

Short-Term Responses of Birds to Forest Gaps and Understory: An Assessment of Reduced-Impact Logging in a Lowland Amazon Forest¹

Joseph M. Wunderle, Jr.²

International Institute of Tropical Forestry, USDA Forest Service, Sabana Field Research Station, HC 02 Box 6205, Luquillo, Puerto Rico 00773, U.S.A.

Luiza Magalli Pinto Henriques

Museu Paraense Emilio Goeldi, C.P. 3999, 66017-970, Belem, Pará, Brazil

and

Michael R. Willig

Ecology Program, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409-3131, U.S.A.

ABSTRACT

We studied physiognomy-specific (i.e., gaps vs. understory) responses of birds to low harvest (18.7 m³/ha), reduced-impact logging by comparing 3500 mist net captures in control and cut blocks of an Amazonian *terra firme* forest in Brazil at 20–42 mo postharvest. Species richness did not differ significantly between control (92 species) and cut (85) forest based on rarefaction to 1200 captures. Fifty-six percent of all species were shared between control and cut forest, compared to the 64 percent shared between control blocks. Higher captures of nectarivores and frugivores in cut forest likely occurred as a consequence of postharvest resource blooms. Higher captures of some insectivores in cut as compared to control forest were unexpected, attributable to increased wandering or shifts from association with midstory to understory as a consequence of habitat alteration. Logging influenced capture rates for 21 species, either consistently, or via positive interaction with physiognomy or time (13 species higher in cut forest and 8 species higher in control forest). Cut understory sites had lower diversity (H') and scaled dominance than understory and gap sites in control forest. Temporal changes in captures may have resulted from successional dynamics in cut forest: two guilds and three species increased in abundance. Increases in abundances of guilds and particular species were more prevalent in control than in cut forest, suggesting that logging displaced birds to control forest. In general, the effects of logging were relatively minor; low harvest rates and reduced-impact methods may help to retain aspects of avian biodiversity in Amazon forest understories.

RESUMO

Nós estudamos as respostas fisionômico-específicas (ou seja, clareiras vs. sub-bosque) das aves à exploração madeireira de impacto-reduzido (18.7 m³/ha) comparando 3,500 capturas com redes em parcelas controle e exploradas de uma floresta de terra firme na Amazônia Brasileira entre 20 a 42 meses após a exploração. A riqueza de espécies não diferiu significativamente entre a floresta controle (92 espécies) e a floresta explorada (85), com base na rarefação de 1,200 capturas. Cinquenta e seis por cento das espécies eram compartilhadas entre a floresta controle e a floresta explorada, enquanto que 64% das espécies eram compartilhadas entre as parcelas controle. A maior incidência de aves nectarívoras e frugívoras na floresta explorada provavelmente ocorreu em consequência da proliferação temporária de recursos após a exploração. As maiores taxas de captura de alguns insetívoros em floresta explorada em relação à floresta controle foram inesperadas, e são atribuídas ao incremento da mobilidade das aves ou a um deslocamento de espécies associadas ao médio-bosque para o sub-bosque em resposta às alterações de hábitat. A exploração madeireira influenciou as razões de captura de 21 espécies, tanto diretamente como através da interação positiva com a fisionomia ou com o tempo (13 espécies foram mais comuns na área explorada e 8 espécies foram mais comuns na área controle). Os sítios em sub-bosque explorado apresentaram diversidade (H') e dominância menores do que os sítios em sub-bosque e clareira da floresta controle. Mudanças temporais nas taxas de captura podem ter resultado da dinâmica de sucessão da floresta explorada: duas guildas e três espécies incrementaram em abundância. Incrementos na abundância das guildas e de algumas espécies em particular foram mais frequentes na floresta controle do que na floresta explorada, sugerindo que a exploração madeireira deslocou aves para dentro da floresta controle. Em geral, os efeitos da exploração madeireira foram relativamente pequenos; exploração de baixa intensidade e métodos de baixo impacto podem ajudar a manter aspectos importantes da diversidade avifaunística do sub-bosque da floresta Amazônica.

Key words: Amazonia; Brazil; disturbance; forest birds; forest management; logging effects; reduced-impact logging; treefall gaps; understory birds.

TREEFALL GAPS PLAY AN IMPORTANT ROLE IN DETERMINING THE distribution, abundance, and diversity of forest organisms (e.g., Pickett 1976, Brokaw 1982a, 1985a) by contributing to structural heterogeneity. When a tree falls and opens the forest canopy, it initiates a dynamic succession: a continuum of states differing in structure and composition, beginning with a gap phase, character-

ized by little or no canopy, and ending in a mature phase with closed canopy (Whitmore 1978, Brokaw 1985a, b). The gap phase represents a period of rapid plant growth and colonization (e.g., Burton & Mueller-Dombois 1984, Denslow *et al.* 1990) as well as increased flower and fruit production (Smith 1987, Levey 1988a, Smith *et al.* 1992). These conditions often contrast sharply with those in the surrounding forest understory with respect to microclimate (Hallé *et al.* 1978, Chazdon & Fetcher 1984), detritus (Whitmore 1978), productivity (Hallé *et al.* 1978), and plant species composition (Brokaw

¹ Received 23 September 2004; revision accepted 8 June 2005.

² Corresponding author; e-mail: Wunderle@coqui.net

1982a, 1985a). Given the gap–understory contrast in physical and biological characteristics, it is not surprising that a variety of animals, such as birds, distinguish between the two habitats (*e.g.*, Schemske & Brokaw 1981, Levey 1988a). Yet the gap–understory contrast is relatively short-lived, as canopy closure for a treefall gap of moderate size occurs in 4–6 yr (van der Meer & Bongers 1996, Fraver *et al.* 1998). However, gaps occur with sufficient frequency in tropical forests (approx. 1% of forest area per year; Denslow 1987, Hartshorn 1990) that 4.3–7.3 percent of their area may consist of gaps (*e.g.*, Lang & Knight 1983, Yavitt *et al.* 1995). Thus, treefall gaps produce a shifting mosaic of habitat patches in tropical forests that enhance forest diversity (Brokaw 1985a, b).

Some selectively logged gaps may resemble natural treefall gaps, at least at very low logging intensities (Whitman *et al.* 1998). Nonetheless, the effects of selective logging are superimposed on those of natural disturbances. Consequently, as logging intensifies, its effects diverge from those produced by natural treefalls (Fimbel *et al.* 2001a). Not only does gap density increase in selectively logged forests, but gaps produced by logging are often larger than natural gaps (Riera & Alexandre 1988, Putz *et al.* 2001). Moreover, clearing for roads, skidder trails, and log storage further increases canopy loss in cut forest (*e.g.*, Uhl & Guimarães 1989). As a result, more light reaches the forest floor of logged forests, producing hotter and drier conditions, and eventually a dense thicket of understory vegetation, as plants respond to increased light. This alteration of forest microclimate and vegetation has important consequences for the biota and may result in the reduction of avian diversity in logged forests (Johns 1991, Thiollay 1992, Mason 1996). Understory species disappear in some selectively logged forests (Mason 1996), and some gap specialists may disappear (Thiollay 1992), suggesting that birds respond to subtle differences between natural and artificial gaps.

Avian responses to vegetative changes following selective logging depend on extraction rate and time after harvest (Guilherme & Cintra 2001, Mason & Thiollay 2001). In addition, mode and tempo of forest recovery differ in a site-specific manner (Chapman & Fimbel 2001) with a region's natural disturbance regime, potentially accounting for differences in avian responses to logging (Whitman *et al.* 1998). In general, as logging activities open the canopy, canopy-dwelling bird abundance and species richness in gaps increase (Mason 1996), whereas abundance of forest understory species, especially insectivores, decreases (Johns 1991, Thiollay 1992, Mason 1996). As the most prevalent group of understory species in Neotropical forests, insectivores, particularly those that join mixed-species foraging flocks or follow army ants, may be especially susceptible to forest disturbances (Mason & Thiollay 2001). In contrast, some gap species may increase, especially nectarivores and frugivores that benefit from increased flowering and fruiting in logged gaps (Mason 1996). Although general patterns of avian response to selective logging of Neotropical forests are beginning to emerge, details of the responses at the guild- and species-level are known poorly, as are the factors that contribute to differences among forests in avian responses to logging (Mason & Thiollay 2001). Finally, little is known of the time scale over which various avian guilds and species respond to selective logging, and how responses differ between gap and understory physiognomies.

In this study, we compared the response of birds to reduced-impact selective logging in gaps and forest understory of an Amazonian *terra firme* forest over a 22-mo period. This approach facilitated addressing four interrelated questions: (1) what species and guilds are affected by selective logging, and does the effect correspond to use of natural gaps and forest understory by species or guilds?, (2) do assemblages of birds in cut gaps and understory differ in composition, diversity, evenness, dominance, rarity, or species richness from those in the corresponding habitat in natural forest?, (3) in what other strata or habitats are birds in cut gap and understory found, and how do they differ from the strata or habitats in which birds of natural gap and understory occur?, and (4) do bird distributions in cut and natural gaps as well as in undisturbed understory change over a short time interval (*ca* 2 yr)? This research differs from previous studies by comparing bird populations in gaps and understory of lightly logged forest with those in nearby natural gaps and understory, while also characterizing the short-term responses after logging during the period when plant growth is most rapid.

METHODS

STUDY SITE.—Research was conducted in the Tapajós National Forest (henceforth Tapajós Forest), a 560,000 ha area managed by the Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis. The Tapajós Forest is located on the east bank of the lower Tapajós River near the mouth of the Tapajós River in the western part of the state of Pará, Brazil (see map in Henriques *et al.* 2003). The climate, soils, and vegetation are described by Silva *et al.* (1985), Daly and Prance (1989), Silva (1989), and Parrotta *et al.* (1995). Average annual rainfall is 1920 mm, with the heaviest rains in December to May and a short dry season (August–October) during which monthly precipitation is less than 60 mm. Average monthly temperatures vary from 24.3°C to 25.8°C.

Our study was conducted in sites accessible from km 83 on the Santarém–Cuiabá Highway (BR 163), where *terra firme* or dry land forest covers gently undulating upland terrain and is characterized by emergent tree species such as *Bertholletia excelsa*, *Couratari* spp., *Dinizia excelsa*, *Hymenaea courbaril*, *Manilkara huberi*, *Parkia* spp., *Pithecellobium* spp., and *Tabebuia serratiolia* (Silva *et al.* 1985). Heights of forest canopy range from 30 to 40 m, with occasional emergents reaching approximately 50 m. Palms are rare and the understory is relatively open with frequent occurrence of the shrubs *Rinorea flavescens*, *R. guianensis*, and *Duguetia echinophora* (Silva 1989).

At km 83, a system of roads and trails provides access to the forest. Here, our study occurred on a 5000 ha grid (3°21'21'S, 54°56'58'W) established for demonstration forestry. Our netting was conducted in two adjacent 100 ha control blocks (C-2 and C-3) and two nonadjacent 100 ha harvest or cut blocks (T-18 and T-2). Each control block was bounded by undisturbed forest on three sides, and a block in which selective logging (at approximately 40 m³/ha) occurred on a fourth side (north). A small stream bisected both the control blocks. All net sites in the control blocks were situated at least 30 m from the stream and from the border adjoining

the selectively logged block. The two cut blocks were each bounded by undisturbed forest on one side and selectively logged forest (40 m³/ha) on the remaining three sides, where timber harvest continued throughout our study. The two cut blocks were separated by 2.5 km, and each was separated from the control blocks by 1–2.3 km. Subsistence hunting by neighboring settlers, primarily for monkeys, tapirs, and peccaries, occurred throughout all blocks, both before and after timber harvest. No evidence suggested that hunting pressure differed among blocks or between treatments, or changed over time.

Timber harvest on the two cut blocks was completed in December 1997, 20 mo before the initiation of our study. The two cut blocks were harvested at low intensity to demonstrate reduced-impact logging (J. Zweedie, pers. comm.) with minimal forest damage due to felling, skidding, or log processing (see Fimbel *et al.* 2001b for reduced-impact guidelines). Timber on block T-2 was harvested at a rate of 18.70 m³/ha for a total 1870.490 m³ (geometric volume) or 394 trees removed on a 100 ha block. Timber on T-18 was harvested at a rate of 18.73 m³/ha for a total of 1872.708 m³ or 379 trees removed on a 100 ha block (1200 × 800 m).

BIRD SAMPLING.—Mist nets were used to sample birds because they allow similar and simultaneous sampling of numerous sites and provide an indication of avian activity at a site (Karr 1981) while avoiding the difficulties of detecting and identifying birds at a distance by sight or sound. Also, observers may differ in field identification abilities and may not detect species that rarely vocalize or are difficult to see. The use of mist nets circumvents some of these problems and facilitates comparisons among studies in different forests by different observers. Furthermore, the method focuses on understory birds, the avian component most likely to be affected by logging activities (reviewed by Mason & Thiollay 2001); however, mist nets do not obtain a random sample of bird species (see Karr 1981, Bierregaard 1990a, b, Remsen & Good 1996), and consequently recommendations are to only compare capture rates within a species or group of behaviorally similar species (Karr 1981, Bierregaard 1990a, b). We previously discussed biases associated with net samples in the Tapajós Forest (Henriques *et al.* 2003) and interpret results in relation to these biases and augmented by knowledge of the avifauna that has been obtained by field observations over a 9-yr period.

Two different habitat types were selected for net placement based on physiognomies: treefall gaps and intact forest understory (henceforth gap and understory, respectively). Each physiognomy was sampled in control and cut blocks, and was designated with the prefix control or cut, respectively, to indicate the block type in which they were situated. A gap is defined as “a vertical hole in the forest extending through the canopy to within 2 m of the forest floor” (Brokaw 1982b). All of our gaps resulted from treefalls due either to natural treefalls in control blocks or logging in cut blocks. Understory sites were established under continuous forest canopy and initially were separated from the nearest gap by at least 25 m. Two or more mist nets (various combinations of 6 or 12 m length nets) were set at each net site to provide a total length of 24 m. Nets were arranged in various configurations (*e.g.*, at right

angles, T-shaped, L-shaped, or straight line) to fit within gaps; nets in understory sites were set to match these configurations. All nets were set to 2.6 m height and contained four shelves and 35 mm mesh.

