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## USE OF AMAZONIAN FOREST FRAGMENTS BY UNDERSTORY INSECTIVOROUS BIRDS<sup>1</sup>

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**Abstract.** We sampled understory insectivorous birds in Amazonian forest fragments from before isolation through 9 yr after isolation. We accumulated 3658 mist net captures of 84 insectivorous species in five 1-ha fragments and four 10-ha fragments. Abundance and species richness declined dramatically after isolation, even though fragments were separated from continuous forest by only 70–650 m. Three species of obligate army ant followers disappeared within the first 2 yr after isolation. Mixed-species flocks containing 13 commonly netted species disintegrated within 2–3 yr after isolation, although three species that dropped out of flocks persisted in fragments. Among insectivores not associated with flocks or army ants, only two species of edge specialists were unaffected by fragmentation. Overall, loss of forest insectivores was not compensated for by an increase in nonforest or previously uncommon species.

Secondary vegetation surrounding fragments strongly affected use of fragments after isolation. Fragments surrounded by *Vismia*, the dominant regrowth where felled forest was burned and temporarily used as cattle pasture, remained depauperate. In contrast, many species returned to fragments by moving through regenerating forest dominated by *Cecropia*, which occurred in areas where the felled forest was not burned. Both 1- and 10-ha fragments surrounded by *Cecropia* were used by ant followers by 5 yr after isolation. Mixed-species flocks reassembled in 10-ha fragments surrounded by *Cecropia* by 7–9 yr after isolation, and augmented their group territories by foraging in secondary forest outside fragments. Solitary species were more variable in their responses, although several species returned to 10-ha fragments surrounded by *Cecropia*. Terrestrial insectivores, such as *Scelerurus* leafscrapers and various antbirds, did not return to any fragments, and appear to be the group most vulnerable to fragmentation.

Ordination of the insectivore community showed that 1-ha fragments diverged from their pre-isolation communities more than did 10-ha fragments. Communities in 10-ha fragments surrounded by *Cecropia* were more closely associated with pre-isolation communities than those in fragments surrounded by *Vismia*. Over time, communities in 10-ha fragments surrounded by *Cecropia* became more like pre-isolation communities, although communities in other fragments generally continued to diverge.

**Key words:** Amazonia; bird communities; Brazil; *Cecropia*; colonization; *Dendrocolaptidae*; *Formicariidae*; fragmentation; *Furnariidae*; insectivory; *Vismia*.

### INTRODUCTION

Fragmentation of forest habitat affects the diversity and abundance of plants and animals in various forest types (e.g., Galli et al. 1976, Gottfried 1979, Shreeve and Mason 1980, Weaver and Kellman 1981, Main 1987, Klein 1989). For birds, studies in North America have generally indicated that forest birds, especially forest interior species, are vulnerable to fragmentation of breeding habitat (reviewed by Askins et al. 1990). The effects of fragmentation on tropical birds have been less thoroughly studied (but see Leck 1979, Willis 1979a, Bierregaard and Lovejoy 1989, Kattan et al. 1994). Available data suggest that some tropical spe-

cies may be even more vulnerable to fragmentation than temperate species. Neotropical forest birds, especially in the Amazon basin, are generally more specialized in their foraging techniques, use narrower habitats and microhabitats, are more sedentary, and have larger territories than temperate forest birds (Orlans 1969, Willis 1974, Remsen and Parker 1984, Karr et al. 1990, Terborgh et al. 1990).

To understand the effects of fragmentation, it has become increasingly important to examine fragments as part of a larger matrix that includes fragments of various sizes, continuous forest, and intervening disturbed areas (e.g., Askins et al. 1987, Keller and Anderson 1992, Fahrig and Merriam 1994). A related aspect of fragmentation that has received little attention is the effect of changing land use in the matrix surrounding fragments (e.g., Askins and Philbrick 1987). These landscape and temporal effects influence fragment use by birds. Moreover, interspecific variation in response to landscape effects are likely to be signifi-

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cant, especially among the sedentary, specialized birds of the Neotropics.

