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EFFECTS OF INTENSITY AND AGE OF SELECTIVE LOGGING AND TREE GIRDLING ON AN UNDERSTORY BIRD COMMUNITY COMPOSITION IN CENTRAL AMAZONIA, BRAZIL.

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Resumo. Uma comunidade de aves de sub-bosque em Floresta de Terra-Firme na Amazônia central foi amostrada em três parcelas experimentais, divididas em seis quadrados de 4 hectares cada, e tendo corte seletivo de 4 a 10 anos antes da amostragem, e onde o anelamento comercial de árvores de diferentes intensidades ocorreu em 1987, 1988, e 1993. As capturas das aves usando redes ornitológicas ocorreu entre julho de 1996 e janeiro de 1997, totalizando 8620 horas-rede e resultando em 1805 capturas de aves representado 80 espécies. Não houve significantes efeitos das diferentes intensidades do corte seletivo na riqueza de espécies de aves, abundância de aves e a frequência em que elas usaram as áreas de 4 hectares. Os resultados de uma analise de ordenação (Escalonamento não métrico multidimensional), mostraram que a intensidade de corte seletivo não afetou significativamente a composição da comunidade de aves. Contudo, a riqueza de espécies de aves, a abundância de aves e a frequência de uso das áreas experimentais foram fortemente afetadas pela idade do corte seletivo. Uma análise das cinco maiores guildas do subbosque mostrou que especialistas de bordas de floresta, e insetivoros e nectarívoros especialistas em clareiras foram os mais beneficiados com o recente corte seletivo de espécies arbóreas florestais.

Abstract. An understory bird community in central Amazonian upland (*terra firme*) forest was sampled in three experimental plots, divided into six plots of 4 ha each, and logged 4 to 10 years before sampling. Commercial tree girdling and selective logging of different intensities was carried out in 1987, 1988, and 1993. Trapping of birds using mist nets were carried out from July 1996 to January 1997, totaling 8,620 net-hours and resulting in 1,805 bird captures representing 80 species. There were no significant effects of the different intensities of selective logging on bird species richness, bird abundance, or on their frequency of use of the 4-ha areas. Results from an ordination analysis (non-metric multiple dimensional scaling) indicated that, in general, intensity of selective logging did not significantly affect bird community composition. However, bird species richness, bird abundance, and their frequency of use of the areas were strongly affected by the age of selective logging. An analysis of the five major understory bird guilds in the study area showed that edge and gap-specialist insectivorous and nectarivorous birds benefited most from recent selective logging. *Accepted 12 September 2001.*

Key words: *Selective logging, tree girdling, bird community, bird species richness, Amazon forest, forest management, Brazil.*

INTRODUCTION

Tropical countries in South America have been trying to minimize the deforestation of the Amazon rainforest, the world's last large area of continuous tropical forest, in order to conserve its biological and genetic variability and to help maintain the stability of the global climate.

There are considerable forest resources in the Amazon region, and sustainable silvicultural management could be a way of replacing agricultural colonization of the forest after its exploitation (IUCN 1990). Selective logging, as a traditional and practical silvicultural method has become extremely important in the context of the sustained development of the Amazon (Higuchi 1996). Therefore evaluation of the impact of selective logging on the fauna and flora is of fundamental importance to promote sustainable development and conserve vanishing tropical natural resources.

Most studies of wildlife conservation in tropical areas of selective logging have been concentrated in southeast Asia and Africa (Whitmore 1975, Higuchi & Wood 1987, Higuchi 1996). The effects of selective logging on the bird community and other verte-

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brates are clearly related to the degree of disturbance of the forest (Wilson & Wilson 1975, Johns 1991, Mason 1996), time since logging (Wong 1985, Thiollay 1992, Welsh & Healy 1993), and hunting effects on medium and large vertebrates (Bennet & Dahaban 1995).

In the last four years, several studies have analyzed the effects of selective logging on different taxa in central Amazonia. These studies have included the significant effects of selective logging on the litter frogs (Ortiz-Suárez 1997), distribution and growth of palm trees of the genus *Astrocaryum* (Ortiz Brasil 1997), community composition of small mammals (Rittl 1998), two termite species (Lima *et al.* 2000), tree regeneration (Magnusson *et al.* 1999), and understory plant distribution (Costa 2000).

The present study was undertaken as part of a larger multidisciplinary project that seeks to evaluate the effects of an experimental simulation of forest exploitation of an area of upland *terra firme* forest near Manaus in central Amazonia. This project is being executed by the Amazonian National Research Institute (INPA) (Higuchi & Vieira 1990).

The objective of this study is to evaluate the impact of intensity and age of selective logging on understory bird community composition in central Amazonia. We asked the following questions: (1) How does the intensity of selective logging affect the frequency of use of the logged areas by understory birds? (2) Are there differences in bird community structure and composition between areas logged in 1988 and areas logged in 1993 (3) Are different guilds of birds affected differently by selective logging?

SITE AND METHODS

The work was undertaken in *terra firme* forest at the Experimental Station for Tropical Forestry (EEST) of the Instituto Nacional de Pesquisas da Amazônia (INPA). The EEST is located between Km 14 and Km 21 of the local road ZF-2 approximately 90 km to the north of the city of Manaus (2° 37' to 2° 38'S and 60° 09' to 60° 11' W). The climate of the area is warm and humid with annual average precipitation of 2200–2500 mm and annual average temperature of 26°C (Higuchi *et al.* 1985, Higuchi and Vieira 1990, Higuchi 1991).

The study was conducted in a randomized-block design, part of the project "Ecologia e Manejo Florestal" described by Higuchi *et al.* (1985), which consists of three blocks of 24 hectares each. Each block was divided into six plots of four hectares of 200 by 200 m. Each plot had eight parallel 200-m-long trails 25 m distant from each other. The plots were subject to one of the following logging treatments: (1) Selective logging treatments (T1, T2, T3, and T4, see Table 1) in which different wood volumes of species of commercially valuable in local timber markets were removed (Higuchi *et al.* 1985). (2) Treatment T5, tree girdling, consisted in the killing of trees via two incisions with continuous and parallel cuts around the outside of the standing trunks to remove their bark, including the cambium (Jardim 1995). In the blocks managed with this treatment the girdling was done only on those species without commercial value in the local market. The objective of the girdling was to reduce competition for space, light and nutrients with the species considered to have commercial value. According to Jardim (1995) the dead girdled trees produce the effect of small openings in the forest canopy that benefit the growth of opportunistic species, limiting vine proliferation and pioneer species. (3) Plots bearing natural and intact forest without any silvicultural treatment and maintained as Controls (T0). Details about location, time, and intensity of the silvicultural interventions in the managed plots are presented below (Table 1).