Sampling occurred in four 100-ha blocks: two control and two cut. Each block was subdivided into four quadrats in which net sites were stratified to insure adequate dispersion of sampling effort throughout a block. Within a quadrat, net sites were paired (gap and understory) so that within a pair, each site was closer to each other than to other sites, and each site was at least 30 m from the nearest site in a different pair. Consequently, 16 gap and 16 understory net sites were established per control block. In contrast, two gap and two understory net sites were established in each quadrat in the cut blocks. Thus, a total of eight net sites per physiognomy (gap, understory) were sampled per cut block.

Birds were sampled during eight 2-d mist netting sessions during eight periods: 19 August to 4 September 1999; 25 November to 16 December 1999; 21 March to 7 April 2000; 12–28 June 2000; 7–26 September 2000; 24 November to 9 December 2000; 11–26 May 2001; and 11–26 June 2001. Although intervals between netting sessions were not equal (mean = 94 d ± 42 SD, range 30–168 d), no relationship was found between capture rates and interval between netting sessions ($r = 0.29$, $N = 7$, $P = 0.54$), suggesting that net avoidance did not reduce capture rates (regardless, empirical capture rates actually increased during this study).

During a session, nets at each site were opened in half of a block for two consecutive days (0600–1400 h, day 1; 0600–1200 h, day 2) and operated simultaneously before moving to the other sites in the other half of a block. Thus, a session involved 16 d to sample the four blocks, although netting days were not always consecutive. Open mist nets were inspected at least every hour, and all captured birds, with the exception of hummingbirds, were provisioned with a numbered aluminum ring or colored plastic ring before release. We clipped a tail or wing feather of hummingbirds before release for identification of recaptures during a netting session. All birds were identified to species. During a session, we recorded each new capture as well as recaptures of previously ringed birds. Capture rates from gaps are interpreted as minimum values because gap nets were exposed to direct sunlight for much of the day, thereby reducing capture effectiveness relative to shaded understory nets.

HABITAT MEASUREMENTS.—Foliage height profiles were used to quantify vegetation structure at the end of the study (June 2001), using a modification of the methods of Schemske & Brokaw (1981), as described by Wunderle *et al.* (2005). Profiles were obtained by establishing two parallel transects, one on each side of a net, situated 2 m from the net and equal in length to the sampled net. A 3-m pole (2.0 cm diameter) marked at 0.5-m intervals was placed vertically at each sample point (13 per transect), with the presence or absence of foliage touching the pole recorded for each height interval. For height intervals above 3 m, we recorded the presence or absence of foliage along the sight line of the pole, and estimated height intervals. Height intervals above the ground (in meters) were: 0–0.5, 0.5–1, 1–2, 2–3, 3–4, 4–6, 6–8, 8–10, 10–12, 12–15, 15–20, and >20. Percent cover was estimated for each height interval at a site

based on the number of points sampled along the transects. Profiles were obtained for each of the 88 sites.

Canopy cover was obtained with a spherical densiometer held 1 m from the ground at each site. Measurements of canopy cover were made in the four cardinal directions in the middle of each net, and an average percent cover calculated per site. Canopy cover was measured during two periods: 10–22 June 2000 and 10–26 June 2001. Estimation of gap area (10–26 June 2001) was based on the formula for a rectangle ($L \times W$). We measured the maximum length (L) of the gap, and the longest right-angle distance (W) across the opening (width).

ANALYSIS.—Capture rates are an index of abundance and are presented as captures per 1000 net hours, where net hour refers to 12 m of net open for 1 h. We excluded all recaptures of individuals during the same 2-d session, but included recaptures between sessions. Analysis of capture rates involved a repeated measures (time, eight sessions; physiognomy, gap vs. understory; management, control vs. cut forest) ANOVA in which block was nested in management and physiognomy (2) with time (8) as a repeated measure. The ANOVAs were conducted for capture rate per site for particular species, as well as for diet guilds based on an established ecological classification (Bierregaard 1990b, Henriques *et al.* 2003). Generally, P values without reference to a statistical test, pertain to results of the repeated measures ANOVA. Although considerable controversy surrounds the practice (Hurlbert 2003, Moran 2003), the Bonferroni sequential adjustment (Rice 1989) often is applied to individual P values for a suite of statistical analyses to prevent inflation of experiment-wise error rate. As such, we apply the adjustment in circumstances where a number of comparable analyses were executed for multiple species or for multiple guilds, but do so for comparative purposes only. We consider it more important to identify potential effects of management than to underestimate the effects of selective logging on the avifauna.

Guild classification included both a simple and complex categorization of species (Bierregaard 1990b, Henriques *et al.* 2003). Simple guilds included nectarivores, frugivores, and insectivores. Determination of complex guilds involved a subdivision of some of the simple guilds, and included army ant-followers, solitary insectivores, solitary insectivore-frugivores, mixed-species flock insectivores, mixed-species flock insectivore-frugivores, solitary frugivores, solitary frugivore-insectivores, and mixed-species flock frugivore-insectivores. The term solitary can refer to species in which pairs forage together, but do not join flocks.

In general, we estimated means and standard errors for each of a number of diversity indices using a bootstrap approach (Manly 1991) written in Matlab (Mathworks 1995). Diversity measures included Camargo's (1993) index of evenness, Shannon's index of diversity (Pielou 1975), Berger–Parker index of dominance (Berger & Parker 1970), species richness (*i.e.*, cumulative number of unique species), and rarity (*i.e.*, the number of species with a relative frequency of capture less than the inverse of species richness; Camargo 1993, Gaston 1994). To ensure that large values of all indices represent high levels of biodiversity, we scaled the Berger–Parker index by calculating its inverse and denoting it as scaled dominance (Stevens

& Willig 2000). Simulations for estimating parameters of biodiversity for gap and forest were conducted by randomly selecting N individuals, with replacement, from a universe defined by the corresponding species abundance distribution for gap and understory, separately. N was equal to the total number of individuals in net samples from the physiognomy with the lowest number of total captures (*i.e.*, 537 captures in cut understory), and each of the four indices of biodiversity was estimated for the four physiognomies based on these data. This process was iterated 1000 times, followed by the calculation of the mean and standard error for each index in each physiognomy. For each physiognomy, separately and in combination, we separately constructed species accumulation curves (richness as a function of number of individuals) for control and for cut forest based on empirical sequences of captures. To facilitate statistical comparisons of species accumulation curves, we conducted bootstrapped simulations based on 1000 iterations for regular increments of captures, and estimated means and standard errors based on simulation results. We used the Jaccard's coefficient of similarity (S) in which $S = C/(A + B - C)$, where C is the number of species shared by cut and control forests, and A and B are the total number of species in cut and control forests, respectively (Krebs 1989).

Statistical tests follow Sokal & Rohlf (1995) using SPSS (SPSS 1990). Paired t -tests were used to evaluate significance of the difference in mean foliage density per height class between control and cut forests. We evaluated the significance of the difference in the coefficient of variation of foliage density per height class between the two forest types using a Wilcoxon signed rank test. A Kolmogorov–Smirnov two-sample test compared rank abundance distributions between physiognomies within each forest type. A χ^2 contingency test assessed differences in species or guild composition between blocks and physiognomies. Spearman rank correlation (r) evaluated the association of capture rates (all species combined and individual species) with time.

TERMS.—Based on Wunderle *et al.* (2005), we used the terms “gap specialist” or “understory specialist” to designate species with significantly more captures in a particular habitat in the control blocks. The habitat classification system for birds of the Tapajós Forest follows that of Cohn-Haft *et al.* (1997) and Henriques *et al.* (2003). Terrestrial birds are those that primarily forage on the ground. Understory birds are species that forage mostly within 5 m of the ground in shrubs and small trees in closed canopy forest. Midstory birds generally forage above 5 m, but below the canopy.

RESULTS

VEGETATION.—The vertical distribution of vegetation at the end of the study differed considerably between gap and understory sites in control and cut forests (Fig. 1). In both forest types, most gap foliage occurred within 6 m of the ground, in contrast to understory sites where most foliage occurred above 6 m. Overall, foliage density was greater in cut than in control forests for 11 of 12 foliage height classes in gaps (paired t -test, $t = 4.00$, $df = 11$, $P = 0.002$) and

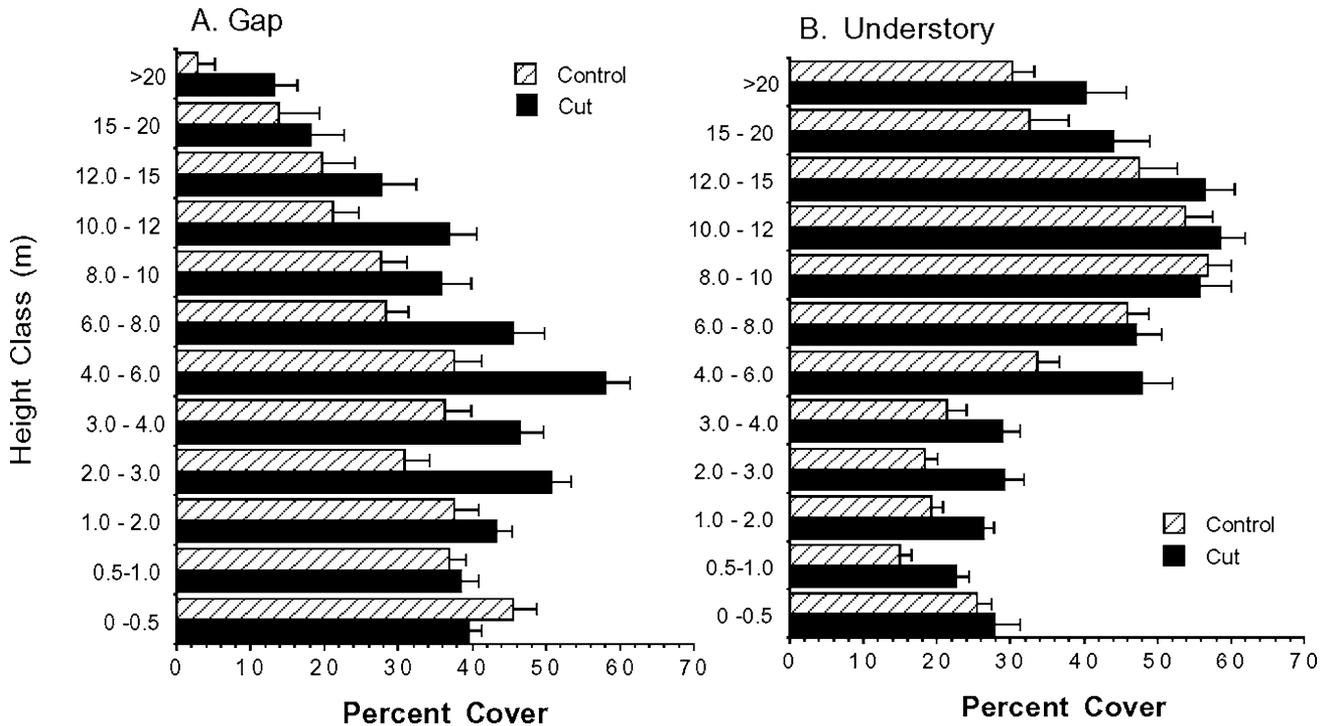


FIGURE 1. Foliage height profiles for 32 control gap and 16 cut gap sites (a) and 32 control understory and 16 cut understory sites (b) in *terra firme* forest in the Tapajós Forest, Brazil. Mean \pm SE are for percent cover in each height class. Foliage profiles were measured at the end of the study (June 2001), which occurred 42 mo after timber was harvested at 18 m³/ha with reduced-impact methods in the cut forest.

in understory sites (paired *t*-test, $t = 5.14$, $df = 11$, $P < 0.001$). Although foliage density was greater in cut than in control gaps, variation in foliage density among the 12 foliage height classes in gaps was significantly (Wilcoxon signed rank test, $Z = 2.98$, $P = 0.003$) greater in control (median coefficient of variation = 42.6) than in cut gaps (median coefficient of variation = 32.7).

The denser canopy above understory than above gap sites in control and cut forests was corroborated by the spherical densiometer readings (Table 1). A higher percentage of canopy was open above gaps than above understory. However, within a physiognomy (gap or understory), little difference in percent openness was found between control and cut forest, especially for understory sites. Canopy closure between June 2000 and June 2001 generally was greater in

gaps than understory in both control and cut forests. Mean gap areas (m²) did not differ significantly ($t = 0.73$, $df = 46$, $P = 0.47$) between control (mean = 286 \pm 37 SE, range 65–760) and cut forest (mean = 219 \pm 55 SE, range 35–999).

BIRD COMMUNITY RESPONSE.—In 21,504 net hours during 8 time periods spanning approximately 2 yr, we recorded 3500 captures representing 134 species in 27 families (Appendix). Assuming an infinite number of samples for the combined gap and understory physiognomies, the bootstrap procedure (sampling with replacement) predicted a species richness of 102 species and 86 species in control ($N = 2216$ captures) and cut ($N = 1284$ captures) forests, respectively (Fig. 2). However, species richness did not differ significantly (*i.e.*, overlapping 95% confidence intervals) between control (92 species) and cut (85) forest based on rarefaction to 1200 captures. Although species accumulation in gap alone and in combined gap and understory physiognomies of the control forest were indistinguishable, species accumulation in gap alone lagged behind that of combined physiognomies for cut forest.

A statistical assessment (*i.e.*, bootstrapped estimates for samples [random sampling with replacement] that have been rarefied to $N = 537$) of biodiversity for each combination of management and physiognomy documented that none of the five indexes differed among control understory, control gap, and cut gap scenarios. All comparisons that were significant involved cut understory, which was different from (1) control gap for richness, (2) all other treatment

Table 1. Mean (\pm SE) canopy openness (%) in gap and understory of control and cut *terra firme* forest in June 2000 and June 2001 in the Tapajós Forest, Brazil. Cut forest was selectively cut using reduced-impact methods at a harvest level of 18 m³/ha completed in December 1997.