Part of the reason temporal effects are poorly known is related to the design of most studies of forest fragmentation. In most cases, response to fragmentation has been inferred from comparisons among fragments of various sizes sampled at the same time. These comparisons of fragments are useful for examining habitat associations (e.g., Ambuel and Temple 1983, Freemark and Merriam 1986, Blake and Karr 1987) or how fragment size influences species richness (e.g., Bolger et al. 1991, McCoy and Mushinsky 1994). The only direct measure of the effects of fragmentation, however, is to sample the same plot before and after it is isolated (e.g., Lovejoy et al. 1986). Repeated sampling also allows examination of successional processes, structural deterioration, and other gradual changes in fragments (Lovejoy et al. 1986, Robinson et al. 1992, Stouffer and Bierregaard 1995).

Here we examine the effects of fragmentation on the diversity and abundance of understory insectivorous birds at a site in Amazonian Brazil. These fragments were sampled from before isolation through 9 yr after isolation. We consider fragments of two sizes, 1 and 10 ha, that are surrounded by two distinct types of secondary growth. Patterns of human disturbance in the Brazilian Amazon often result in small forest fragments and abandoned fields like the ones we studied (e.g., Uhl 1987, Dale et al. 1994). Completely isolated fragments of this size can support no more than one or two pairs of even the commonest understory birds (Terborgh et al. 1990), so fairly rapid extinction is inevitable (e.g., Diamond 1984). Because of rapid extinction, small fragments provide the opportunity to study recolonization on a relatively short temporal scale (see discussion in Rosenzweig and Clark 1994). Our emphasis on recolonization stresses the interaction of the fragments with the temporally variable matrix in which they are imbedded.

We describe the sequence of species loss and subsequent recolonization, how social organization and foraging behavior affect vulnerability to isolation, and the extent to which loss of forest insectivores is compensated for by increased abundance of nonforest species or previously uncommon species. Based on these results, we predict the species that are most likely to be threatened in a fragmented Amazonian landscape. We also suggest research that could further assess habitat requirements for persistence and recolonization of vulnerable birds.

#### STUDY SITE

##### *The biological dynamics of forest fragments project study site*

This study was conducted in terra firme forest 80 km north of Manaus, Brazil (2°30' S, 60° W). Here we include data for five fragments of 1 ha and four frag-

TABLE 1. Characteristics of 1- and 10-ha forest fragments at the BDFFP site. Number refers to the reserve code used in other publications (see Lovejoy et al. 1986 for detailed descriptions of the fragments). Code refers to the codes used here, and indicates fragment size, type of secondary growth, and the number of the replicate.

Code	Num- ber	Location	Size (ha)	Year of isola- tion	Secondary growth
1V-1	1104	Colosso	1	1980	<i>Vismia</i>
10V-1	1202	Colosso	10	1980	<i>Vismia</i>
1C-1	1112	Cidade Powell	1	1983	<i>Cecropia</i>
10C-1	1207	Cidade Powell	10	1983	<i>Cecropia</i>
1C-2	3114	Porto Alegre	1	1983	<i>Cecropia</i>
10C-2	3209	Porto Alegre	10	1983	<i>Cecropia</i>
1V-2	2107	Dimona	1	1984	<i>Vismia</i>
1V-3	2108	Dimona	1	1984	<i>Vismia</i>
10V-2	2206	Dimona	10	1984	<i>Vismia</i>

ments of 10 ha (see Lovejoy et al. 1986, Lovejoy and Bierregaard 1990, Bierregaard et al. 1992 for more detailed descriptions of the site). These fragments are located on three adjacent cattle ranches, with  $\approx 40$  km separating the most distant fragments (Table 1). Although some parts of the area have been cleared for cattle ranching, these local disturbances are within an area that is mostly unbroken forest for hundreds of kilometres (see Vitousek 1994 for a LANDSAT image of the site).

Canopy height averages 30–35 m with occasional emergents up to 55 m. The understory is relatively open and dominated by palms. Density of understory plants is low compared to other Neotropical sites, probably because of poor soils (Gentry and Emmons 1987). Rainfall at Reserva Ducke, 50 km south of the study site, averaged  $\approx 2500$  mm/year from 1966 to 1990, with annual peaks from January to April and a pronounced dry season from June to September (Stouffer and Bierregaard 1993).