Experimental design. Understory birds were captured in 12 × 2.3 m mist nets with 36 mm mesh. The unit of sampling was ten mist nets arranged in a continuous line approximately 120 m along parallel tracks which had been opened in the plots before logging. The mist nets were opened between 05:45 and 06:00 h and checked each half hour until 12:00 h. The lines of 10 mist nets were open during two mornings in each transect of each logging treatment. All birds caught were measured, weighed, and tagged (except those too small such as hummingbirds, and predators such as falcons) with numbered bands. The bands were supplied by the Center of Research for Conservation of Wild Birds (CEMAVE), which is linked to the Brazilian Environmental Agency (IBAMA).

For each plot a capture effort 480 net-hours in 4 capture sessions was used over a period of approximately six months. Each capture cycle represented a capture effort of 120 net-hours covering the entire plot. One of the eight transects was sampled in each plot in each capture session. At the end of the captures there were 4 transects sampled for each of the 18 plots.

An abundance index was standardized to facilitate comparison with other studies. The capture rate was calculated in units of 1000 net-hours for each bird species trapped in each treatment. For this index, recaptures of the same individual in the same treatment were not considered (Table 2).

The relative frequency of use of each plot for each bird species was estimated from the following formula: Frequency of relative use = Ccap\Tcap × 100,

where Ccap = the number of times that each bird species was captured in the plot and Tcap = total number of bird species captured in every study area.

The term guilds used in this study follows that proposed by Root (1967), who defined a guild as a group of bird species that exploit the same type of environmental resources (insects, fruits, nectar, etc.) using similar foraging strategies.

According to Bierregaard (1990), the understory birds in central Amazonian rainforest can be divided into seven main guilds. Mist nets commonly capture the following five guilds: (1) Insectivorous species that follow army-ants; (2) insectivores participating in mixed-species flocks (Munn 1985); (3) small understory frugivorous birds represented mainly by the manakins (Pipridae); (4) nectarivores (hummingbirds), and (5) the tree-fall gap specialists (Schemske & Brokal 1981).

Although there are about 80 bird species commonly trapped in mist nets in Central Amazonian *terra firme* forest (Bierregaard 1990), not all are readily included in clearly defined ecological guilds. In the statistical analysis for this part of the study only those bird species from the above five guilds were used.

Statistical analysis. The effects of different selective logging intensities on the community composition of understory birds were investigated with two simple linear regression analyses (Sokal & Rohlf 1981, Wilkinson 1991). The species richness or abundance of birds was used as the dependent variable, and the different intensities of selective logging as the independent variable (Table 1). Data from the logging in 1993 were excluded to standardize the effect of the age of logging. Analysis of residuals was used to check regression assumptions (Sokal & Rohlf 1981).

The effect of the age of selective logging on the richness and abundance of birds was tested using

TABLE 1. Selective logging treatments used in the managed forest plots.

Blocks	Treatments (plots)	Logging of trees (dbh)*	Wood volume logged (m3)	Year
1	0	Control	(without logging)	
1	1	= 55cm	51.78	1987
1	2	= 50cm	61.33	1987
1	3	= 40cm	67.4	1988
1	4	= 50cm	101.61	1993
1	5	Girdling	–	1985/1986
2	0	Control	(without logging)	
2	1	= 55cm	61.33	1987
2	2	= 50cm	70.3	1987
2	3	= 40cm	98.18	1988
2	4	= 50cm	44.23	1993
2	5	Girdling	–	1985/1986
4	0	Control	(without logging)	
4	1	= 55cm	84.18	1987
4	2	= 50cm	61.86	1987
4	3	= 40cm	106.77	1988
4	4	= 50cm	89.16	1993
4	5	Girdling	–	1985/1986

* dbh = diameter at breast height

Note: Block 3 was not used because it was located in a different habitat (Campinarana)

TABLE 2. Bird species captured in each logging treatment (numbers are rate of capture/1000 Net - hours).

Bird species	BLOCK 1 Logging treatments						BLOCK 2 Logging treatments						BLOCK 4 Logging treatments						p/Total area
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	
FALCONIDAE																			
Micrastur ruficollis														0.11					0.11
M. gilvicollis										0.11				0.11				0.11	0.34
STRIGIDAE																			
Otus watsonii														0.11					0.11
COLUMBIDAE																			
Geotrygon montana	0.11							0.11											0.26
TROCHILIDAE																			
Phaethornis bourcieri		0.11	0.34		0.34	0.23		0.46	0.11		0.23	0.11			0.11		0.34		2.43
P. superciliosus			0.34		0.58	0.46		0.34	0.11		0.34		0.11	0.11	0.23		0.23	0.11	2.90
Campylopterus largipennis					0.23		0.11				0.11				0.11		0.23		0.81
Florisuga mellivora							0.11			0.23									0.34
Thalurania furcata		0.11			0.11					0.11						0.23	0.11		0.69
Heliothryx aurita			0.11					0.11											0.26
TROGONIDAE																			
Trogon rufus							0.11							0.11					0.26
MOMOTIDAE																			
Momotus momota			0.11	0.11			0.11	0.11	0.11	0.11			0.23	0.11				0.11	0.92
GALBULIDAE																			
Galbula albirostris					0.34		0.11	0.23			0.81					0.11	0.11		1.62
BUCCONIDAE																			
Malacoptila fusca							0.11												0.11
Bucco tamatia								0.11											0.11
RAMPHASTIDAE																			
Selenidera culik								0.11											0.11
DENDROCOLAPTIDAE																			
Deconychura longicauda	0.11		0.23		0.11			0.11	0.34	0.11		0.11	0.11	0.11					1.16
D. stictolaema	0.11	0.11	0.11		0.23		0.11	0.11					0.11	0.11	0.11			0.23	1.04
Dendrocincla fuliginosa				0.23	0.11				0.11	0.23	0.11	0.11		0.23	0.11	0.11			1.04
D. merula	0.58	0.23	0.34	0.92			0.11	0.11	0.23	0.11	0.11	0.11				0.11	0.34	0.34	2.66
Dendrocolaptes certhia			0.11			0.11													0.26
Glyphorynchus spirurus	0.34	1.16	0.58	0.34	1.27	0.69	0.81	0.23	0.69	0.11	0.23	0.69	0.81	0.34	0.69	0.69	1.04	1.16	8.23
Xiphorhynchus pardalotus	0.11		0.11	0.11	0.11	0.23	0.23	0.34	0.11	0.23	0.34	0.11	0.11	0.11	0.11	0.23	0.46	0.23	2.32