Forest type	Gap		Understory	
	June 2000	June 2001	June 2000	June 2001
Control	14.45 \pm 0.77	12.43 \pm 0.75	6.25 \pm 0.24	5.32 \pm 0.17
Cut	15.03 \pm 1.27	10.82 \pm 0.96	5.81 \pm 0.32	5.60 \pm 0.30

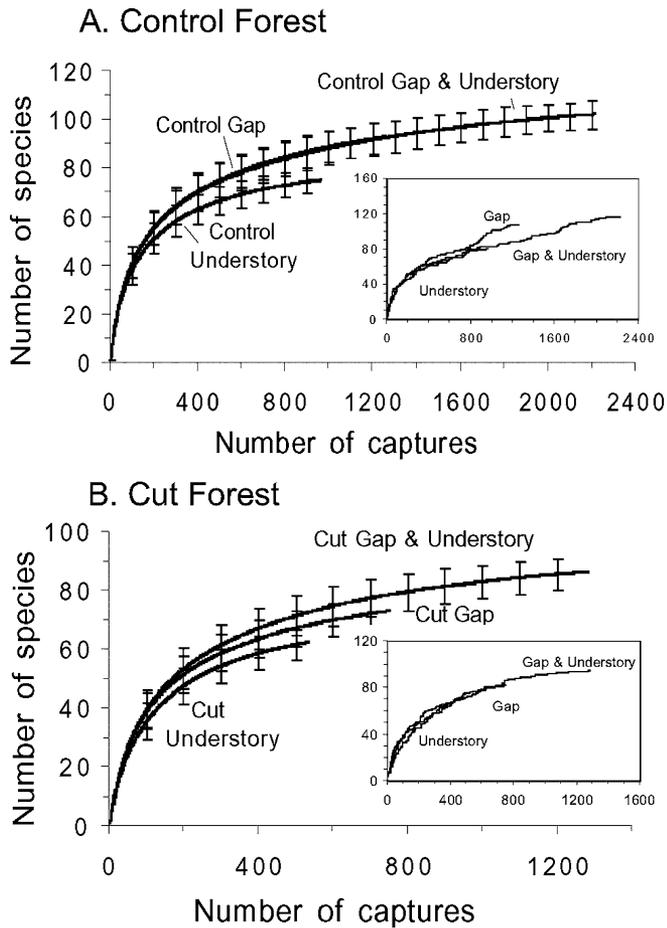


FIGURE 2. Species accumulation curves based on a bootstrap procedure for gap and understory physiognomies in control (a) and cut (b) *terra firme* forest in Tapajos Forest, Brazil. Inserts within each panel represent empirical species accumulation curves based on the actual order of captured specimens in the field. The study was initiated 20 mo after timber had been harvested in cut forest at a level of 18 m³/ha with reduced-impact methods.

combinations for diversity, and (3) control gap and control understory for scaled dominance (Fig. 3).

The proportion of species shared between gaps and understories were nearly identical in control forest (68%) and cut forest (63%). The percentage of shared species in gap and understories within a forest type was approximately equivalent or slightly higher than that between the same physiognomy in different forest types. For example, 58 percent of the species were shared between cut and control understory, whereas 54 percent of the species in gaps were shared between forest types. Disregarding physiognomy, 56 percent of the species were shared between control and cut forest, a value only slightly lower than the 64 percent of species shared between the control blocks or between cut blocks (58%). Similarity between control and cut forest increased slightly (61% species shared), when the analysis was restricted to species with more than two captures.

Gap and understory assemblages differed in rank abundance distributions (Kolmogorov–Smirnov test, $Z = 1.70$; $N = 108$, 108;

$P = 0.006$) only within control forest. This reflects the greater species diversity and rarity in control gaps than in control understories. Timber harvest did not significantly affect the rank abundance distributions of cut forest relative to control forest, although the difference was suggestive (Kolmogorov–Smirnov test, $Z = 1.26$; $N = 114$, 114; $P = 0.08$). Thus, the marked difference in rank abundance distributions between gap and understory in control forest was not apparent in cut forest.

Proportional representation of simple diet guilds (*i.e.*, nectarivores, frugivores, and insectivores) differed between gap and understory only within the control forest. A block effect on diet guild composition characterized control gaps ($\chi^2 = 16.74$, $df = 3$, $P < 0.001$) in which captures of nectarivores (10.4 vs. 6.1%) and frugivores (20.0 vs. 15.0%) were higher, and captures of insectivores (69.4 vs. 78.9%) were lower in block 2 as compared to block 3. The proportional representation of diet guilds differed significantly between control gap and understory ($\chi^2 = 15.48$, $df = 3$, $P = 0.001$). Control gap captures ($N = 1256$) differed from understory gap captures ($N = 960$) in having higher representation of frugivores (17.6 vs. 14.4%) and nectarivores (8.3 vs. 5.0%), but lower representation of insectivores (74.1 vs. 80.6%). Habitat differences in the relative abundance of diet guilds did not characterize cut forest ($P > 0.10$).

SPECIES AND GUILD-SPECIFIC RESPONSES TO MANAGEMENT.—Of the 134 species captured in both forest types, 48 percent had higher capture rates in control forest and 50 percent had higher capture rates in cut forest; most differences were not significant (Appendix). Significant and consistent management effects characterized only four species (Table 2). However, management affected 17 species through an interaction with physiognomy (P), time (T), or physiognomy and time (Table 2). For 12 species, the response to management was dependent on physiognomy, with the difference between gap or forest understory accentuated in one forest type ($M \times P$, positive synergism). For five species, the magnitude of the preference for a forest type (control vs. cut) varied over time, so that during a netting session, captures in one forest type were always greater or equal to those in the other forest type ($M \times T$ interaction, positive synergism). Three species showed both significant $M \times P$ and $M \times T$ interactions. For three species, the response to management was dependent on physiognomy and time ($M \times P \times T$). Thus forest management affected capture rates for 21 species, either directly or via positive interactions with physiognomy or time. Of the 21 species for which an effect of management was detected, 13 species were most abundant in cut forest and 8 species were most abundant in control forest.

At the simple guild-level, forest management affected captures of each guild, although the response to management depended on physiognomy, time, or both (Table 3, Fig. 4). Captures of simple guilds showed significant positive $M \times P$ interactions (*i.e.*, positive synergism), but differed as to the forest type in which capture differences between gap and understory were accentuated most. In addition, captures of frugivores and insectivores showed significant management effects that depended on time (*e.g.*, positive

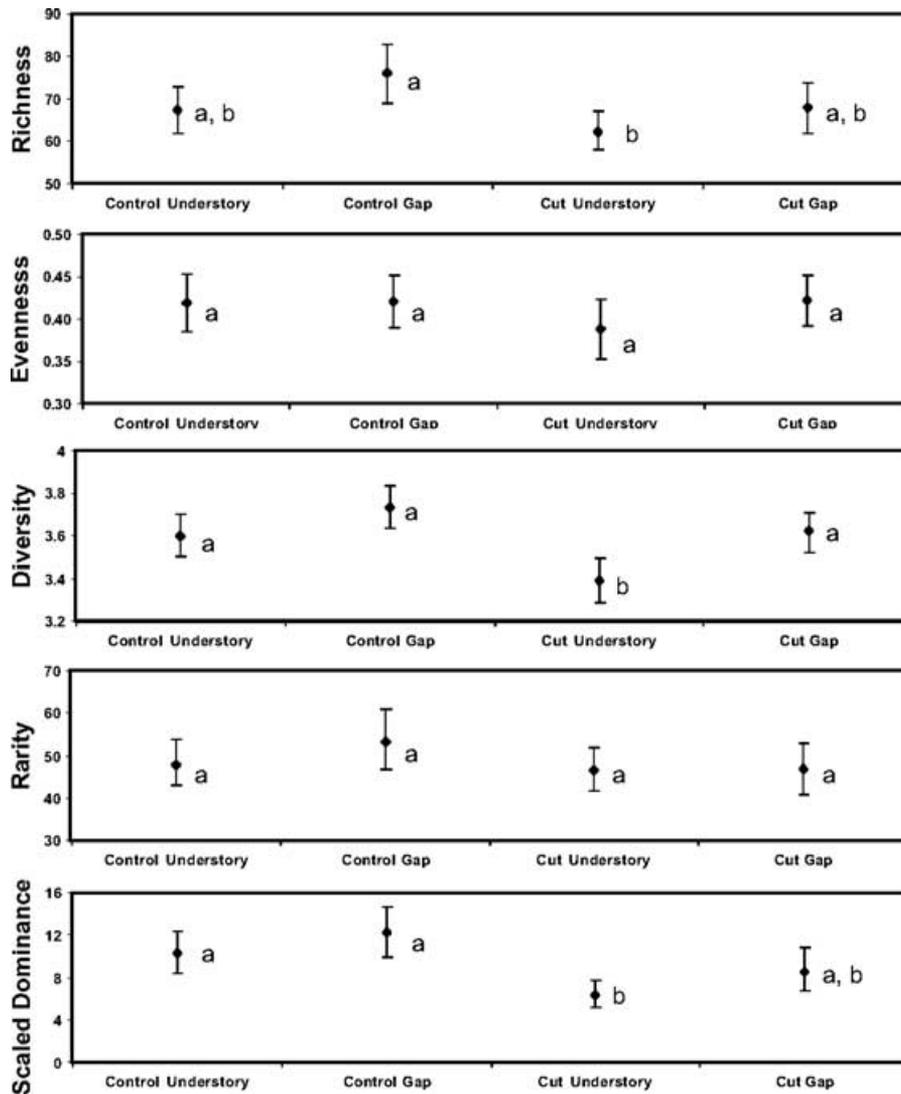


FIGURE 3. Bootstrap estimates after rarefaction ($N = 537$) of bird species richness, Camargo's index of diversity, Schannon's index of diversity, rarity, and scaled dominance from control understory, control gap, cut understory, and cut gap in *terra firme* forest of the Tapajós Forest, Brazil. Error bars represent 95 percent confidence intervals of the simulated values. Simulated values with overlapping confidence intervals are indicated by shared letters.

synergisms). Captures of each of the simple guilds were higher in cut than in control forest.

THE EFFECT OF PHYSIOGNOMY ON MANAGEMENT RESPONSE.—The response to management depended on physiognomy for total captures, species diversity, captures of most guilds, and for captures of 12 species (Tables 2 and 3, Fig. 4). In all but one instance, taxa that were captured more commonly in gaps or understories within a forest type consistently showed the same physiognomic bias in the alternative forest type. Nonetheless, the magnitude of the difference differed between control and cut forest (*i.e.*, positive synergism). Only in the solitary insectivore-frugivore guild did the physiognomic bias of captures differ between control (understory bias) and cut forest (gap bias). This negative synergism resulted from an interplay of abundances of constituent species (*i.e.*, *Cyphorhinus aradus*,

Arremon taciturnus) which showed gap preferences that differed with forest type.

The simple guilds showed gap bias for captures within each forest type, as well as did some of the constituent complex guilds (*i.e.*, solitary frugivores and mixed-species flock insectivores). Of the species that evinced a significant $M \times P$ interaction, a gap bias characterized eight species and an understory bias characterized three species. Gap biases were evident in species captured most commonly in cut forest (eight species in gap vs. one species in understory in cut forest compared to two species in gap vs. one species in understory in control forest). Although a gap bias was most apparent in cut forest, the difference between gap and understory within a forest type was accentuated in the control relative to cut forest for seven species, as compared to five species in which differences between the two physiognomies were accentuated in cut forest.

Table 2. Mean capture rate per 1000 net hours for species that exhibit a significant response to reduced-impact logging in terra firme forest in the Tapajós Forest, Brazil. The effects of management were assessed through a repeated measures ANOVA with management and physiognomy as categorical factors, and time as a repeated measure within combinations of management and physiognomy. M refers to management (control vs. cut forest); P refers to physiognomy (gap vs. understory); and T refers to time (eight netting sessions from 19 August 1999 to 26 June 2001). All P values for interactions indicate positive interactions. Levels of significance after Bonferroni sequential adjustment (P') are indicated by superscripts associated with P values ($^@0.10 \geq P' > 0.05$; $*0.05 \geq P' > 0.01$; $**0.01 \geq P' > 0.001$; $***0.001 \geq P'$). The study was initiated 22 months after timber had been harvested in cut forest at a level of 18 m^3/ha using reduced-impact methods.

