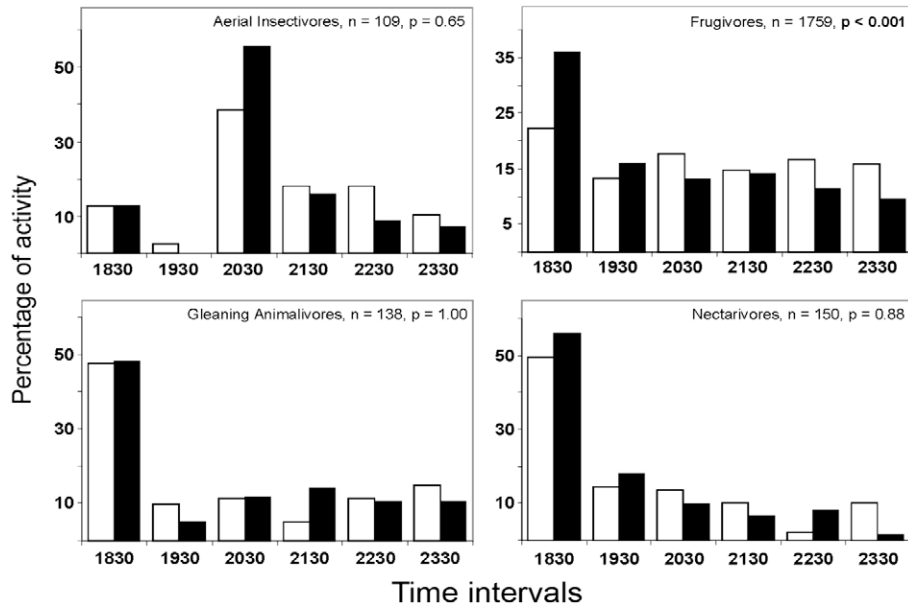
For each species (*A. lituratus*, *C. brevicauda*, and *C. perspicillata*) that exhibited management-specific activity patterns, activity was greater during early night in control forest than in RIL forest (Fig. 1). Moreover, modes of activity in control forest were more pronounced than those in RIL forest. Reductions in activity during twilight in response to RIL are consistent with hypotheses of increased predation risk in open habitats. Although bat species



**Fig. 1.** Comparison of activity patterns between control (black) and RIL (white) forest for each of seven common bat species sampled with understorey mist nets in the Tapajós National Forest, Brazil. Sample sizes are indicated by  $n$  and  $P$ -values correspond to results from Kolmogorov–Smirnov two-sample tests (see Table 1). Times denote the mid-point of each temporal sampling interval.

may have activity peaks during the first hour after sunset (Brown, 1968; LaVal, 1970; Eckert, 1982; Marinho-Filho and Sazima, 1989), some reduce their activity during the first hours of night in human-created open areas (Rodríguez-Duran and Lewis, 1985; Duvergé et al., 2000; Presley et al., 2009a) or in naturally occurring open areas (Fenton et al., 1994; Weinbeer and Meyer, 2006). Such reductions in activity likely are responses to greater risk of predation by birds (Baker, 1962; Ibañez et al., 1992; Fenton et al., 1994; Chacón-Madriral and Barrantes, 2004). Indeed, predator avoidance is an important factor in determination of emergence time for cave-dwelling bats (Jones and Rydell, 1994; Duvergé et al., 2000). Because diurnal raptors are among the main predators of bats (e.g., Fenton et al., 1994; Rodríguez-Duran and Lewis, 1985; Chacón-

Madriral and Barrantes, 2004), increased risk of predation may occur during twilight hours, especially in open areas where slow flying bats are more vulnerable to visually-oriented avian predators (Baker, 1962; Rodríguez-Duran and Lewis, 1985). In Tapajós, likely avian predators of bats in the understorey of control and RIL forest (Wunderle et al., 2006) include falcons (*Micrastur ruficollis* and *M. gilvicollis*) and even canopy raptor species (e.g., *Accipter* spp., *Falco rufigularis*, *Falco columbarius*) occasionally prey on bats by descending to lower levels in large openings or forest gaps (Rodríguez-Duran and Lewis, 1985; Wunderle, unpublished observations). In addition, non-raptorial nocturnal (Ibañez et al., 1992) and diurnal (Chacón-Madriral and Barrantes, 2004) birds prey opportunistically on bats in the Neotropics.