Bird species	BLOCK 1 Logging treatments						BLOCK 2 Logging treatments						BLOCK 4 Logging treatments						p/Total area
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	
Campylorhamphus procurvoides					0.11	0.11		0.11			0.11	0.11							0.26
Hylexetastes perrotii				0.11															0.11
FURNARIIDAE																			
Synallaxis rutilans	0.11		0.11		0.34	0.23		0.23			0.11	0.23					0.11		1.50
Philydor erythrocercus								0.34				0.11							0.34
Automolus infuscatus	0.34	0.11				0.23		0.46		0.11	0.11	0.11	0.34	0.11	0.11	0.23	0.46	0.34	2.08
A. ochrolaemus	0.11	0.11	0.11	0.46		0.23	0.11		0.23	0.23	0.11	0.11		0.11	0.11	0.11		0.11	1.74
A. rubiginosus					0.11		0.11	0.11		0.11	0.23	0.23	0.11		0.11	0.11	0.23	0.23	0.46
Sclerurus caudacutus		0.34	0.11			0.11				0.11									0.46
S. rufigularis	0.23							0.11				0.11				0.11			0.46
S. mexicanus					0.11														0.11
Xenops minutus	0.11		0.23			0.23		0.23	0.23	0.23	0.11	0.23	0.11		0.11			0.11	1.50
FORMICARIIDAE																			
Cymbilaimus lineatus														0.11					0.11
Frederickena viridis				0.11	0.11														0.11
Thamnophilus murinus		0.11	0.23	0.11	0.11		0.23	0.11				0.11	0.11	0.11		0.11	0.11	0.11	1.62
Thamnomanes ardesiacus	0.11	0.23	0.46	0.23	0.34	0.34	0.46	0.11	0.11	0.11	0.11	0.34	0.69	0.34	0.11	0.23	0.46	0.34	3.59
T. caesius		0.11	0.11	0.23	0.11	0.23	0.23	0.69	0.11	0.46	0.23	0.69	0.34	0.23	0.34		0.23		3.48
Myrmotherula guttata		0.23		0.23		0.23			0.11	0.11			0.11						0.81
M. gutturalis		0.11	0.11		0.11	0.23	0.23			0.34	0.23	0.11	0.23	0.11	0.23	0.23	0.11	0.11	1.85
M. axillaris		0.11			0.11	0.11					0.11		0.23		0.11	0.11		0.23	0.92
M. longipennis	0.34		0.11		0.11	0.11	0.34			0.11	0.11	0.11	0.11					0.11	1.16
M. menetriessii			0.11		0.34	0.11	0.11	0.11			0.11	0.11		0.11		0.11			1.27
Hypocnemis cantator			0.23		0.58	0.11		0.58	0.11	0.11	0.46	0.23			0.23	0.23	0.34	0.34	3.01
Percnostola rufifrons		0.34	0.11	0.69	0.34	0.46	0.11	0.92	0.11	0.11	1.16	0.34	0.23	0.34	0.23	0.69	0.34	0.23	5.22
Myrmeciza ferruginea			0.11	0.11	0.11												0.11		0.46
Pithys albifrons	1.74	0.34	1.85	3.24	0.46	2.08	0.69	0.81	0.92	0.92	0.69	0.58	1.50	0.58	1.04	1.50	1.16	2.43	11.8
Gymnopithys rufigula	0.69	0.11	0.58	1.39	0.46	1.27	0.11	0.46	0.58	0.46	0.46	0.58	0.34	0.23	0.58	0.69	0.92	1.04	6.14
Hylophylax poecilinota	0.34	0.23	0.58	0.69	0.11	0.58	0.34	0.34	0.34	0.81	0.23	0.23	0.34	0.11	0.58	0.34		0.34	4.75
Formicarius colma	0.34	0.11	0.11	0.34	0.11	0.11	0.23	0.23		0.23	0.11	0.23	0.23	0.23	0.46	0.23	0.34	0.23	2.90
F. analis		0.11																	0.11
Myrmornis torquata	0.34	0.23		0.34		0.11	0.23									0.11			1.04
Conopophaga aurita														0.11					0.11
COTINGIDAE																			
Laniocera hypopyrrha													0.11						0.11

Bird species	BLOCK 1 Logging treatments						BLOCK 2 Logging treatments						BLOCK 4 Logging treatments						p/Total area
	0	1	2	3	4	5	0	1	2	3	4	5	0	1	2	3	4	5	
PIPRIDAE																			
Pipra erythrocephala	0.11						0.11				0.11				0.11		0.23		0.69
P. pipra	0.23	0.92	0.34	1.16	0.69	0.11	0.46	1.16	0.81	0.34	0.58	0.23	0.34	0.46	0.69	0.81	0.69	0.69	9.28
P. serena	0.11			0.11	0.11	0.23	0.23	0.11		0.69	0.34	0.46		0.11	0.34	0.23			2.43
Corapipo gutturalis												0.11	0.34						0.46
Neopipo cinnamomea		0.11												0.11					0.26
Schiffornis turdinus							0.11	0.11	0.11	0.11		0.23						0.11	0.58
TYRANNIDAE																			
Attila spadiceus									0.11				0.11						0.26
Corythopis torquata																		0.11	0.11
Hemitriccus zosterops											0.11								0.11
Rhynchocyclus olivaceus	0.11											0.11						0.11	0.34
Rhytipterna simplex																0.11			0.11
Terenotriccus erythrurus					0.11	0.23	0.11				0.23	0.11	0.34		0.23	0.11	0.11		1.62
Myiobius barbatus	0.11						0.34		0.11								0.11		0.58
Platyrinchus saturatus			0.34	0.34	0.34			0.69	0.23	0.11	0.58	0.23				0.34	0.11	0.23	2.32
Mionectes macconnelli	0.11	0.34		0.11	0.11	0.11	0.34	0.11	0.11	0.11	0.23	0.11	0.11	0.23	0.11	0.11	0.34	0.23	2.78
TROGLODYTIDAE																			
Thryothorus coraya					0.23					0.11	0.69		0.11		0.11		0.23		1.39
Microcerculus bambla				0.23	0.11	0.23		0.46	0.46	0.23	0.11	0.11		0.46	0.23	0.23		0.23	1.85
Cyphorhinus arada					0.34							0.11			0.11				0.46
MUSCICAPIDAE																			
TURDINAE																			
Turdus albicollis	0.11	0.23	0.11	0.23		0.34	0.11		0.11				0.23	0.11			0.11	0.11	1.85
SYLVIINAE																			
Microbates collaris	0.11	0.23			0.46	0.11	0.11	0.11		0.11			0.23			0.11		0.11	1.62
VIREONIDAE																			
Hylophilus ochraceiceps	0.11	0.11			0.34	0.23	0.23			0.11	0.11	0.11	0.23	0.23	0.11				1.50
EMBEREZIDAE																			
THRAUPINAE																			
Tachyphonus surinamus				0.11	0.11				0.11	0.11			0.11	0.46					1.04
T. cristatus								0.11											0.11
CARDINALINAE																			
Cyanocompsa cyanoides		0.23	0.11	0.23	0.46	0.11					0.34		0.11			0.23	0.23		1.27
Arremon taciturnus					0.34						0.11				0.11				0.46