	Mean capture rate				Overall and p -adjusted significance level						
	Control		Cut		M	P	T	$M \times P$	$M \times T$	$P \times T$	$M \times P \times T$
	Gap	Understory	Gap	Understory							
Control forest species											
<i>Cyphorhinus aradus</i> (IF) ^a	3.49	1.81	3.35	0.56				0.007			
<i>Dendrocincla merula</i> (AA)	7.95	12.28	2.51	6.42				0.005			
<i>Myrmotherula longipennis</i> (MFI)	12.97	8.79	6.14	5.86					0.020		
<i>Phaethornis bourcieri</i> (N)	1.81	1.53	0.84	0.23	0.030						
<i>Pipra iris</i> (F)	10.88	6.00	8.65	3.91			0.008	0.006			
<i>Platyrynchus coronatus</i> (I)	1.67	4.46	0	0	0.001*						
<i>Schiffornis turdinus</i> (F)	2.09	2.22	0	0.28	0.005						
<i>Xiporhynchus spixii</i> (MFI)	2.65	3.77	1.40	3.91	0.002 [@]						
Cut forest species											
<i>Arremon taciturnus</i> (IF)	0.55	0.42	4.74	0.56							<0.001**
<i>Glyphorynchus spurrus</i> (MFI)	11.86	11.44	16.46	23.44					0.001*		
<i>Hylophylax poecilonota</i> (I)	5.71	9.35	5.30	11.44			0.040	0.005			
<i>Hypocnemis cantator</i> (I)	3.07	0.56	6.98	0.56				<0.001**			
<i>Myrmotherula leucophthalma</i> (MFI)	9.38	2.63	12.28	2.51			0.001*	<0.001***			
<i>Myrmotherula menetriesii</i> (MFI)	3.08	0.40	3.07	0.84				0.017	0.009	0.035	
<i>Phaethornis longuemareus</i> (N)	3.97	0.67	3.91	3.07			0.014	0.024			
<i>Phlegopsis nigromaculata</i> (AA)	2.63	0.98	8.37	2.23							0.013
<i>Pipra rubrocapilla</i> (F)	12.70	4.74	24.5	17.30				0.001*	<0.001***		
<i>Thamnomanes caesi</i> (MFI)	6.07	3.35	9.77	7.53				0.048	<0.001**		
<i>Thamnophilus aethiops</i> (MFI)	1.40	0.56	4.19	2.23				0.030			
<i>Thamnophilus schistaceus</i> (MFI)	2.93	0.28	5.58	1.67				<0.001**			
<i>Xenops minutus</i> (MFI)	2.46	1.74	6.14	1.40							0.044

^aCode designates a diet guild based on classification in Henriques *et al.* (2003), AA = ant-follower; F = solitary frugivore; I = solitary insectivore; IF = solitary insectivore-frugivore; MFI = mixed-species flock insectivore; N = nectarivore.

TEMPORAL RESPONSES.—The response to management depended on time for one simple guild (frugivores), three complex guilds (solitary frugivores, ant-followers, mixed-species flock insectivores), and five species (Tables 2 and 3, Figs. 4–6). For these guilds and species, no significant negative correlation between number of captures and time characterized either forest type (Table 4). However, significant positive correlations between number of captures and time occurred in control forest for three simple guilds (nectarivores, frugivores, insectivores), one complex guild (solitary frugivores), and four species (Table 4). In addition, captures of mixed-species flock insectivores showed a suggestive ($P = 0.07$) positive correlation with time in control forest (Table 4, Fig. 7). In contrast, significant positive correlations of captures with time in cut forest occurred in ant-followers and a constituent species (*Rhegmatorhina*

gymnops), although the $M \times T$ interaction in this species (Fig. 5) was not quite significant ($P = 0.06$).

The temporal response to management depended on physiognomy ($M \times T \times P$) in one complex guild and three species (Tables 2 and 3). Temporal increases in control gaps ($r = 0.77$, $N = 8$, $P = 0.02$) were registered for mixed-species flock insectivore-frugivores (mostly tanagers of the genus *Tachyphonus*), and not in the other combinations of physiognomy and management ($P > 0.05$). Moreover, species richness increased over time only in control gaps ($r = 0.81$, $N = 8$, $P = 0.02$) but not elsewhere ($P > 0.45$), indicating that the temporal response to management involved an interaction with physiognomy ($M \times T \times P$, $P = 0.006$). In contrast, temporal increases occurred only in cut gaps for an ant-follower (*Phlegopsis nigromaculata*, $r = 0.79$, $N = 8$, $P = 0.02$)

Table 3. Mean capture rate per 1000 net hours for total captures and avian feeding guilds that exhibit a significant response to reduced-impact logging in terra firme forest in the Tapajós Forest, Brazil. The effects of management were assessed through a repeated measures ANOVA with management and physiognomy as categorical factors, and time as a repeated measure within combinations of management and physiognomy. M refers to management (control vs. cut forest); P refers to physiognomy (gap vs. understory); and T refers to time (eight netting sessions from 19 August 1999 to 26 June 2001). Significance levels in bold indicate a positive interaction. Bonferroni sequential adjustments were applied separately to results for major guilds and for complex guilds, with levels of significance after adjustment (P') indicated by superscripts associated with P values ($^@ 0.10 \geq P' > 0.05$; $* 0.05 \geq P' > 0.01$; $** 0.01 \geq P' > 0.001$; $*** 0.001 \geq P'$). The study was initiated 22 months after timber had been harvested in cut forest at a level of 18 m³/ha using reduced-impact methods.

	Mean capture rate				Overall and p -adjusted significance level						
	Control		Cut		M	P	T	$M \times P$	$M \times T$	$P \times T$	$M \times P \times T$
	Gap	Understory	Gap	Understory							
Total captures	175.09	133.93	209.32	149.02				0.023			0.038
Nectarivores	14.55	6.65	13.13	10.09			0.047	0.002**			
All frugivores	30.80	19.24	41.88	26.83				<0.001***	<0.001***		
Solitary frugivores	26.25	13.30	37.23	23.97				<0.001***	<0.001***		
Solitary insectivore-frugivore	4.60	6.00	4.74	2.79							
All insectivores	128.71	106.74	154.06	106.56				<0.001***	<0.003**		
Solitary insectivores	35.30	34.88	41.29	30.97							0.049
Solitary insectivore-frugivore	5.85	7.54	12.23	3.04				0.043	<0.001**	0.024	
Ant-followers	16.07	19.15	17.86	17.02						0.013[@]	
Mixed-species flock insectivores	68.53	45.00	81.79	57.86				<0.001***	0.003*		
Mixed-species flock insectivores-frugivores	2.77	0.13	0.80	1.43							0.006*

and a mixed-species flock insectivore (*Xenops minutus*, $r = 0.84$, $N = 8$, $P = 0.01$), while slight and nonsignificant temporal changes in captures of these species occurred in other physiognomies ($M \times T \times P$, Fig. 6). Cut gaps also showed temporal changes in a solitary insectivore-frugivore (*A. taciturnis*) that peaked in captures early in the study and then declined for the rest of the study, a pattern that did not correspond to captures in other physiognomies ($M \times T \times P$, Fig. 6).

High temporal variation of captures within a forest type that did not coincide between forest types ($M \times T$, negative synergism) characterized a complex guild (solitary insectivore-frugivores), a constituent species (*Mionectes maconnelli*, $P < 0.001$, Fig. 5), and a nectarivore (*Thalurania furcata*, $P = 0.03$, Fig. 5). Captures varied consistently with time (main effect) regardless of forest type or physiognomy for one guild (nectarivores) and four species (Table 2). In all these instances, the trend reflected a positive correlation of captures with time, which was significant for captures of nectarivores in control forest (Table 4) and suggestive for captures of a mixed-species flock insectivore (*Myrmotherula leucophthalma*) in control forest ($P = 0.09$) and captures of a nectarivore (*Phaethornis longuemareus*) in cut forest ($P = 0.07$).

HABITAT AFFINITIES OF GAP AND FOREST SPECIES IN CONTROL AND CUT FORESTS.—The habitat distribution of birds in the Tapajós Forest (Henriques *et al.* 2003) facilitated an assessment of the habitat breadth of species as well as a determination of potential sources of rare species (Table 5). Species designated as understory species (*i.e.*, understory > gap captures) were most typically found in forest

understory, followed by mid-canopy, with least frequent occurrences in second growth, forest edge, and canopy, as well as on the forest floor. However, understory species in the cut forest differed from those in control forest by occurring most often in mid-canopy and less often in other categories, except the forest floor. Occurrences of gap species (*i.e.*, gap > understory captures) were similar to those of understory species, with most occurrences in forest understory followed by mid-canopy, and with fewest occurrences in the other habitats. Gap species in control and cut forests differed little in their occurrences with respect to the other habitats.

The habitat affinities of rare species generally corresponded in cut and control forests, but slightly more occurred in the forest midstory and on the ground for the rare species in cut forest. Rare cut-gap species occurred more often than did control-gap species in all habitats, except second growth forest.

DISCUSSION

GENERAL EFFECTS.—Reduced-impact logging and timing of our study were expected to minimize the likelihood of detecting effects of management on bird populations and guilds. Trees were harvested selectively at relatively low rates (about half the rate for commercial logging in this region). Careful felling of trees and placement of skidding trails limited collateral damage to the forest. Although roads and log storage sites contributed to canopy loss in cut blocks, these sites contributed a maximum loss of 5–7 percent of the canopy cover in management blocks. Moreover, our study began shortly after harvest (20–42 mo), well before the most severe effects of

Captures per 1000 Net Hours

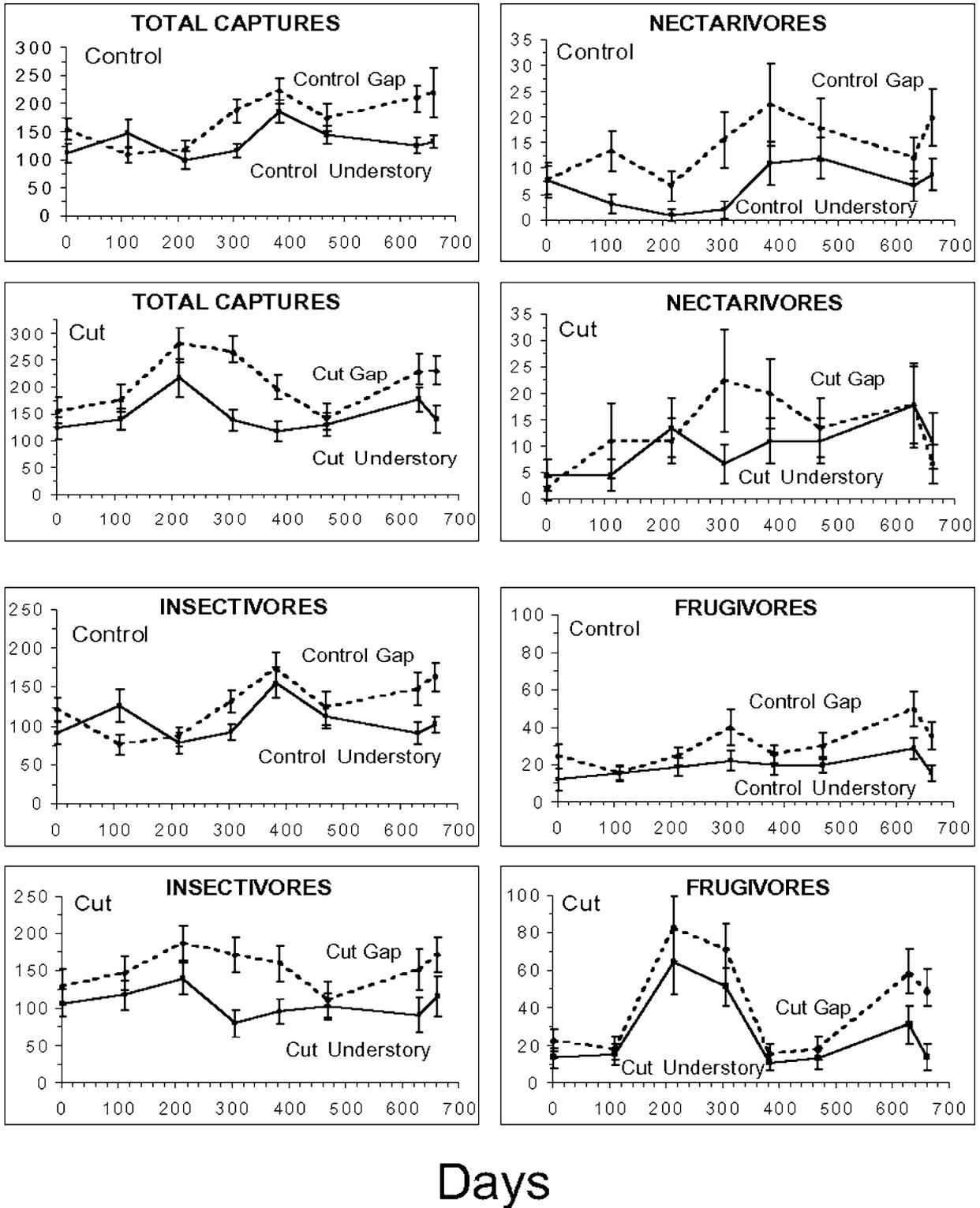


FIGURE 4. Mean (\pm SE) bird captures per 1000 net hours in control gap and control understory sites of control forest (upper) and in cut gap and cut understory sites of cut forest (lower) in *terra firme* forest of the Tapajós Forest, Brazil, during eight netting sessions from 19 August 1999 through 26 June 2001. Capture rates in control and cut forests are shown for total captures, all insectivores, all nectarivores, and all frugivores. The study was initiated 20 mo after timber had been harvested in cut forest at a level of 18 m³/ha with reduced-impact methods.