Fragments were isolated when ranchers cut the surrounding vegetation during the dry season (see discussion in Bierregaard 1990a). Fragments were separated by distances of 70–650 m from the nearest continuous forest, although six of the nine fragments we consider were separated by 100–200 m. Following cutting, treatments differed among the fragments (Table 1). Cut areas around the Colosso and Dimona fragments were burned, but the fallen timber was not burned at Porto Alegre and Cidade Powell. The area around the Colosso and Dimona fragments has been partially cleared and used by grazing cattle at irregular intervals, but too infrequently to prevent regeneration of patches of dense secondary growth dominated by trees in the genera *Vismia* (Clusiaceae) and *Bellicia* (Melastomataceae). By 1991 this growth had reached a height of 3–7 m around the Dimona reserves and 5–10 m in some areas around the Colosso reserves. The areas surrounding the Cidade Powell and Porto Alegre reserves regenerated rapidly into a forest with a closed canopy of

*Cecropia sciadophylla*. By 1991 this growth had reached 12–15 m.

#### *The understory bird community at the site*

The avifauna of central Amazonia is extremely rich in species;  $\approx 400$  species of birds have been recorded from our forest sites and adjacent secondary areas (Stotz and Bierregaard 1989, Karr et al. 1990). Among  $\approx 200$  diurnal species that regularly occur within the forest, most species restrict their activity to one or two strata. The understory community has been quantitatively sampled with ground-level mist nets. This group of birds includes  $\approx 40$  species that are terrestrial or restrict their activity to the first 2–3 m of the understory. About 56 species use the understory and the midstory, but only about half of these are regularly captured in ground-level mist nets. Over 100 species occur in the canopy, but these are almost never netted. Our analysis here is restricted to insectivorous birds in the mist net sample. Most of these insectivores, especially the ovenbirds, woodcreepers, and antbirds that dominate the sample, feed almost exclusively on small invertebrates (see accounts in Hilty and Brown 1986). We also include four uncommonly netted species, *Attila spadiceus*, *Laniocera hypopyrrha*, *Pachyrhamphus minor*, and *Celeus elegans*, that take some fruit but appear to be primarily insectivorous at our site (Hilty and Brown 1986, Mesquita 1989; P. C. Stouffer, *personal observation*). Our analysis excludes raptors, hummingbirds, and birds that are strongly frugivorous. Based on fecal samples and observations of foraging birds, we also exclude commonly netted birds that regularly consume both fruit and insects, such as *Mionectes macconnelli*.

In addition to the familiar social structure of pairs or family groups defending territories, many species participate in multispecies assemblages. Ten to 20 understory and midstory species regularly travel together in mixed-species flocks. These flocks use areas of 8–12 ha at our site, and are led by a nuclear species, *Thamnomanes caesi*, whose vocalizations orient the flock (Powell 1985, Stotz 1993). A second multispecies assemblage forms at army ant (*Eciton burchelli*) swarms, feeding on arthropods fleeing from the marauding ants (Willis and Oniki 1978, Harper 1987). Three common species, the woodcreeper *Dendrocincla merula* and the antbirds *Pithys albifrons* and *Gymnopithys rufigula*, feed almost exclusively at ant swarms, often with several pairs of *Pithys* and *Gymnopithys* feeding at the same swarm (Willis and Oniki 1978, Willis 1979b). Several other species, especially the woodcreepers *Dendrocincla fuliginosa* and *Dendrocolaptes picumnus* and the antbirds *Hylophylax poecilinota*, *Percnostola rufifrons*, and *Formicarius colma*, feed at swarms that pass through their territories, but do not follow swarms as they enter a neighboring territory (Willis 1972, 1982a, b, Hilty and Brown 1986). Army ants are not restricted to forest; they swarm into

secondary growth, although most forest birds will not accompany them into young secondary growth (Willis and Oniki 1978, Willis 1979b, 1982b).

Previous analysis showed a strong pulse in abundance of understory birds in fragments just after isolation, presumably due to the influx of birds that previously lived in the deforested area (Bierregaard and Lovejoy 1989, Bierregaard 1990a). Following this brief peak, capture rates declined, and by 1 yr after isolation were below pre-isolation levels. Obligate army ant followers declined in abundance rapidly, and flocks disintegrated within 2 yr (Bierregaard and Lovejoy 1989).

## METHODS

### *Netting*

Before isolation, trails were cut through the areas that were to be isolated. Lines of eight mist nets (NEB-BA-type ATX, 36-mm mesh, 12  $\times$  2 m), set with the bottom of the net at ground level, were used to sample 1-ha fragments. Lines of 16 nets were used in 10-ha fragments. Each line was netted for 1 d at a time. Nets were kept open from 0600 to 1400. Generally, sites were sampled about once every 2 mo from before isolation until  $\approx 3$  yr after isolation, less frequently until 1991, and every 6 wk from 1991 to 1992. Data included here are based on 40 245 net hours (nh), 11 208 before isolation and 29 037 after isolation. With the exception of 1C-2, all fragments were sampled at least 5 times over at least 5 mo before isolation (mean = 14 samples over 19 mo). Fragment 1C-2 was only sampled twice in the month before isolation, so the pre-isolation community in this fragment is less well characterized.