analysis of covariance (ANCOVA) in the SYSTAT program (Wilkinson 1991). The data from the treatments of 1987, 1988, and 1993 were used to run the ANCOVA. The control treatments (Table 1) were not used in these analyses because their age was not known. For both the analysis of simple linear regression and ANCOVA the data of 61.33 m^3 and 67.4 m^3 from Block I were not used because of the presence of army ants in these areas. The army ants attract a great number of bird species, most of them obligatory ant-followers (Willis & Oniki 1978). This is a relatively infrequent event in the area and causes a sudden increase in the local bird abundance. A longer-term study would be necessary to include this phenomenon in all plots.

To test the relationship between the frequency of use of the areas by bird species and the different intensities of selective logging, a linear regression analysis was used, using the frequency of use of the areas by the birds as the dependent variable and the logging intensity as the independent variable. To separate *a priori* the effect of time since logging in the regression we did not use the logging data from 1993. Instead they were used together with those from 1987 and 1988 in an analysis of covariance (ANCOVA), to test whether the covariate age of the selective logging would affect the frequency of use of the areas by birds in the different selective logging treatments.

The effect of the age of the selective logging on bird community composition was also investigated by constructing a dissimilarity matrix calculated with the Bray-Curtis index and using the absolute abundance of the species collected in each treatment. The matrix was reduced to two dimensions using multidimensional scaling. The program PATN (Belbin 1992) was used to build the dissimilarity matrix and to do the non-metric multiple dimensional scaling ordination analysis (NMDS). To test the significance of the two axes (MDS 1 and MDS 2) in relation to the ages of the selective logging we used analysis of variance (ANOVA) in the Systat program (Wilkinson 1991).

The Bray-Curtis index has been used and recommended for ecological studies and analysis of bird community composition (Beals 1960, Schemske & Brokal 1981, MacNally 1994). More details and clear explanations on the NMDS ordination analysis, used for plant community in the same study area are available in Magnusson *et al.* (1999).

In the NMDS ordination analysis the data of the intensities of selective logging of 61.33 m^3 and 67.4 m^3 conducted respectively in the Block I (Treatment 2 and Treatment 3) were also not used due to presence of army ants in that area.

To verify the effects of the age and the different intensities of selective logging on the composition (species richness and abundance) of the five avian guilds, we ran two linear regression analyses using the species richness and bird abundance of each guild as dependent variables and the intensity of selective logging as the independent variable. In these analyses, the data for the logging treatments from 1993 were not used. The effect of the logging age was investigated using covariance (ANCOVA), in which the dependent variable was species richness or bird abundance, and the independent variable was logging intensity. The covariate in the ANCOVA models, was the logging age. Data for control treatments were excluded because they were not logged and therefore, we do not know the age of the forest in those areas.

RESULTS

Between July 1996 and January 1997 a total of 1,805 birds was captured and 1,010 birds banded. There were over 700 recaptures in a total of 8,620 net-hours in the three experimental blocks.

The birds captured belonged to 80 species in 18 families (Table 2). The total number of species captured in the whole study area in relation to the total capture effort in each treatment indicates that the community of understory birds was well sampled during the six months of captures, reaching the asymptotic value of about 80 species (Fig. 1).

Effects of selective logging on species richness, bird abundance, and frequency of use of the logged areas. There was no significant relationship between species richness, bird abundance, or frequency of use of the areas by birds, and the intensities of selective logging (species richness $r^2 = 0.104$; n = 10; $P = 0.75$; bird abundance $r^2 = 0.001$; n = 10; $P = 0.99$; frequency of use $r^2 = 0.175$; n = 12; $P = 0.58$). However, there were significant relationships between species richness $F_{1,7} = 5.94$; $P = 0.045$ (Fig. 2a), bird abundance $F_{1,7} = 20.45$; $P = 0.003$ (Fig. 2b), and frequency of use of the areas by birds ($F_{1,9} = 12.18$; $P = 0.007$) and time since selective logging.

Effects of selective logging on the obligate army-ant-following bird guild. Of the three species of obligatory army-ant-following birds present in the study area. *Pithys albifrons* and *Gymnopithys rufigula* were the first and third most abundant bird species overall. For this group of birds there was no significant relationship between species richness and intensity of selective logging ($r^2 = 0.167$; n = 12; $P = 0.60$), or between bird abundance and intensity of selective logging ($r^2 = 0.046$; n = 12; $P = 0.88$). There were no significant effects of time since logging on species richness (analysis of covariance, $F_{2,8} = 1.80$; $P = 0.22$) or bird abundance ($F_{2,8} = 2.64$; $P = 0.10$) in this guild.

Effects of selective logging on mixed-species flocks. In the study area there are many species of insectivorous birds that forage regularly in mixed-species flocks with the nuclear species *Thamnomanes caesius*. Neither species richness (analysis of regression $r^2 = 0.511$; n = 12; $P = 0.089$) nor bird abundance ($r^2 = 0.434$; n = 12; $P = 0.15$) were significantly affected by different intensities of selective logging. Also the different years (ages) of selective tree logging did not significantly affect the species richness of this guild (ANCOVA $F_{2,8} = 0.249$; $P = 0.78$), nor bird abundance ($F_{2,8} = 0.625$; $P = 0.55$).

Effects of selective logging on gaps and forest-edge specialists. The five bird species in this group commonly caught in the study area were not significantly affected in their species richness ($r^2 = 0.49$; n = 12; $P = 0.10$), or bird abundance ($r^2 = 0.277$; n = 12; $P = 0.38$) by the differing intensity of selective logging. Also, species richness was not significantly affected by time since logging ($F_{2,8} = 1.54$; $P = 0.27$; Fig. 3a). However, bird abundance was significantly affected by time since logging ($F_{2,8} = 6.06$; $P = 0.025$; Fig. 3b).

Effects of selective logging on frugivores. Manakins (Pipridae) were the most common small-sized frugivorous birds captured in the study area. The most abundant species was *Pipra pipra*, making 6.13% of captures (Table 2). This species was the third most abundant of those trapped.