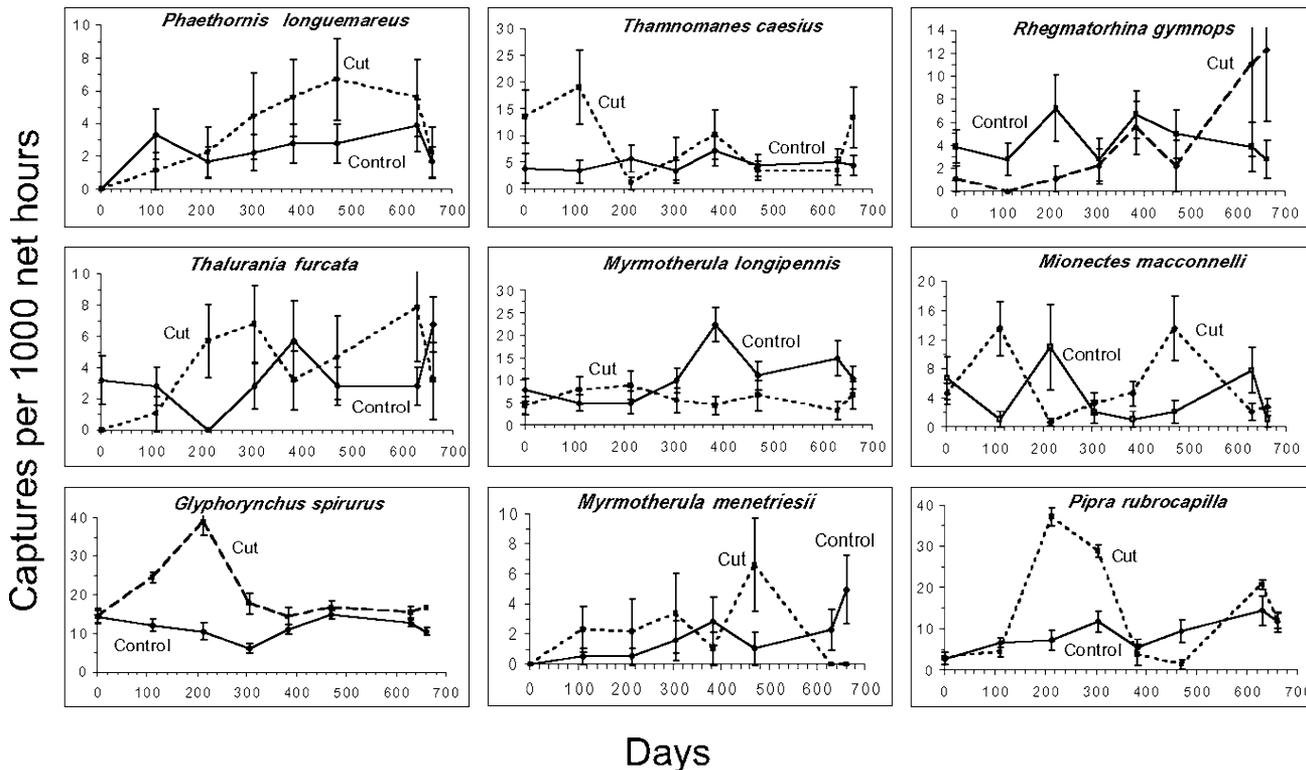


FIGURE 5. Mean (\pm SE) bird captures per 1000 net hours for nine bird species during eight netting sessions from 19 August 1999 through 26 June 2001 in control and cut *terra firme* forests where netting began 20 months after timber had been harvested in cut forest at a level of 18 m³/ha with reduced-impact methods, in the Tapajós Forest, Brazil.

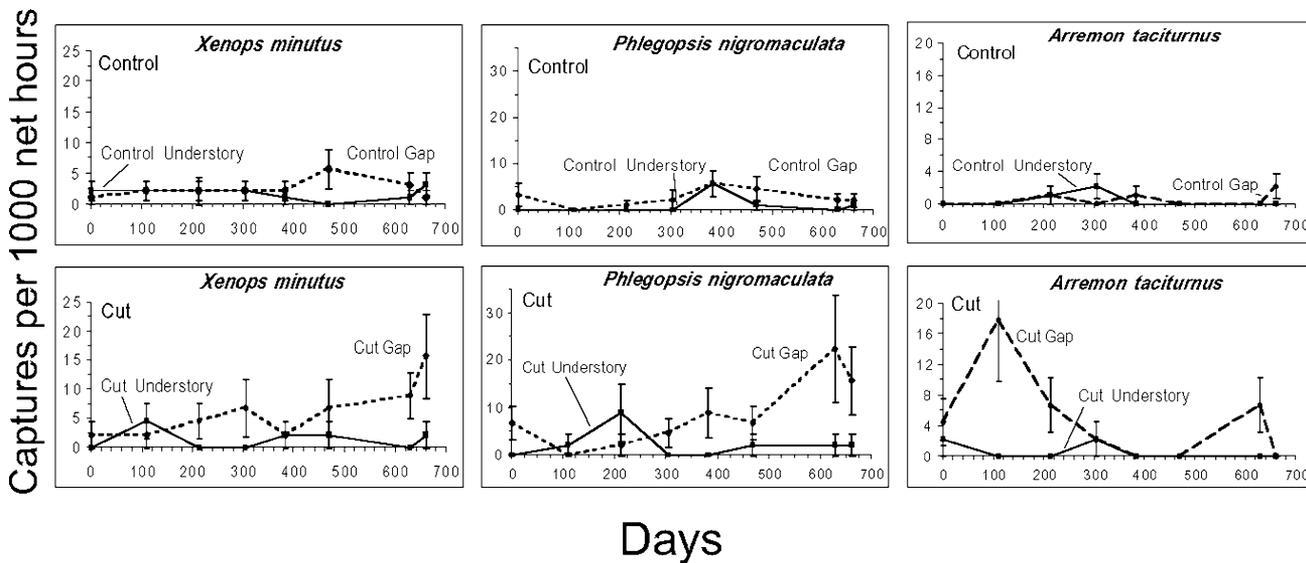


FIGURE 6. Mean (\pm SE) captures per 1000 net hours for three bird species in gap and understory sites of control forest (upper) as well as in gap and understory sites of cut forest (lower) in *terra firme* forest of the Tapajós Forest, Brazil, during eight netting sessions from 19 August 1999 through 26 June 2001. The study was initiated 20 mo after timber had been harvested in cut forest at a level of 18 m³/ha with reduced-impact methods.

Table 4. Guilds and species that showed a significant change in capture rates over eight netting sessions in control or cut forest in terra firme forest of the Tapajós Forest, Brazil. Spearman rank correlations between capture rates and time are shown for control and for cut forest separately. Levels of significance after Bonferroni sequential adjustment (P') are indicated by a superscript associated with P values ($^@ 0.10 \geq P' > 0.05$; $* 0.05 \geq P' > 0.01$). Within each forest type, the adjustment was executed separately for simple guilds, complex guilds, and species.

Guild or species	Forest type			
	Control		Cut	
	r	P	r	P
All nectarivores	0.71	0.047 [@]	0.54	0.066
<i>Phaethornis longuemareus</i>	0.31	0.500	0.66	0.070
<i>Thalurania furcata</i>	0.32	0.444	0.49	0.491
All frugivores	0.79	0.021 [@]	-0.02	0.955
Solitary frugivores	0.83	0.009*	0.17	0.690
<i>Geotrygon montana</i>	0.22	0.608	-0.31	0.453
<i>Pipra iris</i>	0.22	0.601	0.58	0.136
<i>Pipra rubrocapilla</i>	0.74	0.035	0.07	0.867
All insectivores	0.76	0.030 [@]	0	1.000
<i>Hylophylax poecilonota</i>	0.06	0.887	0.49	0.217
Ant-followers	0.26	0.528	0.71	0.047
<i>Rhegmatorhina gymnops</i>	-0.07	0.862	0.92	0.001*
Mixed-species flock insectivores	0.67	0.071	-0.38	0.351
<i>Glyphorhynchus spirurus</i>	-0.08	0.844	-0.17	0.690
<i>Myioborus barbatus</i>	0.39	0.346	0.37	0.362
<i>Myrmotherula leucophthalma</i>	0.64	0.091	0.11	0.799
<i>Myrmotherula longipennis</i>	0.71	0.050	-0.22	0.606
<i>Myrmotherula menetriesii</i>	0.82	0.013	-0.03	0.938
<i>Thamnomanes caesioides</i>	0.39	0.346	-0.35	0.399
Insectivore-frugivores	0.07	0.857	-0.39	0.346

logging are expected for birds (Mason & Thiollay 2001). Given these relatively benign effects, it was not surprising that estimated bird species richness did not differ significantly between control and cut forest (92 vs. 85 species, respectively, in samples of 1200 captures). Moreover, 56 percent of the species were shared between control and cut forest, a value only 8 percent lower than the natural variation observed in the percentage of species shared between the two control blocks (64%).

Total captures were higher in cut than in control forests as well as captures of nectarivores, frugivores (including solitary frugivores), and insectivores (including mixed-species flock insectivores). Increased captures of nectarivores and frugivores following timber harvest were expected, given the reliance of these guilds on food resources that are widely dispersed and often patchy, or available for a short time (e.g., Feinsinger 1976, Levey 1988b). Consequently, some nectarivores and frugivores may be preadapted to take advantage of postharvest increases in flowering and fruiting that are

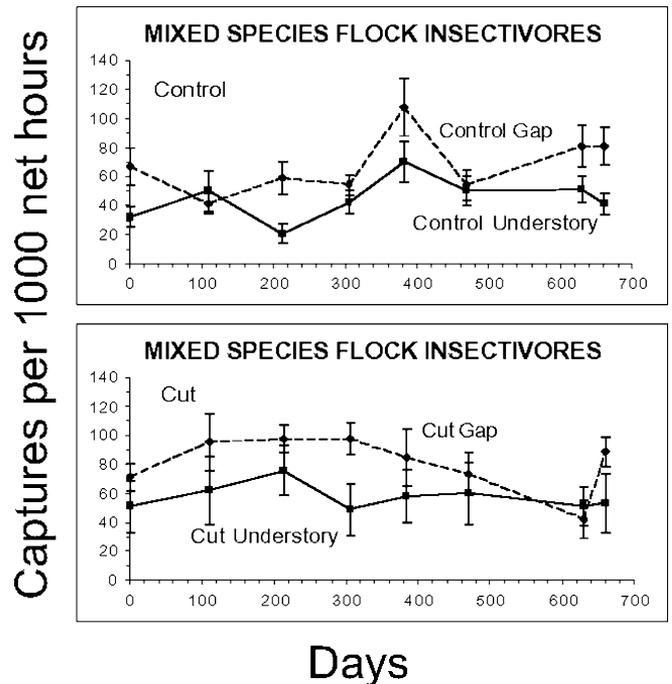


FIGURE 7. Mean (\pm SE) captures per 1000 net hours of mixed-species flock insectivores in gap and understory sites of control forest (upper) and in gap and understory sites of cut forest (lower) in terra firme forest of the Tapajós Forest, Brazil, during eight netting sessions from 19 August 1999 through 26 June 2001. The study was initiated 20 months after timber had been harvested in cut forest at a level of 18 m³/ha with reduced-impact methods.

associated with increased light levels after tree-felling. Not surprisingly, members of these guilds frequently are resistant to logging, at least in the short-term (e.g., Johns 1988, Mason 1996).

Higher capture rates of insectivores in cut vs. control forest were inconsistent with findings that understory and terrestrial insectivores are especially sensitive to timber harvest (Johns 1991, Thiollay 1992, Mason 1996). This sensitivity has been attributed (Mason 1996) to the specialized foraging modes of insectivores (Sherry 1984, Rosenberg 1990), which often require open forest understory, as well as postharvest changes in prey availability (Holloway *et al.* 1992). Indeed, capture rates of five insectivore species were significantly higher in control than in cut forest. Nonetheless, capture rates of 11 insectivore species were significantly higher in the cut forest. Insectivore declines might not occur until several years after tree-felling (e.g., Stouffer & Bierregaard 1995a). Our study probably occurred while many insectivores, recently displaced by habitat loss, were wandering widely in search of vacant territories and therefore were more likely to be captured. Given more time, however, wandering birds as well as territorial birds may abandon sites as they become inappropriate due to successional changes in foraging substrate (*i.e.*, foliage) or food abundance. Similarly, an initial phase of abundance, due to increased wandering by birds that abandoned defoliated sites, followed by population declines

Table 5. *Habitat associations of bird species classified by affinity for gap or understory in control and in cut terra firme forest in the Tapajós Forest, Brazil. Percentages do not sum to 100, because a species may be typical of more than one habitat type. Habitats are defined in Henriques et al. (2003). The term “gap species” refers to species with more total captures in gap than in understory within a forest type; and “understory species” refers to species with more total captures in understory than in gap within a forest type. “Rare species” are those with proportional abundances less than 1/S, where S = richness (Camargo 1993, Gaston 1994).*

Classification	No. of species	Percent of species within the specified habitat					
		Terrestrial	Understory	Midstory	Canopy	Forest edge	Second growth
Control gap species	72	7	56	46	11	15	22
Cut gap species	66	11	58	45	12	17	11
Control understory species	28	7	53	32	14	11	18
Cut understory species	30	13	50	47	7	7	0
Control gap rare species	79	11	44	46	15	13	13
Cut gap rare species	60	12	48	52	17	13	5
Control understory rare species	58	12	52	38	16	12	21
Cut understory rare species	51	14	49	43	12	12	4

associated with plant recovery characterized insectivorous birds in a hurricane-impacted forest (Wunderle 1995).

An initial response to habitat loss followed by a response to succession likely characterized mixed-species flock insectivores in which capture rates in cut forest, especially cut gaps, surpassed those in the control forest during the first half of the study. Species captured most often in cut forest were members of the mixed-species flock insectivores; individuals in this guild were captured commonly in cut gaps. The concentration of mixed-species flock insectivores in cut gaps was similar to the situation in the central Amazon shortly after forest fragmentation, when flocks shifted from forest understory to the edge of newly formed fragments for several months before disbanding (R. O. Bierregaard, pers. comm.).

PHYSIOGNOMY.—We expected that logging would have the greatest effect on birds in the understory surrounding cut gaps, given the results of previous logging studies (e.g., Thiollay 1992) as well as the negative response of some understory species to forest openings (e.g., Willis & Oniki 1978) and to dense understory foliage (Marra & Remsen 1997, Merry 2001). Consistent with this expectation were observations that two of four previously (Wunderle *et al.* 2005) identified understory specialist species (*Dendrocincla merula*, *Platyrhynchus coronatus*) were significantly more abundant in control than in cut forests. Both scaled dominance and diversity were significantly lower in cut than in control understories. Moreover, estimated species richness was lower in cut than in control understory, albeit only slightly (62 vs. 67 species each in 537 captures) and nonsignificantly. Thus, even at a relatively low harvest rate and only few years postharvest, some effects of reduced-impact logging were evident in the understory bird community, although increased wandering of displaced understory species may have masked actual population declines.