**Fig. 2.** Comparison of activity patterns between control (black) and RIL (white) forest for each of the four common feeding guilds sampled with understorey mist nets in the Tapajós National Forest, Brazil. Sample sizes are indicated by *n* and *P*-values correspond to results from Kolmogorov–Smirnov two-sample tests (see Table 1). Times denote the mid-point of each temporal sampling interval.

Twilight avoidance is comparable to the reduction in activity by bats during times of greater lunar illumination (i.e., “lunar phobia”; Crespo et al., 1972; Morrison, 1978; Kalko and Handley, 2001), a phenomenon generally considered to be a response to increased predation risk. Indeed, in the absence of significant risk from pre-

**Table 2**

Results for interspecific comparison of temporal activity patterns within management types (blocks pooled) for common frugivorous bats sampled with understorey mist nets in the Tapajós National Forest, Brazil, based on Kolmogorov–Smirnov two-sample tests.

	Aja	Ali	Aob	Cbr	Cpe
Aja		0.655	0.995	<b>0.030</b>	0.827
Ali	0.814		0.930	<b>&lt;&lt;0.001</b>	<b>&lt;&lt;0.001</b>
Aob	0.253	0.268		<b>&lt;&lt;0.001</b>	0.126
Cbr	0.585	0.506	1.000		<b>0.001</b>
Cpe	<b>0.004</b>	<b>&lt;&lt;0.001</b>	0.794	0.977	

Significance values above the diagonal correspond to results from control forest and those below the diagonal correspond to RIL forest.

Sample sizes are as in Table 1.

Significant *P*-values are bold.

Species abbreviations are: Aja, *Artibeus jamaicensis*; Ali, *Artibeus lituratus*; Aob, *Artibeus obscurus*; Cbr, *Carollia brevicauda*; and Cpe, *Carollia perspicillata*.

**Table 3**

Interguild comparisons of activity patterns within management types (blocks pooled) for phyllostomid bats sampled with understorey mist nets in the Tapajós National Forest, Brazil, based on Kolmogorov–Smirnov two-sample tests.

	AI	FR	GA	NE
AI		<b>&lt;&lt;0.001</b>	<b>&lt;&lt;0.001</b>	<b>&lt;&lt;0.001</b>
FR	0.100		0.245	<b>0.009</b>
GA	<b>&lt;&lt;0.001</b>	<b>0.001</b>		0.114
NE	<b>&lt;&lt;0.001</b>	<b>&lt;&lt;0.001</b>	0.489	

Significance values above the diagonal correspond to control forest and those below the diagonal correspond to RIL forest.

Sample sizes are as in Table 1.

Significant *P*-values are bold.

Guild abbreviations are: AI, aerial insectivores; FR, frugivores; GA, gleaning animalivores; and NE, nectarivores.

dators, bats do not exhibit lunar phobia (Gannon and Willig, 1997). Avoidance of open areas during times of greater illumination may have an evolutionary basis (Roll et al., 2006), with species exhibiting this behaviour regardless of the proximate presence of predators. Reduction of activity at dusk by bats is not dependent on the size of the open area, as it occurs in large tracts (~4 ha) subject to agricultural use (Presley et al., 2009a) as well as in RIL forest with small gaps (0.2 ha) created by tree removal (Presley et al., 2009b). In general, canopy-foraging species exhibit stronger lunar phobia because they fly through open areas, such as space above the canopy, more often than do understorey-foraging species (Kalko and Handley, 2001; Thies et al., 2006). Although forest subjected to RIL does not suffer much canopy loss, RIL does create open areas (e.g., canopy gaps from tree removal, log storage sites) in all forest strata. Such forest openings may decrease activity of bats during times of greater illumination (e.g., twilight, full moon). Nonetheless, changes in activity during twilight hours in response to RIL were greater for species that forage in the understorey (*Carollia*) than for species that forage throughout the vertical extent of the forest (*Artibeus*). Because light levels in forests generally decrease with proximity to the ground, it could be expected that multi-strata species (e.g., *Artibeus*) would avoid upper levels of the forest during twilight hours, which could manifest as an increase in temporal activity during those times. That such a pattern did not occur indicates that these species did not exhibit twilight phobia or that they did so by being less active during those times and not by shifting location of activity to less illuminated habitats.