There were no significant relationships between the species richness ($r^2 = 0.264$; n = 12; $P = 0.40$) or bird abundance of frugivore species ($r^2 = 0.61$; n = 12; $P = 0.13$) and the different intensities of selective logging. Bird richness of frugivorous species was not affected by the time since selective logging ($F_{2,8} = 0.90$; $P = 0.44$), nor was bird abundance ($F_{2,8} = 1.28$; $P = 0.32$).

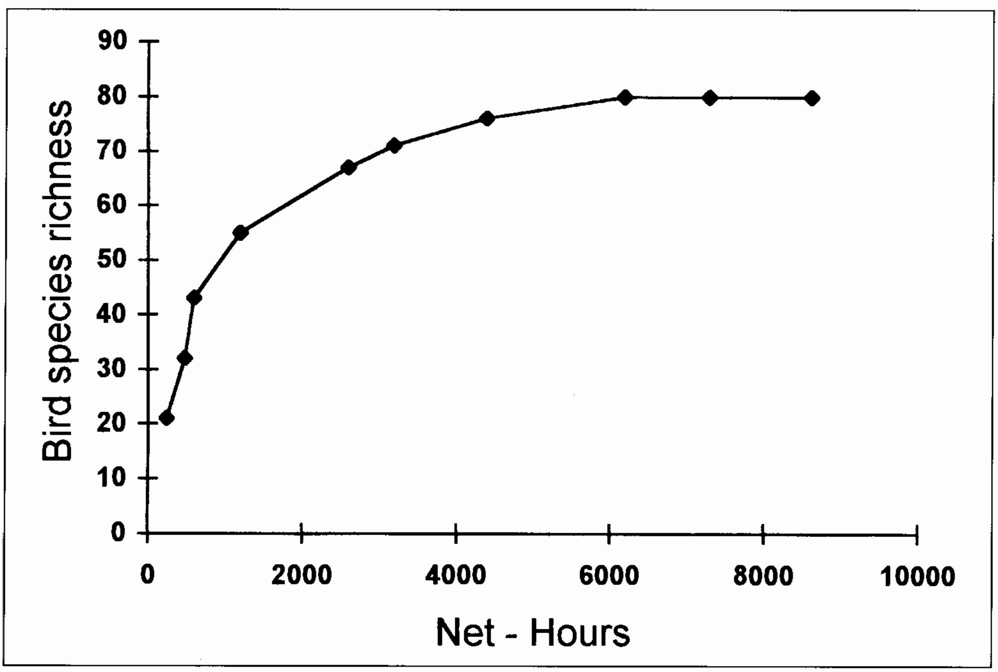

FIG. 1. Number of bird species captured in *terra firme forest*, central Amazonia, in relation to capture effort.

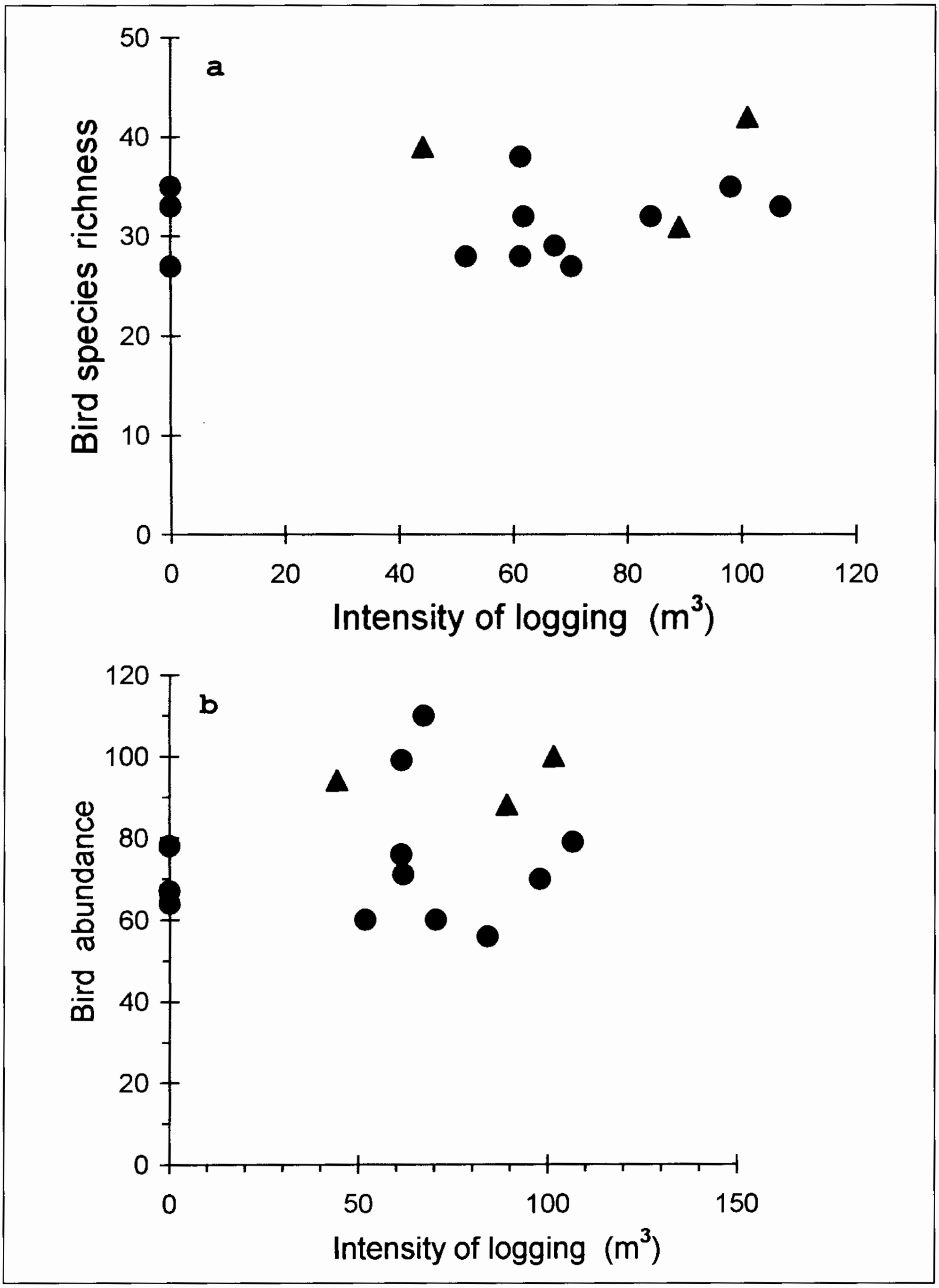

FIG. 2. Bird species richness (a) and bird abundance (b) in relation to the different intensities of selective logging. The triangles indicate the results in plots logged in 1993 and the dots indicate the results in treatment controls and in plots logged in 1987 and 1988.