By increasing light, logging produced a denser understory with presumably more flowers and fruits, thus making it more attractive for some gap species than would be the darker, more open control

understory. Consistent with these expected postharvest changes, the relative abundance of the simple guilds was similar in cut gap and understory, whereas proportionately more nectarivores and frugivores occurred in gaps than in understory in control forest. For some guilds and constituent species, the distinction between gap and understory was less marked in cut than in control forests. This was evident for nectarivores, for which 69 percent of all captures in control forest occurred in gaps, whereas 57 percent of all captures in cut forest occurred in gaps. Furthermore, for the 12 gap specialists (previously identified by Wunderle *et al.* 2005) that were present in both forest types, all showed a predominance of captures in cut gaps relative to cut understory, but their proportional representation in gaps relative to understory was lower in cut than in control forests. Avian response to treefall gaps is influenced by characteristics of the gap and by traits of the surrounding forest. The response to gaps is context-dependent (Wunderle *et al.* 2005).

Our findings were consistent with the expectation that gap specialists would increase following timber harvest, whereas understory specialists would decrease. Of the 13 species with more captures in cut than in control forest, 10 were gap specialists and only 1 (*Hylophylax poecilonata*) was an understory specialist. In contrast, of the eight species with higher captures in control forest, two were gap specialists and two were understory specialists. Captures of the gap specialists, the manakin *Pipra iris* and the antwren *Myrmotherula longipennis*, were each higher in control than in cut forest, illustrating the subtle requirements of some gap specialists. This also suggests that tree-felled gaps are not necessarily equivalent to natural gaps for some gap specialists (Thiollay 1992). Presumably successional changes in the cut forest will cause cut gaps to be more attractive to these and other gap specialists, as was observed in the antbird *P. nigromaculata*; its captures increased with time in cut gaps.

Many mid-canopy birds may be reluctant to descend into a relatively open understory, but may readily descend into the more dense understory of logged forests (Mason 1996). Support for a

vertical shift is evident in a higher tally of cut understory species (47%) with mid-canopy affinities relative to the control understory species (32%) with mid-canopy affinities. The high percentage of cut understory species with mid-canopy affinities was comparable to that for gap species in cut (45%) and control (46%) gaps, providing another example of the convergence of bird community composition in gap and understory of the cut forest. Although documented in other logged forests (Mason 1996), a shift of canopy dwellers into gaps or understory of the cut forest did not occur in the Tapajós Forest. We previously attributed the rarity of canopy dwellers in gaps to the tall stature of the Tapajós Forest and noted that canopy dwellers occurred in gaps of larger size than those that we studied (Wunderle *et al.* 2005).

TEMPORAL EFFECTS.—By initiating our study 20 mo postharvest, we studied avian response to logging during a period of intensive plant growth and colonization, especially in the cut gaps. When netting began, shrub and herb densities in cut gap appeared comparable to that of the surrounding forest understory, except for areas damaged by felled trees. This suggests that our study began at the end of a lag in plant response to increased sunlight (*e.g.*, Oberbauer & Strain 1985). It was not until after 25–30 mo post-felling that plant growth accelerated markedly in gaps, as observed in artificial gaps in Panama, where gap seedling growth rates were highest during 10–40 mo post-felling (Fraver *et al.* 1998). Although gap canopy closure was not complete when our study ended (42 mo post-felling), closure due to ingrowth and gap plant growth was appreciable. Gap closure for an average 286 m² gap in the Tapajós Forest may require about 5 yr, an estimate within the range of 4–5 yr for gap closure elsewhere (Fraver *et al.* 1998, Costa & Magnusson 2003).

We assume that the natural gap frequencies in control and cut forests were equivalent prior to logging. Consequently, cut gaps and associated clearings (log storage sites and access roads) increased the number of canopy openings and increased light levels in the cut forest understory. The higher foliage density of the cut understory relative to the control understory sites was consistent with this expectation. Given a rapid postharvest successional response of vegetation in gap and understory of cut forest, we expected a variety of temporal responses by birds in the cut forest, especially in cut gaps, where microclimate, food resources, and vegetation structure and composition rapidly changed with time.

Temporal responses of captures consistent with postharvest successional changes were evident at both the guild- and species-level in the cut forest. Temporal responses of captures only occurred in cut gaps (*i.e.*, three insectivorous species changed with time). For example, attractiveness of cut gaps was short-lived, at least for the sparrow *A. taciturnus*, a solitary insectivore-frugivore, which invaded cut gaps early in the study and subsequently declined. In contrast, captures of the ovenbird *X. minutus* in cut gaps increased with time. This result may have been associated with increased abundance of dead twigs and branches, a favored substrate for these members of the mixed-species flock insectivore guild (Skutch 1969). Also, captures increased over time in cut gaps for the antbird *P. nigromaculata*, an ant-follower and gap specialist, suggesting that gap suitability for

this species improved with time. Although not specific to a physiognomy, another ant-follower, the antbird *R. gymnops*, increased only in the cut forest. The response of these antbirds contributed to the guild's increase in cut forest. Although many ant-followers are affected negatively by selective logging (Thiollay 1992, Mason 1996) and forest fragmentation (*e.g.*, Bierregaard & Lovejoy 1989), ant-followers use second growth habitats and recolonize deforested areas once second growth cover is present (Stouffer & Bierregaard 1995a, Borges & Stouffer 1999). Similarly, captures of ant-followers increased as vegetation cover increased in cut forest. By the study's end, the average capture rate of ant-followers was equivalent in the two forest types, despite lower captures in cut forest of a common guild member, the woodcreeper *D. merula*, an understory specialist.

The temporal response of members of mixed-species insectivore flocks in cut forest was more variable than the response of members of the ant-follower guild. This greater variability in cut forest was likely due to use of a greater variety of foraging modes, substrates, and prey that might undergo successional changes. Although flock members are predominantly leaf gleaners, others forage by flycatching or gleaning from twigs, branches, or vines. In addition, members of mixed-species flocks are more likely to use the midstory and forage above the net-level compared to ant-followers, a guild restricted to net-level in the understory (Stouffer & Bierregaard 1995a). Thus, heterogeneity of temporal response by members of the mixed-species insectivore flock guild likely resulted from species-specific use of a variety of foraging modes, substrates, heights, and prey, which differentially changed during secondary succession.

The influx of frugivores into cut forest was consistent with expected bursts of gap or understory fruiting associated with increased gap and edge habitat (*e.g.*, Levey 1988a, b, Loiselle & Blake 1991). This response was mostly due to the manakin *Pipra rubrocapilla*, which peaked during the third and seventh netting sessions in cut forest. In contrast, a congener, *P. iris* and the thrush-like manakin *Schiffornis turdinus* primarily remained in control forest. Elsewhere in Amazonia, captures of manakins and other frugivores did not differ significantly among small selectively logged plots differing in postharvest age (4–10 yr) and harvest intensity (Guilherme & Cintra 2001). The response of manakins to logging differs among species (Thiollay 1992, Mason 1996), indicating that even closely related taxa can differ in habitat requirements. Divergent responses to logging indicate that close phylogenetic affinity is not necessarily a good predictor of response to timber harvest (see also the divergent responses of the hermits *Phaethornis bourcierii* and *P. longuemareus*).

Species that track resources of short temporal availability (*e.g.*, some flowers and fruits) might move in and out of cut and control forests at different times, as resources wax and wane asynchronously. Two species showed patterns of captures consistent with a response to a temporal alternation of resource availability between forest types. In this instance, dominance of captures shifted between control and cut forests in different netting sessions for both the flycatcher *M. macconnelli* and the hummingbird *T. furcata*. The latter species uses canopy and understory nectar resources (Stouffer

& Bierregaard 1995b), such that variation in dominance between forests might reflect vertical shifts in foraging sites.

Temporal effects were not confined to the cut forest. Captures of some guilds and species increased with time in the control forest. This suggests that some birds were displaced by nearby logging activities (Wunderle *et al.* 2005). Others have documented influxes of birds into Amazonian forests patches as sites nearby are deforested (Bierregaard & Lovejoy 1989, Bierregaard 1990a). Guilds and species that showed significant increases in captures over time in the control forest in the absence of corresponding increases in cut forest support the displacement hypothesis. This pattern was evident in captures of all frugivores, all insectivores, and solitary frugivores, and was suggestive ($P = 0.07$) for the mixed-species flock insectivores. The displacement hypothesis is supported further by the observation that all guilds or species with significant or suggestive ($P < 0.10$) changes in capture rates increased over time. Consistent with an influx hypothesis, captures of two understory specialists increased with time in the control forest (Wunderle *et al.* 2005). An influx of displaced birds from nearby logging sites might increase competition with residents of intact forests reserves. Consequently, effects of logging may extend beyond the logged forest. However, some of the influx may have resulted from birds responding to changes in the control forest, especially to successional changes in gaps where total captures and total insectivore captures increased over time (Wunderle *et al.* 2005).

Not all increases in captures were confined to control forest, as nectarivores increased in both forest types during the study. Nectarivore increases were attributable mostly to increased captures of understory hummingbirds (mostly hermits, *Phaethornis* spp.), and not as a result of canopy dwellers shifting to the understory over time. For nectarivores, increases were most likely a consequence of a combination of factors including displacement due to nearby logging activities as well as a response to increased flowering in the cut forest.

PREVIOUS STUDIES AND MANAGEMENT IMPLICATIONS.—Comparisons of studies on the effects of selective logging on bird communities are difficult, given the differences in logging intensities, postharvest sampling time, forest type, and sampling methods and design. A study somewhat comparable to ours involved a comparison of logging effects on understory and gap birds 1 yr after highly selective harvest ($1.8 \text{ m}^3/\text{ha}$) in a subtropical moist forest in Belize (Whitman *et al.* 1998). That study showed no effect of logging on species richness. Moreover, 26 avian guilds were unaffected by the harvest, although 13 of 66 common species were twice as likely to be found in control forest or in cut understory than in cut gaps. The absence of logging effects on the bird community differs from our findings as well as those of previous studies. Whitman *et al.* (1998) attributed the absence of response by the bird community to low harvest rates, and high natural and anthropogenic background rates of disturbance. The very low harvest rate may have been important in minimizing logging effects on birds. Indeed, the harvest rate in Belize was well below that in our study or in those of previous studies (*e.g.*, $11\text{--}90 \text{ m}^3/\text{ha}$, Thiollay 1992 & Lambert 1992, respectively).

Background disturbance rates may be an important factor contributing to differences between our study and those of Whitman *et al.* (1998). The Belize study was conducted in an area with a high rate of natural disturbance—hurricanes are frequent and subsequent fires occur occasionally (Lynch 1991). In addition, there is a long history of broad-scale disturbance by the indigenous Maya, which combined with high natural disturbance rates, may have eliminated disturbance-sensitive species, leaving an avifauna relatively insensitive to low levels of disturbance (Whitman *et al.* 1998). In contrast, natural disturbance rates are lower in the Amazon. Although there may have been a long history of anthropogenic disturbance by indigenous people (*e.g.*, Meggers 1985, Heckenberger *et al.* 2003), their impacts may have been localized relative to the broad expanse of forest. Consequently, Amazonian birds may have evolved a high degree of habitat specialization, as evidenced by the relatively high proportion of disturbance-sensitive species (Stouffer & Bierregaard 1995a, Robinson & Terborgh 1997), as well as the low proportion of forest species that use secondary habitats (Stotz *et al.* 1996). Sensitivity to disturbance needs to be considered in formulating management prescriptions to sustain diversity of Amazonian birds in logged forests.

Logging effects on most birds found in this study were relatively minor, although the effects of clearing for roads and log storage sites, which often have the greatest impact on wildlife (*e.g.*, Fimbel *et al.* 2001b), were not studied. Also, the study was conducted shortly after harvest, possibly well before some of the most severe effects of logging appear (Mason & Thiollay 2001). Eight species were especially sensitive to logging, as shown by higher capture rates in control than in cut forests; however, low harvest rates and use of reduced-impact logging methods may reduce some of the negative effects of logging. Cut forest supported only 7 percent fewer species than control forest in net samples of 1200 captures. The percentage of species shared between cut and control forests was only 8 percent lower than percentage of species shared between control blocks. Many of the absent species were rare in control forest. However, these rare species are found in other habitats or forest strata (often where they are not rare). Although understory specialist species had lower captures in cut than in control forest, only one of four understory specialists was absent from cut forest. Insectivores, one of the understory guilds most sensitive to logging, had higher capture rates in cut than in control forest. This trend, however, may have resulted from an increase in wandering by birds displaced by habitat loss, as well as a shift from midstory (*e.g.*, mixed-species flock insectivores). Ant-follower recovery in cut forest was well underway at the time of this study. Many of these birds use regenerating cut gaps, such that overall capture rates were equivalent in the two forest types. Continued monitoring of the cut forest is warranted to document possible population changes and to identify appropriate rotation periods, which may require 30–40 yr or more for recovery of the most sensitive understory species. Thus, low harvest rates and reduced-impact methods may help reduce some of the effects of logging on sensitive understory bird communities. As recommended by others (Fimbel *et al.* 2001b, Mason & Putz 2001), these approaches should be coupled with long rotation periods and

establishment of forest reserves to maintain high avian diversity in tropical forests.

ACKNOWLEDGMENTS

Field assistance was provided by Laércio Damasceno Cabral, Sidnei de Melo Dantas, Gilson de Jesus Oliveira, Rosimar Pantoja Oliveira, and Luis Nélio Saldanha. David C. Oren assisted in many ways. Assistance with data analysis was provided by Stephan Cox, Steven Presley, and Richard Stevens. We are particularly grateful to Kathleen Harris, Jay McMilen, and Mary Camp for logistics support with respect to a number of administrative challenges. The manuscript benefited from the constructive comments of Nicholas V. L. Brokaw, Robin L. Chazdon, Eileen Helmer, Bette A. Loiselle, Ariel E. Lugo, and Scott K. Robinson. Cooperation, logistics support, and permission to use field stations were provided by the Instituto Brasileiro de Meio Ambiente e Recursos Naturais Renováveis (IBAMA) and the Large-Scale Biosphere Atmosphere Ecology Project (LBA). We thank IBAMA for providing collecting permits and permission to work in the Tapajós National Forest. Funding was provided by Museu Paraense Emílio Goeldi, Conselho Nacional de Desenvolvimento Científico e Tecnológico, Fundo Estadual de Ciência Tecnologia do Estado do Pará, Fundação O Boticário, and USDA Forest Service. The study was conducted under a cooperative agreement between IBAMA and USDA Forest Service, as well as a cooperative agreement between FADESP and Texas Tech University. This research was conducted in cooperation with the University of Puerto Rico and Texas Tech University.