Alternatively, movement of individuals among patches of forest may account for apparent reductions in activity during twilight hours in forest subjected to RIL. Some bat species may preferentially roost in undisturbed forest because of the presence of more large trees and forage in RIL forest that harbors greater abundances of early successional plants (*Piper*, *Solanum*, *Cecropia*) on which they feed (Gorchoy et al., 1993). Because mist nets intercept bats as they travel, capture rates likely reflect distance travelled during particular time intervals. Thus, greater numbers of captures in control forest during twilight hours could reflect travel of individuals from roosting habitat to foraging habitat. This is consistent with the observation that during the first hour of darkness, *Carollia*

**Table 4**

Indices of assemblage-wide temporal overlap and mode clustering for five common frugivorous phyllostomids and for four guilds sampled with understorey mist nets in the Tapajós National Forest, Brazil.

Group	Treatment	Temporal overlap				Mode clustering	
		Pianka index		Czechanowski index		MC	P-value
		Observed overlap	P-value	Observed overlap	P-value		
Species	Control forest	0.850	<b>0.002</b>	0.714	<b>0.002</b>	2.97	<b>0.022</b>
	RIL forest	0.891	0.765	0.801	0.661	4.31	<b>0.001</b>
Guilds	Control forest	0.759	<b>0.010</b>	0.676	<b>0.012</b>	2.40	0.095
	RIL forest	0.741	0.140	0.668	0.199	2.40	0.095

Analyses were conducted separately for control forest and for RIL forest.

Significance is indicated by bold font.

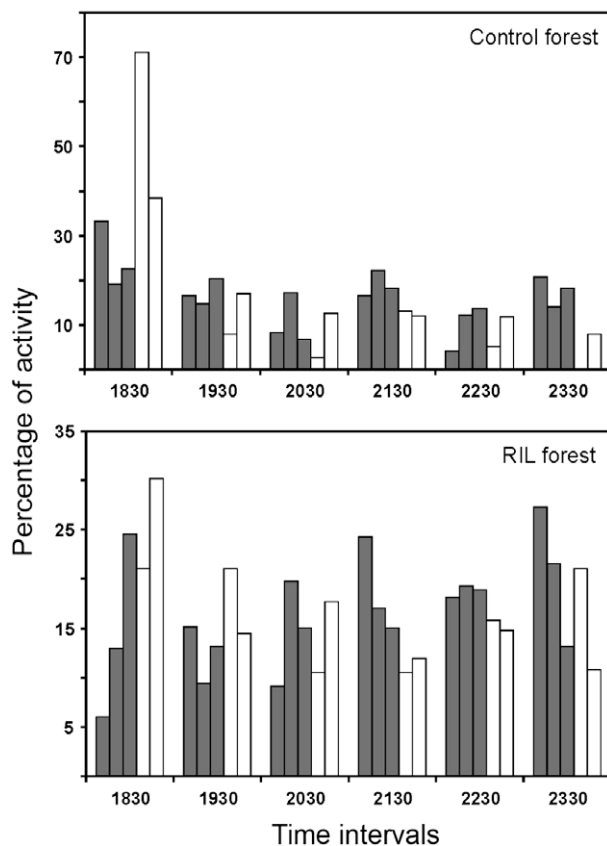
All significant results reflect more temporal overlap or greater mode clustering than expected by chance.

travels toward or searches for suitable feeding areas, with reduced travel thereafter (Fleming, 1988). RIL may have a small effect on roost availability because few large trees are removed (i.e., < 4 trees/ha, which represents only 7% of trees with dbh > 35 cm; Keller et al., 2001). Nonetheless, selection of roost sites by bats in logged forest may be affected by factors beyond the loss of particular trees, although these factors are poorly understood (Crampton and Barclay, 1998; Evelyn and Stiles, 2003; Kunz and Lumsden, 2003; Elmore et al., 2004; Hayes and Loeb, 2007). As a result, changes in activity during twilight in response to RIL may indicate which species have specialized roost requirements and which species roost less discriminately in the forest. Specialized roost requirements often necessitate farther travel to foraging areas,