Effects of selective logging on nectarivores. Five hummingbird species of this guild were captured (Table 2) and *Phaethornis superciliosus* and *P. bourcieri* were the most abundant.

There were no significant relationships between the richness of nectarivore species and the different intensities of selective logging (r^2 = 0.084; n = 12; P = 0.79), or bird abundance (r^2 = 0.187;n = 12; P = 0.56) and the different intensities of selective logging. However both richness of nectarivore species ($F_{2,8}$ = 15.71; P = 0.002, Fig. 3c) and bird abundance ($F_{2,8}$ = 6.69, P = 0.020, Fig. 3d) were signicantly affected by time since logging.

Effects of selective logging on bird community composition. There was no significant effect of time since logging on bird community composition (ANOVA using MDS1 as the dependent variable, $F_{1,8}$ = 1.16; P = 0.31). However there was significant effect of time since logging on bird community composition when testing the axis MDS2 as the dependent variable ($F_{1,8}$ = 6.034; P = 0.040). The logging treatments of 1987 and 1988 were in an advanced stage of regeneration and together with the controls formed a separate group from the logging carried out in 1993 (Fig. 4).

Effects of tree girdling on species richness. Due to the small number of replicates in the girdling treatment we decided not to do statistical analysis. However, our results suggest that species richness and bird abundance in the blocks under girdling were not different from the control areas (intact forest).

DISCUSSION

A relatively high number of understory birds (80 species) was trapped considering the amount of effort employed in an area of 72 hectares. Similar results

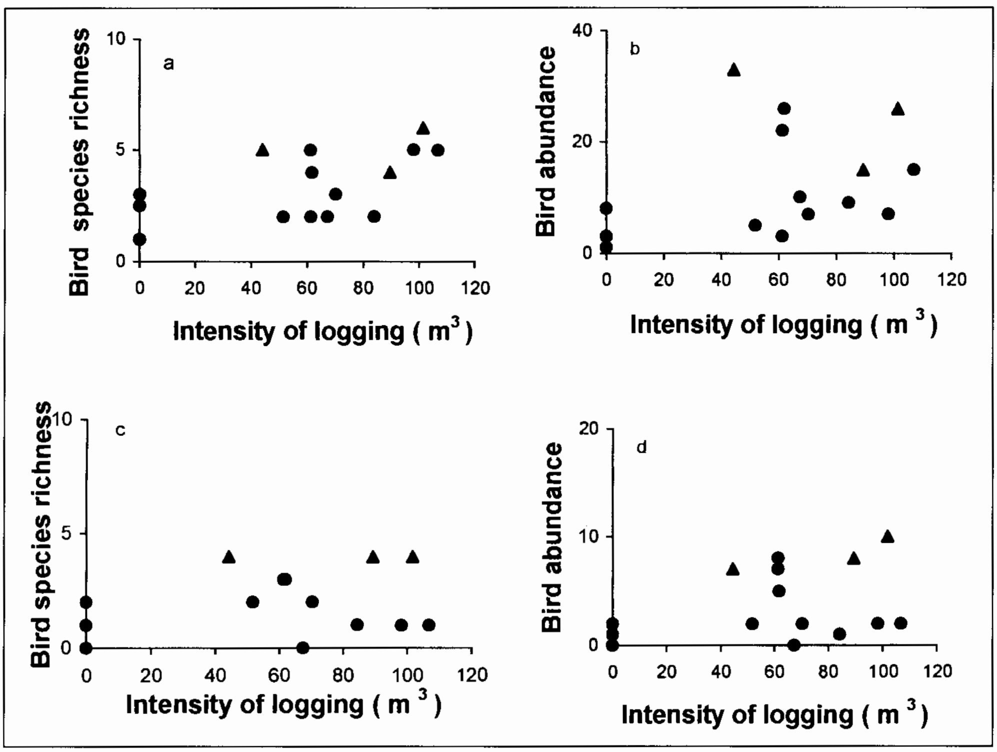

FIG. 3. Bird species richness and bird abundance of guilds in relation to the intensity of logging. Guilds: (a) and (b) specialist insectivores at gaps and forest edge; (c) and (d) nectarívores. For explanation of triangles and dots see Figure 2.

were found by Wong (1985), who captured 73 species in an area of 16 ha in Malaysia, where selective extraction of timber occurred 25 years ago. Mason (1996) captured 117 understory bird species in an area of undisturbed forest with selective logging in the Venezuelan Amazon rainforest. However, his area was much larger, and his capture effort and that by Wong were much more than ours.

Cohn-Haft *et al.* (1997) presented a checklist and revision of the bird species occurring around Manaus identifying 352 species. From that total 167 were canopy and understory inhabitants, and forest edge and ground specialists. A high number of these species could be present in our study area, however they were not captured in the mist nets.

Effects of selective logging on species richness and bird abundance. The low variation we found in species richness and bird abundance could be due to the proximity of the plots. Most of the birds in the Amazon rainforest have home ranges larger than the area (4 hectares) of each selective logging treatment used in this study (Terborgh *et al.* 1990). Because the birds are in constant movement in the area, this may in-