LITERATURE CITED

- BERGER, W. H., AND F. L. PARKER. 1970. Diversity of planktonic Foraminifera in deep sediments. *Science* 168: 1345–1347.
- BIERREGAARD, R. O. JR. 1990a. Avian communities in the understory of Amazonian forest fragments. In A. Keast (Ed.), *Biogeography and ecology of forest bird communities*, pp. 333–343. Academic Publishing, The Hague, The Netherlands.
- . 1990b. Species composition and trophic organization of the understory bird community in a central Amazonian terra firme forest. In A. H. Gentry (Ed.), *Four Neotropical rainforests*, pp. 161–181. Yale University Press, New Haven, Connecticut.
- , AND T. E. LOVEJOY. 1989. Effects of forest fragmentation on Amazonian understory bird communities. *Acta Amazon.* 19: 215–241.
- BORGES, S. H., AND P. C. STOUFFER. 1999. Bird communities in two types of anthropogenic successional vegetation in Central Amazonia. *Condor* 101: 529–536.
- BROKAW, N. V. L. 1982a. Treefalls: Frequency, timing and consequences. In J. E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.), *The ecology of a tropical forest: Seasonal rhythms and long-term changes*, pp. 101–108. Smithsonian Institution Press, Washington, DC.
- . 1982b. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14: 158–160.
- . 1985a. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682–687.
- . 1985b. Treefalls: Regrowth, and community structure in tropical forests. In S. T. A. Pickett and P. S. White (Eds.), *The ecology of natural disturbances and patch dynamics*, pp. 53–69. Academic Press, Orlando, Florida.
- BURTON, P. J. A., AND D. MUELLER-DOMBOIS. 1984. Response of *Metrosideros polymorpha* seedlings to experimental canopy opening. *Ecology* 65: 779–791.
- CAMARGO, J. A. 1993. Must dominance increase with the number of subordinate species in competitive interactions? *J. Theor. Biol.* 161: 537–542.
- CHAPMAN, C. A., AND R. A. FIMBEL. 2001. An evolutionary perspective of natural disturbance and logging: Implications for forest management and habitat restoration. In R. A. Fimbel, A. Grajal, and J. G. Robinson (Eds.), *The cutting edge: Conserving wildlife in logged tropical forests*, pp. 511–522. Columbia University Press, New York, New York.
- CHAZDON, R. L., AND N. FETCHER. 1984. Photosynthetic environments in a lowland tropical rainforest in Costa Rica. *J. Ecol.* 72: 553–564.
- COHN-HAFT, M., A. WHITTAKER, AND P. STOUFFER. 1997. A new look at the “species-poor” Central Amazon: The avifauna north of Manaus, Brazil. *Ornithol. Monogr.* 48: 205–235.
- COSTA, R. C., AND W. W. MAGNUSSON. 2003. Effects of selective logging on the diversity and abundance of flowering and fruiting understory plants in a Central Amazonian forest. *Biotropica* 35: 103–114.
- DALY, D. C., AND G. T. PRANCE. 1989. Brazilian Amazon. In D. G. Campbell and H. D. Hammond (Eds.), *Floristic inventory of tropical countries*, pp. 401–426. New York Botanical Garden, New York.
- DENSLow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431–451.
- , J. C. SCHULTZ, P. M. VITOUSEK, AND B. R. STRAIN. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71: 165–179.
- FEINSINGER, P. 1976. Organization of a tropical guild of nectarivorous birds. *Ecol. Monogr.* 46: 257–291.
- FIMBEL, R. A., A. GRAJAL, AND J. G. ROBINSON (Eds.). 2001a. *The cutting edge: Conserving wildlife in logged tropical forest*. Columbia University Press, New York.
- , ———, AND ———. 2001b. Logging and wildlife in the tropics. In R. A. Fimbel, A. Grajal, and J. G. Robinson (Eds.), *The cutting edge: Conserving wildlife in logged tropical forest*, pp. 667–695. Columbia University Press, New York.
- FRAVER, S., N. V. L. BROKAW, AND A. P. SMITH. 1998. Delimiting the gap phase in the growth cycle of a Panamanian forest. *J. Trop. Ecol.* 14: 673–681.
- GASTON, K. J. 1994. *Rarity*. Chapman and Hall, London, England.
- GUILHERME, E., AND R. CINTRA. 2001. Effects of intensity and age of selective logging and tree girdling on an understory bird community composition in Central Amazonia, Brazil. *Ecotropica* 7: 77–92.
- HALLÉ, F., R. A. A. OLDEMAN, AND P. B. TOMLINSON. 1978. *Tropical trees and forests: An architectural analysis*. Springer-Verlag, Berlin, Germany.
- HARTSHORN, G. S. 1990. An overview of neotropical forest dynamics. In A. H. Gentry (Ed.), *Four Neotropical forests*, pp. 585–599. Yale University Press, New Haven, Connecticut.
- HECKENBERGER, M. J., A. KUIKURO, U. T. KUIKURO, J. C. RUSSELL, M. SCHMIDT, C. FAUSTO, AND B. FRANCHETTO. 2003. Amazonia 1492: Pristine forest or cultural parkland? *Science* 301: 1710–1714.
- HENRIQUES, L. M. P., J. M. WUNDERLE, JR., AND M. R. WILLIG. 2003. Birds of the Tapajós National Forest, Brazilian Amazon: A preliminary assessment. *Ornitol. Neotrop.* 14: 307–338.
- HOLLOWAY, J. D., A. H. KIRK-SPRIGGS, AND C. V. KHEN. 1992. The response of some rain forest insect groups to logging and conversion to plantation. *Philos. Trans. R. Soc. Lond. B* 335: 425–436.
- HURLBERT, S. H. 2003. Design and analysis: Uncertain intent, uncertain result. *Ecology* 84: 810–812.
- JOHNS, A. D. 1988. Effects of “selective” timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica* 20: 31–37.
- . 1991. Responses of Amazonian rain forest birds to habitat modification. *J. Trop. Ecol.* 7: 417–437.
- KARR, J. R. 1981. Surveying birds with mist nets. *Stud. Avian Biol.* 6: 62–67.
- KREBS, C. J. 1989. *Ecological methodology*. Harper Collins Publishers, New York.

- LAMBERT, F. R. 1992. The consequences of selective logging for Bornean lowland forest birds. *Philos. Trans. R. Soc. Lond. B* 335: 443–457.
- LANG, G. E., AND D. H. KNIGHT. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. *Ecology* 64: 1075–1080.
- LEVEY, D. J. 1988a. Tropical wet forest treefall gaps and distribution of understory birds and plants. *Ecology* 69: 1076–1089.
- . 1988b. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58: 251–269.
- LOISELLE, B. A., AND J. G. BLAKE. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72: 180–193.
- LYNCH, J. F. 1991. Effects of Hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. *Biotropica* 23: 488–496.
- MANLY, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York.
- MARRA, P. P., AND J. V. REMSEN, JR. 1997. Insights into the maintenance of high species diversity in the Neotropics: Habitat selection and foraging behavior in understory birds of tropical and temperate forests. *Ornithol. Monogr.* 48: 445–483.
- MASON, D. 1996. Responses of Venezuelan understory birds to selective logging, enrichment strips, and vine cutting. *Biotropica* 28: 296–309.
- , AND F. E. PUTZ. 2001. Reducing the impacts of tropical forestry on wildlife. *In* R. A. Fimbel, A. Grajal, and J. G. Robinson (Eds.). *The cutting edge: Conserving wildlife in logged tropical forests*, pp. 474–487. Columbia University Press, New York.
- , AND J. M. THIOLLAY. 2001. Tropical forestry and the conservation of Neotropical birds. *In* R. A. Fimbel, A. Grajal, and J. G. Robinson (Eds.). *The cutting edge: Conserving wildlife in logged tropical forests*, pp. 167–191. Columbia University Press, New York.
- MATHWORKS, I. 1995. The student edition of MATLAB Version 4 User's Guide. Prentice Hall, Englewood Cliffs, New Jersey.
- MEGGERS, B. J. 1985. Aboriginal adaptation to Amazonia. *In* G. T. Prance and T. E. Lovejoy (Eds.). *Key environments: Amazonia*, pp. 307–327. Pergamon Press, Oxford, England.
- MERRY, E. A. 2001. Effects of vine-cutting on understory birds in a Bolivian lowland forest: Implications for management. M.S. Thesis, University of Florida, Gainesville, Florida.
- MORAN, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* 100: 403–405.
- OSBERBAUER, S. F., AND B. R. STRAIN. 1985. Effects of light regime on the growth and physiology of *Pentaclethra macroloba* (Mimosaceae) in Costa Rica. *J. Trop. Ecol.* 1: 303–320.
- PARROTTA, J. A., J. K. FRANCIS, AND R. ROLO DE ALMEIDA. 1995. Trees of the Tapajós—A photographic field guide. General Technical Report, U. S. Department of Agriculture, Forest Service, International Institute of Tropical Forestry, Rio Piedras, Puerto Rico.
- PICKET, S. T. A. 1976. Succession: An evolutionary interpretation. *Am. Nat.* 110: 107–119.
- PIELOU, E. C. 1975. *Mathematical ecology*. Wiley, New York.
- PUTZ, F. E., L. K. SIROT, AND M. A. PINARD. 2001. Tropical forest management and wildlife. *In* R. A. Fimbel, A. Grajal, and J. G. Robinson (Eds.). *The cutting edge: Conserving wildlife in logged tropical forest*, pp. 11–34. Columbia University Press, New York.
- REMSSEN, J. V., JR., AND D. A. GOOD. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* 113: 381–398.
- RICE, W. R. 1989. Analyzing tables of statistical results. *Evolution* 43: 223–225.
- RIERA, B., AND D. Y. ALEXANDRE. 1988. Surface des chablis et temps de renouvellement en forêt dense tropicale. *Acta Oecol.* 57: 773–782.
- ROBINSON, S. K., AND J. TERBORGH. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. *Ornithol. Monogr.* 48: 641–672.
- ROSENBERG, K. V. 1990. Dead-leaf foraging specialization in tropical forest birds: Measuring resource availability and use. *Stud. Avian Biol.* 13: 360–368.
- SCHEMSKE, D. W., AND N. BROKAW. 1981. Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62: 938–945.
- SHERRY, T. W. 1984. Comparative dietary ecology of sympatric insectivorous neotropical flycatchers (Tyrannidae). *Ecol. Monogr.* 54: 313–338.
- SILVA, J. N. M. 1989. The behaviour of the tropical rain forest of the Brazilian Amazon after logging. Ph.D. Dissertation, Oxford University, Oxford, England.
- , J. DE LOPES, AND J. O. P. DE CARVALHO. 1985. Inventário florestal de uma área experimental na Floresta Nacional do Tapajós. *Boletim de Pesquisa Florestal* 10/11: 38–110.
- SKUTCH, A. F. 1969. Life histories of Central American birds. III. Cooper Ornithological Society, Berkeley, California.
- SMITH, A. P. 1987. Respuestas de hierbas del sotobosque tropical a claros ocasionados por la caída de árboles. *Revista de Biología Tropical (suplemento)* 35: 111–118.
- SMITH, P., K. P. HOGAN, AND J. R. IDOL. 1992. Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. *Biotropica* 24: 503–511.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. W. H. Freeman and Company, New York.
- SPSS. 1990. *The SPSS base system user's guide*. SPSS, Inc., Chicago, Illinois.
- STEVENS, R. D., AND M. R. WILLIG. 2000. Community structure, abundance, and morphology. *Oikos* 88: 48–56.
- STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER, III, AND D. K. MOSKOVITZ. 1996. Neotropical birds: Ecology and conservation. University of Chicago Press, Chicago, Illinois.
- STOUFFER, P. C., AND R. O. BIERREGAARD, JR. 1995a. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76: 2429–2445.
- , AND ———. 1995b. Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conver. Biol.* 9: 1085–1094.
- THIOLLAY, J. M. 1992. Influence of selective logging on bird species diversity in a Guianan rain forest. *Conver. Biol.* 6: 47–63.
- UHL, C., AND R. GUIMARÃES. 1989. Ecological impacts of selective logging in the Brazilian Amazon: A case study from the Paragominas region of the State of Para. *Biotropica* 21: 98–106.
- VAN DER MEER, P. J., AND F. BONGERS. 1996. Formation and closure of canopy gaps in the rain forest at Nouragues, French Guiana. *Vegetatio* 126: 167–179.
- WHITMAN, A. A., J. M. HAGAN, III, AND N. V. L. BROKAW. 1998. Effect of selective logging on birds in northern Belize. *Biotropica* 30: 449–457.
- WHITMORE, T. C. 1978. Gaps in the forest canopy. *In* P. B. Tomlinson and M. H. Zimmerman (Eds.). *Tropical trees as living systems*, pp. 639–655. Cambridge University Press, Cambridge, England.
- WILLIS, E. O., AND Y. ONIKI. 1978. Birds and army ants. *Annu. Rev. Ecol. Syst.* 9: 243–263.
- WUNDERLE, J. M., JR. 1995. Responses of bird populations in a Puerto Rican forest to Hurricane Hugo: The first 18 months. *Condor* 97: 879–896.
- , M. R. WILLIG, AND L. M. P. HENRIQUES. 2005. Avian distribution in treefall gaps and understory of *terra firme* forest in the lowland Amazon. *Ibis* 147: 109–129.
- YAVITT, J. B., J. J. BATTLES, G. E. LANG, AND D. H. YOUNG. 1995. The canopy gap regime in a secondary neotropical forest in Panama. *J. Trop. Ecol.* 11: 391–402.