Mist netting is a technique that can be readily standardized and is relatively free from observer biases, factors essential in a long-term study such as this (Karr 1981a, b). Large species and species that seldom fly are underrepresented by mist netting, as are birds that rarely descend below the midstory. Nevertheless,  $\approx 50$  species are captured regularly enough at our sites to permit statistical comparisons among sites and over time. Mist netting is a particularly important technique for sampling species that are difficult to see and seldom vocalize (Terborgh et al. 1990). At our site, these inconspicuous species include a number of commonly netted birds, such as *Sclerurus* leafscrapers and ant followers moving between ant swarms. The effectiveness of mist netting varies among species (e.g., Remsen and Parker 1983), so capture rates are best compared within species, although comparisons can be made among behaviorally similar species (Karr 1981a, Bierregaard 1990b).

### *Statistics*

We use capture rate (captures/1000 nh) as a standard index of abundance. Hereafter, capture rates will be presented without units. Same-day recaptures are excluded from all analyses. We partitioned time into five

TABLE 2. Repeated-measures ANOVA table. Size refers to fragment size, Type refers to the type of secondary growth surrounding the fragment (see Table 1). In this case, the repeated times are pre-isolation (time 0) and postisolation times 2, 3, and 4.

Effect	df	F calculation
Size	1	MS size/MS error a
Type	1	MS type/MS error a
Error a	6	
Time	3	MS time/MS error b
Time $\times$ Size	3	MS time $\times$ size/MS error b
Time $\times$ Type	3	MS time $\times$ type/MS error b
Error b	18	
Total	35	

periods: pre-isolation (time 0); 0–1 yr after isolation (time 1); 1–3 yr after isolation (time 2); 3–6 yr after isolation (time 3); and 6–9 yr after isolation (time 4). Results from time 1 are not included here, as they have been previously analyzed for some fragments and represent a brief, highly unstable period that is essentially independent of the subsequent loss of species (Bierregaard and Lovejoy 1989, Bierregaard 1990a).

The principal test we used to test for a change in capture rate after isolation was the Wilcoxon signed-ranks test, a nonparametric test that compares paired observations (Sokal and Rohlf 1981:449). Our paired observations were pre- and postisolation capture rates in the same fragment; in the text we report only the *P* value for these tests.

We used repeated-measures ANOVA to analyze time trends from pre-isolation through 9 yr postisolation, with fragment size and type of second growth (either *Cecropia* or *Vismia*) as main effects (Table 2). These data are well suited to repeated measures analysis since the same sites were sampled repeatedly with the same protocol. We report adjusted *P* values from univariate tests with fragment size and type of second growth as among-fragment main effects, and from univariate tests of within-fragment effects of time and its interactions with the main effects (Table 2). Adjusted *P* values are based on adjusted degrees of freedom according to the value of the Huynh-Feldt epsilon, which reflects departures from sphericity in the covariance matrix (Stevens 1990:Chapter 6). In practical terms, these adjustments correct biases that can inflate *F* statistics. We used natural log transformed capture rates in all parametric analyses to reduce the correlation between variance and mean within samples (Sokal and Rohlf 1981: 419).

We used an ordination procedure to identify patterns in mist net samples of all species of insectivores. Detrended correspondence analysis (DCA, using the program DECORANA) uses similarity in associations of species to order sites (Hill and Gauch 1980, Gauch et al. 1981, Gauch 1982, Jongman et al. 1987). DCA is an improvement over reciprocal averaging (also referred to as correspondence analysis) because it reduces

TABLE 3. The 35 most common insectivores in the pre-isolation sample. Guild refers to typical foraging associations: obligate army ant followers (Ants), members of mixed-species flocks (Flock), and solitary species that do not typically participate in mixed-species assemblages (Sol.). Solitary species are further separated into terrestrial (ter.) and arboreal species (arb.), with two gap specialists indicated (see *Results: Pre-isolation*). Abundance is captures/1000 net hours. See Appendix for common names and postisolation abundance.