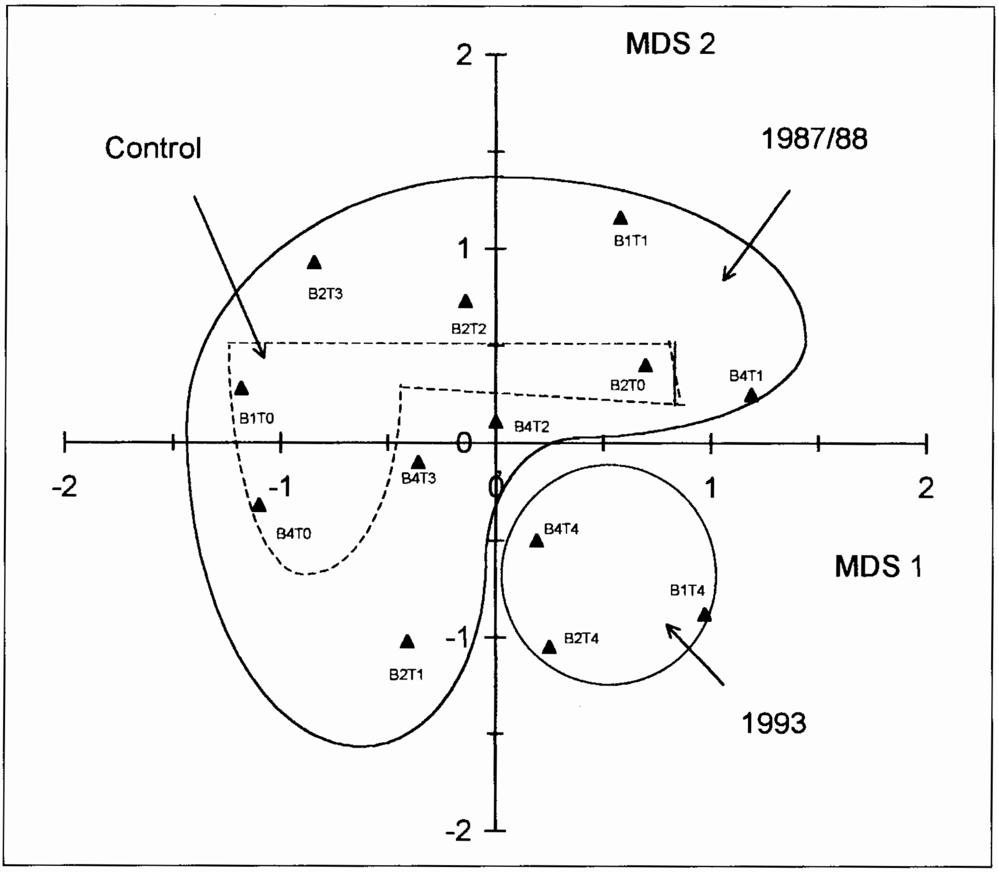

FIG. 4. Results of the Multidimensional Scaling Ordination analysis (MDS) on bird community composition (richness and abundance) from blocks (B) and treatments (T) studied. The semi-circle indicates the logging treatments of 1987/88, inside of which are the treatment controls (stippled line). The small circle represents the results in areas logged in 1993. The blocks B1T2 and B1T3 were not included in this analysis due to the presence of obligate army-ant- following birds during at least two days of sampling.

crease the probability of these species being recaptured several times, not only in the plots but also over all experimental blocks. However, the plots under selective logging in 1993 constitute an exception to the 1987 logging, 1988 logging, and controls. These areas presented higher species richness and bird abundance, indicating that changes in the behavior of the birds can still be detected on a small spatial scale. Although the plots logged in 1993 have short vegetation, they still have some large tree-fall gaps. This modified forest structure may favor colonization by bird species that are associated with disturbance in areas of regeneration, and at the same time maintain those species originally from primary forest which are resistant to disturbances.

In the areas logged in 1987 and 1988, species richness and bird abundance varied more atound the control values rhan those from the logged area in 1993. Today all these areas are under advanced forest regeneration, consisting of young trees above 12 meters in height. This creates a mosaic of vegetation where most species are typical of secondary growth. For example *Cecropia* trees, after reaching the canopy, reduce the light reaching the interior of the forest and consequently create conditions in these areas more similar to the surrounding primary forest. The logging intensities 61.33 m^3 and 67.4 m^3 did not follow the same patterns of the other treatments. They turned out to be two outliers in the analysis, possibly due to a passage of the army ant species *Eciton burchelli* during two days of the sampling (E.G. Silva, obs.). The army-ants may have attracted a large number of species including army-ant-following birds (Oniki & Willis 1972). This additional bird activity in the areas of Treatments 2 and 3 in Block 1 may have increased species richness and bird abundance in those areas.

Effects of selective logging on frequency of use of the areas by birds. The relative frequency of use of the areas by birds, as well as species richness and bird abundance was more affected by the age of the logging than its intensity. More than 20% of all the bird species captured were using the areas logged in 1993. Forest regeneration may have attracted a large number of specialist species to natural gaps and forest edges. It may also attract frugivores and nectarivores skilled in exploring the resources produced by the fast growing secondary vegetation developed soon after the selective logging (Johns 1985). In addition, some insectivores from primary forest may stay in the area due to their tolerance of forest disturbance.

Effects of selective logging on bird guilds. The species richness and bird abundance of the five guilds studied were not affected by the different intensities of logging in the years 1987 and 1988, except insectivorous birds which are forest edge and gap specialists and the nectarivores that were favored by the logging in 1993.

Effects of selective logging on insectivores. Except the woodcreeper *Dendrocincla merula*, which did not occur in some logging treatments, the bird species components of this guild were well represented in the study area. The antbirds *Pithys albifrons* and *Gymnopithys rufigula* were trapped in all logging treatments and in high numbers. This is because these birds are more than 50% dependent in their diet on insects that are disturbed by the army ants (Oniki 1972). In the study area the ant species *Eciton burchelli* has nomadic periods of up to 14 days during the 35 days of its reproductive cycle (Willis & Oniki 1978). In the remaining days the ants are sedentary.

Bird species dependent on army-ants tend to monitor various army ant swarms during the day, and they always locate at least one available bivouac of army-ants. Because of this behavior the home range of these bird species can exceed 200 hectares (Bierregaard 1990). This helps to explain the high rates of capture in the experimental blocks. This higher rate of capture, however, may obscure the potential effect of the intensities of selective logging on this guild, considering that each logging treatment has an area of 4 hectares. In fact Thiollay (1992), working in areas of selective logging in French Guiana, found most of the terrestrial species, including the army-ant-following birds, among the species more affected by selective logging. However Thiollay used a different method, the fixed point count, or registration of those birds that vocalize for a certain time. Stouffer and Bierregaard (1995b) argued that the results found by Thiollay, mainly for the species *Pithys albifrons* and *Gymnopithys rufigula*, can be due to the difficulty in detecting these species through fixed point counts in areas of dense secondary vegetation.

The mixed-species flocks (Winterbottom 1949, Buskirk *et al.* 1972, Moynihan 1979, Munn 1985, Powell 1985) were present in all forest logging treatments and *Thamnomanes caesius* was the nuclear species (E.G. Silva, pers. obs.). In the Amazon forest the bird species that participate in mixed-species flocks have territory sizes ranging from 8 to 12 hectares (Powell 1989). Therefore it would not be easy to detect an effect of the different logging intensities on this type of guild considering that the captures were concentrated in plots of 4 hectares. However, the fact that members of mixed-species flocks were trapped in the nets and were observed foraging in all areas of logging treatments, indicates that they have not abandoned those areas. According to Stouffer & Bierregaard (1995b), the understory mixed-species flocks forage up to a height of 10–20 m and consequently they use areas of secondary growth dominated by *Cecropia* sp. This was the case in the areas where selective logging was conducted in 1987 and 1988. However, in the areas logged in 1993 the secondary forest with four years of regeneration contained trees of 10 m in height. Therefore, for this guild, we found no significant differences in species richness and bird abundance between this area and other areas. In the Amazon region, Cintra (1997) studied the use of forests and savannas by 12 species of insectivorous birds (tyrant flycatchers) and found no significant differences in both their vertical distribution in the vegetation and the foraging behavior when comparing these two habitats. But he did find strong and positive correlations between perch position and tree height. His results suggest that some insectivorous bird species can adjust their behavior to different degrees of vegetation disturbances.