Appendix. Mist net capture rates (captures per 1000 net hours) for birds captured in control gaps and understory sites in two 100-ha control blocks, and in cut gaps and understory sites in two 100-ha cut blocks in which reduced-impact timber harvest occurred at a rate of 18.3 m³/ha, 22 months prior to netting in terra firme forest of the Tapajós Forest, Brazil. Captures were obtained during eight netting sessions from 19 August 1999 to 26 June 2001. The sequence and nomenclature for species in non-Passeriformes families follow Sick (1997). For Passeriformes, the sequence and nomenclature for families and species follow Ridgely and Tudor (1989, 1994), with minor modifications adopted by Sick (1997). Guild and microhabitat classifications follow Henriques et al. (2003).

	Physiognomy and forest type				Guild ^a	Microhabitat ^b
	Control gap	Control understory	Cut gap	Cut understory		
Tinamidae						
<i>Crypturellus variegatus</i>	0.14	0.14	0	0	f	t
Accipitridae						
<i>Accipiter bicolor</i>	0	0.14	0	0	svi	c
<i>Leucopternis albicollis</i>	0.14	0	0	0	svli	c
Falconidae						
<i>Micrastur ruficollis</i>	0.14	0.28	0.28	0	svli	u
<i>Micrastur gilvicollis</i>	0.84	0.84	0	1.12	svli	c
Odontophoridae						
<i>Odontophorus gujanensis</i>	0	0	0	0.28	f	t
Psophidae						
<i>Psophia viridis</i>	0	0.28	0	0	fi	u
Columbidae						
<i>Leptotila rufaxilla</i>	0	0	0	0.28	f	ef
<i>Geotrygon montana</i>	1.95	1.81	2.51	1.95	f	t, u
Cuculidae						
<i>Piaya cayana</i>	0	0	0.28	0	i	c
Trochilidae						
<i>Glaucis hirsuta</i>	0	0.27	0	0	n	s, ef
<i>Threnetes leucurus</i>	0.14	0	0	0	n	u
<i>Phaethornis superciliosus</i>	2.65	0.98	3.91	2.23	n	u, ef
<i>Phaethornis bourcieri</i>	1.81	1.53	0.84	0.28	n	u
<i>Phaethornis longuemareus</i>	3.91	0.70	3.91	3.07	n	u
<i>Campylopterus largipennis</i>	0.56	0.41	0	0	n	c, ef
<i>Florisuga mellivora</i>	0.14	0	0	0	n	c
<i>Thalurania furcata</i>	4.60	2.09	4.19	3.91	n	tf
<i>Hylocharis saphirina</i>	0.14	0	0	0	n	ef
<i>Heliothryx aurita</i>	0.14	0.14	0	0	n	c
Trogonidae						
<i>Trogon violaceus</i>	0.14	0	0	0	mfif	m, ef
<i>Trogon rufus</i>	0.28	0.14	0.28	1.40	mfif	m
Momotidae						
<i>Baryphthengus ruficapillus</i>	0.14	0.28	0	0	if	m
<i>Momotus momota</i>	0	0.14	0	0	if	m
Galbulidae						
<i>Galbula cyanicollis</i>	0.69	0.14	0.56	0	i	m
<i>Galbula dea</i>	0	0	0.28	0.28	i	c, ef
Buconidae						
<i>Bucco capensis</i>	0.14	0	0	0	i	m
<i>Malacoptila rufa</i>	0.70	2.09	0.56	1.40	i	m
<i>Monasa morphoeus</i>	0.14	0.14	0	0.84	svli	m
Ramphastidae						
<i>Selenidera gouldii</i>	0.14	0	0	0	f	c

Appendix. Continued.

	Physiognomy and forest type				Guild ^a	Microhabitat ^b
	Control gap	Control understory	Cut gap	Cut understory		
<i>Rhamphastos vitellinus</i>	0	0.14	0	0	f	c
Picidae						
<i>Celeus jumana</i>	0	0	0	0.28	if	m
<i>Veniliornis affinis</i>	0	0	0.28	0	i	m, u
Furnariidae						
<i>Xenops minutus</i>	2.51	1.81	6.14	1.40	mfi	u, m
<i>Phylidor erythrocerus</i>	0.14	0	0	0.56	mfi	u
<i>Phylidor ruficaudatus</i>	1.26	0.41	0	0.28	mfi	u
<i>Phylidor pyrrhodes</i>	0.28	0.14	0	0	mfi	u
<i>Automolus infuscatus</i>	3.21	3.63	1.40	3.35	mfi	u, ef
<i>Automolus ochralaemus</i>	0.98	0.28	0.28	0	i	u
<i>Sclerurus mexicanus</i>	0.28	0.41	0.56	0.84	i	u
<i>Sclerurus rufularis</i>	0.70	0.97	0.84	0.56	i	u
<i>Sclerurus caudacutus</i>	1.26	1.26	0.28	0.56	i	u
Dendrocolaptidae						
<i>Dendrocincla fuliginosa</i>	1.40	0.84	0.84	1.95	i	u, m
<i>Dendrocincla merula</i>	7.95	12.28	2.51	6.42	aa	u
<i>Deconychura longicauda</i>	0.98	1.12	0.28	0.28	mfi	u
<i>Deconychura stictolaema</i>	0.84	1.8	0	0	mfi	u
<i>Glyphorhynchus spirurus</i>	11.86	11.44	16.46	23.44	mfi	u, m
<i>Hylexetastes uniformis</i>	0.70	1.12	0.56	1.67	aa	m
<i>Dendrocolaptes certhia</i>	0.14	0.41	0.2	0.7	aa	m
<i>Dendrocolaptes picumnus</i>	0.14	0	0	0	aa	m
<i>Xiphocolaptes promeropirhynchus</i>	0	0	0	0.2	i	m
<i>Xiphorhynchus spixii</i>	2.65	3.77	1.40	3.91	mfi	u, m
<i>Xiphorhynchus guttatus</i>	0.42	0.42	1.95	1.40	mfi	c, m
<i>Campylorhamphus procurvoides</i>	0.14	0	1.12	0.56	mfi	c, m
Thamnophilidae						
<i>Cymbilaimus lineatus</i>	0.41	0	1.40	0.28	mfi	u, m, ef
<i>Taraba major</i>	0.14	0	0	0	i	ef
<i>Thamnophilus aethiops</i>	1.39	0.55	4.19	2.23	mfi	u
<i>Thamnophilus schistaceus</i>	2.93	0.28	5.58	1.67	mfi	u
<i>Pygiptila stellaris</i>	0.14	0	0	0	i	u
<i>Thamnomanes caesius</i>	6.0	3.35	9.77	7.53	mfi	u
<i>Microrhopias quixensis</i>	0.14	0.14	0.56	0	i	m, u
<i>Myrmotherula brachyura</i>	0	0	0.56	0	mfi	m, u
<i>Myrmotherula hauxwelli</i>	2.51	1.39	0.56	0.84	mfi	u, m
<i>Myrmotherula leucophthalma</i>	9.35	2.65	12.28	2.51	mfi	u, m
<i>Myrmotherula ornata</i>	0.28	0	0.84	0.28	mfi	m, u
<i>Myrmotherula axillaris</i>	0.14	0	2.51	0.28	mfi	ef
<i>Myrmotherula longipennis</i>	12.97	8.79	6.14	5.86	mfi	u
<i>Myrmotherula menetriesii</i>	3.07	0.41	3.07	0.84	mfi	u, m
<i>Cercomacra cinerascens</i>	0.14	0	0.56	0	i	c, m
<i>Cercomacra nigrescens</i>	0.14	0.14	0.56	0	i	tf, ef, m
<i>Pyriglena leuconota</i>	0	0	1.95	0.84	aa	u
<i>Myrmoborus myotherinus</i>	0.14	0	1.95	2.51	i	u
<i>Dichrozona cincta</i>	0.84	0.56	0	0.28	i	t
<i>Hylophylax naevia</i>	1.12	1.67	0	1.12	i	u

Appendix. *Continued.*

	Physiognomy and forest type				Guild ^a	Microhabitat ^b
	Control gap	Control understory	Cut gap	Cut understory		
<i>Hylophylax punctulata</i>	0.84	0.56	0	0	i	u, I
<i>Hylophylax poecilonota</i>	5.72	9.35	5.30	11.44	i	u
<i>Hypocnemis cantator</i>	3.07	0.56	6.98	0.56	i	u, ef, tf
<i>Sclateria naevia</i>	0.28	0.14	0	0	i	u, I
<i>Schistocichla leucostigma</i>	0.28	0	0	0	i	u
<i>Myrmeciza hemimelaena</i>	0.28	0.42	4.19	1.40	i	u?, tf, ef
<i>Myrmornis torquata</i>	0.28	0.56	0.28	0.84	i	t
<i>Rhagmatorhina gymnops</i>	4.46	4.32	2.79	3.07	aa	u
<i>Phlegopsis nigromaculata</i>	2.65	0.98	8.37	2.23	aa	u
Formicariidae						
<i>Formicarius analis</i>	0.14	0.14	0.56	0.28	i	t
<i>Formicarius colma</i>	0	0	0.28	0	i	t
<i>Myrmothera campanisona</i>	0.14	0.14	0.28	0	i	t, tf
<i>Hylopezus macularius</i>	0.14	0.14	0	0	i	t
Conopophagidae						
<i>Conopophaga aurita</i>	1.26	1.67	0.28	0.56	i	t
Tyrannidae						
<i>Mionectes oleagineus</i>	0	0	0.56	0	if	u
<i>Mionectes macconnelli</i>	4.60	6.56	6.14	2.23	if	u
<i>Lophotriccus galeatus</i>	0.28	0	1.95	0	i	m
<i>Corythopsis torquata</i>	0.55	0.42	0	0	i	u, t
<i>Platyrrinchus platyrhynchos</i>	1.95	1.81	1.12	1.95	i	u, m
<i>Platyrrinchus saturatus</i>	1.53	0.70	1.40	0.28	i	u, m
<i>Platyrrinchus coronatus</i>	1.67	4.46	0	0	i	u
<i>Rhynchociclus olivaceus</i>	0.14	0	0	0	i	m
<i>Ramphotrigon ruficauda</i>	0.14	0.41	0	0	i	m
<i>Onychorhynchus coronatus</i>	0.98	0.98	1.67	0.84	i	u
<i>Myiobius barbatus</i>	3.49	2.23	2.23	0.28	mfi	u
<i>Terenotriccus erythrurus</i>	1.26	0.56	2.79	1.12	i	m, u
<i>Attila spadiceus</i>	0.28	0.28	0.84	0.56	i	c, m
<i>Rhytipterna simplex</i>	0.42	0.14	0.28	0.28	i	m
<i>Pachyramphus marginatus</i>	0.14	0	0	0	if	m
<i>Pachyramphus minor</i>	0	0	0.28	0	i	m, c
Pipridae						
<i>Schiffornis turdinus</i>	2.09	2.23	0	0.28	fi	u
<i>Tyranneutes stolzmanni</i>	0.14	0	0.28	0	f	m
<i>Manacus manacus</i>	0.14	0.14	0	0	f	u
<i>Pipra iris</i>	10.88	6.00	8.65	3.91	f	tf, ef
<i>Pipra pipra</i>	0	0	0.56	0	f	m
<i>Pipra rubrocapilla</i>	12.70	4.74	24.5	17.30	f	u, m
Cotingidae						
<i>Phoenicircus carnifex</i>	0	0.28	0.28	0.28	f	c, m
<i>Laniocera hypopyrha</i>	0.28	0.14	0.56	0	if	m
<i>Lipaugus vociferans</i>	0.28	0	0	0.84	fi	m
Troglodytidae						
<i>Thryothorus coraya</i>	0	0	1.95	0	mfi	ef
<i>Cyborhinus aradus</i>	3.49	1.81	3.35	0.56	i	t, u
<i>Microcerculus marginatus</i>	0	0	1.12	0.56	i	t, u

Appendix. *Continued.*

	Physiognomy and forest type				Guild ^a	Microhabitat ^b
	Control gap	Control understory	Cut gap	Cut understory		
Sylviidae						
<i>Ramphocaenus melanurus</i>	0.70	0	1.40	0	mfi	m, u
Turdidae						
<i>Catharus minimus</i>	0.14	0	0	0	if	u
<i>Turdus albicollis</i>	0.98	2.65	0.28	0.28	fi	u
Vireonidae						
<i>Vireolanus leucotis</i>	0	0	0.28	0	mfi	c, m
<i>Hylophilus ochraceiceps</i>	1.12	1.12	0	0	i	m, u, tf
Emberizidae: Parulinae						
<i>Granatellus pelzelni</i>	0	0	0.28	0	mfi	m, c
<i>Basileuterus rivularis</i>	0.14	0	0	0	i	m
Thraupinae						
<i>Lanio versicolor</i>	0.98	0.70	0	0	mfi	c, m
<i>Tachyphonus cristatus</i>	0.14	0	0	0	mfif	c, m
<i>Tachyphonus surinamus</i>	2.23	0	0	0	mfif	m
<i>Tachyphonus luctuosus</i>	0	0	0.56	0	mfif	m, ef
<i>Habia rubica</i>	0.70	0.42	0.56	0.28	fi	m
<i>Cyanerpes caeruleus</i>	0.28	0	0	0	n	c
Emberizinae						
<i>Oryzoborus angolensis</i>	0.14	0	0.28	0	f	t, u, ef
<i>Arremon taciturnus</i>	0.56	0.42	4.74	0.56	if	u, ef
Cardinalinae						
<i>Pitylus grossus</i>	0	0	0.56	0.28	fi	m
<i>Cyanocompsa cyanooides</i>	0.56	0.42	3.35	0.84	fi	u

^aGuild: aa = ant-follower; f = solitary frugivore; fi = solitary frugivore-insectivore; i = solitary insectivore; if = solitary insectivore-frugivore; mfi = mixed-species flock insectivore; mffi = mixed-species flock frugivore-insectivore; mfif = mixed-species flock insectivore-frugivore; n = nectarivore; svli = small vertebrates and large insects.

^bMicrohabitat: t = terrestrial; u = understory; m = mid-story; c = canopy; ef = edge of forest; tf = treefall.