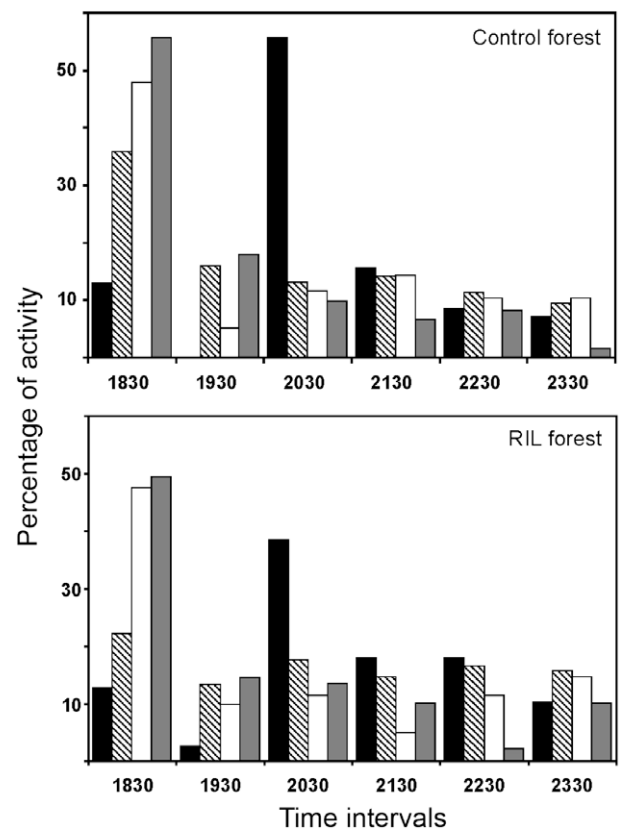
resulting in many early evening captures. In contrast, species with less strict roosting requirements can locate roosts nearer to foraging areas, resulting in a more even distribution of captures throughout the night. Nevertheless, more detailed studies are needed to ascertain effects of RIL on roosting, movements, and foraging of bats.

#### 4.3. Conservation and management implications

To date, the quantified negative effects of RIL on the diversity and abundance of vertebrate species are small (Azevedo-Ramos et al., 2006; Wunderle et al., 2006; Castro-Arellano et al., 2007; Presley et al., 2008), and much less severe than those associated with conventional logging techniques (Davis, 2000). Although RIL



**Fig. 3.** Comparisons of patterns of temporal activity for five common species of frugivore in control or RIL forest sampled with understorey mist nets in the Tapajós National Forest, Brazil. Within each time interval, species are ordered alphabetically, with shading indicating generic affiliation: *A. jamaicensis*, *A. lituratus*, *A. obscurus*, gray; *C. brevicauda*, *C. perspicillata*, white. Times denote the mid-point of each temporal sampling interval.



**Fig. 4.** Comparisons of patterns of temporal activity for four common feeding guilds in control or RIL forest sampled with understorey mist nets in the Tapajós National Forest, Brazil. Within each time interval, guilds are ordered as: aerial insectivores, black bars; frugivores, striped bars; gleaners, white bars; and nectarivores, gray bars. Times denote the mid-point of each temporal sampling interval.

did affect temporal activity patterns of three species of frugivores, such changes generally were restricted to twilight hours. Moreover, each of these species remained abundant in RIL forest (Castro-Arellano et al., 2007), indicating that ecosystem services provided by these species were not greatly affected by logging. Nonetheless, anthropogenically-induced changes to temporal activity patterns may influence energy budgets of bats, potentially affecting fitness. Because frugivorous bats avoid open areas, putatively in response to increased predation risk, during times of greater illumination (e.g., Crespo et al., 1972; Morrison, 1978; Fenton et al., 1994; Kalko and Handley, 2001; Weinbeer and Meyer, 2006; Presley et al., 2009a), gap formation in forests may reduce time available for foraging and may make it difficult for bats to meet daily dietary requirements, especially during times of stress. The combination of loss of roosting habitat, increased risk of predation, and reduced time for foraging may have cumulative detrimental effects on bat populations that require long-term monitoring to detect. Indeed, this study was conducted 2–4 years post-harvest and documents only short-term responses to RIL. Long-term population monitoring of demographics (e.g., turnover, immigration) and fitness indicators (e.g., physiological status, stress hormones; Henry et al., 2007) will provide a more comprehensive assessment of responses of the biota to RIL and of the viability of RIL as a sustainable option for forest management.

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