Effects of selective logging on edge and gap specialists. The tree-fall gaps formed in the forest during selective logging may simulate the natural falling of trees in the primary forest, and may be attractive to those species of insectivores that exploit resources from forest areas in regeneration. In Panama, the guild specializing in tree-fall gaps – apart from a granivore *Cyanocompsa cyanoides* that was also captured in our study area – was mainly composed of insectivores (Schemske & Brokal 1981), and was also different from that found in the adjacent areas of primary forest.

In our study area, the bird abundance of this guild was affected by the logging carried out in 1993. *Percnostola rufifrons* was the most captured in the other logging treatments, while *Thryothorus coraya*, *Hypocnemis cantator*, and *Galbula albirostris* were captured only in logging Treatment IV from 1993. These logging treatments are the only ones that have created large gaps due to tree removal in the area. The same effect was not detected in the controls areas (intact forest) and much less in the areas logged in 1987 and 1988.

These results clearly show that the age of the regeneration is an important factor affecting bird community composition in tropical forests.

Effects of selective logging on frugivores. This guild can be divided into two groups: (1) the large-bodied frugivores such as cracids, tinamids, psophids and phasianids, or birds that depend on fallen fruits of the trees; which represent up to 90% of the biomass of the frugivorous birds in the forest (Terborgh 1986); and (2) the small frugivores, mostly represented by species of the family Pipridae (Bierregaard 1990). Although the first group represents a significant part of the avian biomass in the forest, these species are rarely captured in mist nets because they are too big to be trapped by the small meshes of the nets (Bierregaard 1990). Perhaps because of this only small frugivores were captured in the present study.

Pipra pipra was the most abundant bird captured in all logging treatments, followed by *P. erythrocephala*, *P. serena*, *Schiffornis turdinus*, and *Turdus albicollis* (Table 2). Mason (1996) showed that manakin numbers decreases considerably with the increase in the level of disturbance of the forest. He also found that *P. erythrocephala* increased considerably in numbers in the disturbed forests after selective logging and in linear plantations. Although the methods he used were the same as in this study, at least for this group of species the pattern found by Mason was not confirmed in our area. Bird abundance varied close to the average values found in the control areas, not confirming an effect of age or intensity of selective logging on this avian guild. One of the explanations could be the low production of fruits that occurs in tropical forests during the dry season (Terborgh 1986) when we captured the birds. The abundance of frugivores increased considerably during the period of highest fruit production (Loiselle & Blake 1991, 1993) that occurs in the rainy season (Poulin *et al.* 1992). So, if our bird sampling had been carried out during the rainy season, perhaps a selective logging effect on this guild would have been detected.

Effects of selective logging on nectarivores. In the study area this group is represented by five species of the family Trochilidae. It was the only guild having both species richness and bird abundance benefiting by the most recent logging treatments (in 1993). In fact Costa (pers. comm.), while recording the phenology of trees in our study site, observed that in the 1993 logging treatments, which were not at a flowering peak, were bearing a larger number of flowering plots, such as Heliconiaceae, Rubiaceae, and Melastomataceae, than the other treatments. According to Costa (2000), during the flowering period that difference was not so evident. However, Magnusson *et* *al.* (1999), also working in the area, found a higher abundance of trees (>10 cm dbh) in the plots logged in 1993 and 1987 than in the control. This may explain the largest abundance of nectarivores in these areas and support the findings that *Phaethornis superciliosus* and *P. bourcieri* are the most abundant exploiters of disturbed areas (Johns 1991, Stouffer & Bierregaard 1995a, 1996). Mason (1996) found similar results for this guild in areas of selective logging and linear plantations in Venezuelan Amazon rainforest.

Effects of girdling on birds. The species richness, bird abundance, and their frequency in using the area, were not significantly different between areas with tree girdling and those with controls (intact forest).

Although the object of this treatment would be to kill the standing trees for the opening of small gaps, it would be expected that some bird species associated with forest gaps could benefit by this situation and use them more often. However, the tree girdling treatments have apparently not affected the bird community when compared to the controls. This may be because girdling occurred more than 10 years ago, which probably is enough time to allow forest regeneration and reestablishment the microclimatic environments similat to that found in primary forest.

Bird conservation. In the last few years a substantial literature has been produced aimed at solutions towards the best way to reconcile the economic development of Amazonia and the conservation of its biodiversity. Deforestation for agricultural land or pasture has been increasing the number of forest fragments in areas where previously there was continuous forest. This raises the crucial topic of the minimum fragment size that could support a representative number of species, and could characterize the diversity of the local ecosystem (Lovejoy 1980, Lovejoy & Rankin 1981), considering that the loss of species in small fragments is very high. However, many people use the forest resource, without modifying drastically its original vegetation composition. One method of sustained management of the forest by following its dynamics, for example, could be by using selective logging, which sometimes 'mimics' the formation of tree-fall gaps.

Although most of the studies carried out in areas of selective logging in the tropics have shown that it does have effects on bird community structure, many authors agree that the areas in which selective logging has occurred are still capable of maintaining a great number of bird species that would not survive in small and isolated reserves.

Recent studies in forest fragments, 40 km from the area where we worked, showed that obligate army ant followers are the first birds to disappear, while some components of complex heterospecific mixed-species flocks disappear, from the fragments within two years following isolation (Bierregaard 1989, 1990; Lovejoy & Bierregaard 1990). The results of our study, however, indicate that, independent of the intensity and age of selective logging, the bird species from different functional groups such as insectivores, frugivores, and nectarivores continued using the areas. This suggests that if small forest patches are managed with selective logging, and surrounded by native forest, a great number of bird species that otherwise would not be tolerate to forest disturbance would persist in the logged areas.

The present study indicates that there are few significant effects of logging. Due to the extensive sampling conducted, the results are likely to be representative of the impact of selective logging on bird communities when undertaken on the scale considered here. A subsequent study, using a similar design, but over a much larger area (expetimental blocks of 1000–5000 ha and sampling units of 10 ha) located 250km from our study area, arrived at the same general results (Marcela Torres pers. comm.). The effects of carefully controlled selective logging in central Amazonia on other organisms also appears to be moderate to low (Ortiz Brasil 1997, Ortiz-Suárez 1997, Rittl 1998, Magnusson *et al.* 1999, Costa 2000). Therefore, in some situations, selective logging may be better for conservation than alternative land uses.

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