Species	Guild	Pre-isolation abundance
<i>Pithys albifrons</i>	Ants	16.28
<i>Hylophylax poecilinota</i>	Sol. arb.	12.40
<i>Glyphorhynchus spirurus</i>	Flock	9.73
<i>Gymnopithys rufigula</i>	Ants	9.28
<i>Thamnomanes ardesiacus</i>	Flock	6.33
<i>Myrmotherula gutturalis</i>	Flock	5.26
<i>Xiphorhynchus pardalotus</i>	Flock	5.17
<i>Thamnomanes caesi</i>	Flock	4.64
<i>Microbates collaris</i>	Sol. arb.	4.64
<i>Deconychura stictolaema</i>	Flock	4.55
<i>Dendrocincla merula</i>	Ants	4.19
<i>Pernostola rufifrons</i>	Sol. arb. (gap)	4.10
<i>Myrmotherula longipennis</i>	Flock	4.01
<i>Myiobius barbatus</i>	Flock	3.03
<i>Platyrinchus saturatus</i>	Sol. arb.	3.03
<i>Microcerculus bambla</i>	Sol. arb.	3.03
<i>Automolus infuscatus</i>	Flock	2.86
<i>Myrmornis torquata</i>	Sol. ter.	2.86
<i>Sclerurus rufigularis</i>	Sol. ter.	2.77
<i>Myrmotherula guttata</i>	Sol. arb.	2.77
<i>Hypocnemis cantator</i>	Sol. arb. (gap)	2.77
<i>Formicarius colma</i>	Sol. ter.	2.77
<i>Myrmotherula axillaris</i>	Flock	2.59
<i>Hylophylax naevia</i>	Sol. arb.	2.50
<i>Myrmotherula menetriesii</i>	Flock	2.41
<i>Cyphorhinus arada</i>	Sol. ter.	2.41
<i>Automolus rubiginosus</i>	Sol. arb.	2.23
<i>Hylophilus ochraceiceps</i>	Flock	2.14
<i>Corythopis torquata</i>	Sol. ter.	2.05
<i>Conopophaga aurita</i>	Sol. ter.	1.87
<i>Platyrinchus coronatus</i>	Sol. arb.	1.78
<i>Dendrocincla fuliginosa</i>	Sol. arb.	1.52
<i>Sclerurus caudacutus</i>	Sol. ter.	1.43
<i>Automolus ochrolaemus</i>	Sol. arb.	1.34
<i>Xenops minutus</i>	Flock	1.25

compression at the ends of the first axis and distortion in the shape of second and higher axes (Hill and Gauch 1980, Gauch 1982:Chapter 4, Kenkel and Orlóci 1986).

## RESULTS

### Pre-isolation

A total of 1758 captures of 63 species of insectivores was recorded in the nine fragments before isolation (Appendix). This represents a capture rate of 156.9. The most commonly netted species, *Pithys albifrons*, accounted for 8.5% of total captures. Only three other species, *Hylophylax poecilinota*, *Glyphorhynchus spirurus*, and *Gymnopithys rufigula*, accounted for >4% of total captures (Table 3). The remaining species were distributed as a long tail of uncommonly netted species (see Bierregaard 1990b for more discussion of the sample from continuous forest).

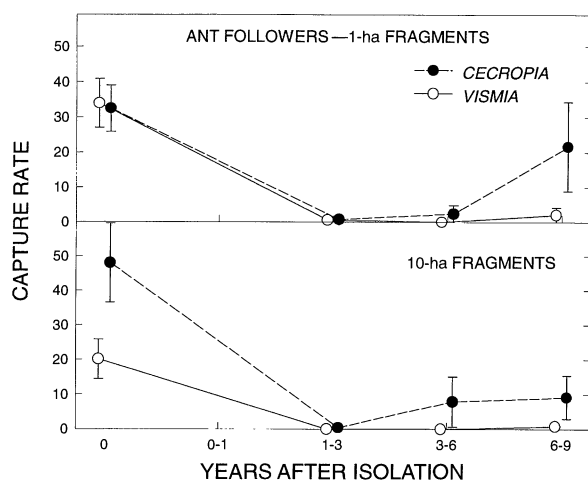


FIG. 1. Capture rate (captures/1000 net hours, mean  $\pm$  1 SE) of three species of army ant followers (see Table 3 for names) in 1- and 10-ha fragments. Open circles represent fragments surrounded by secondary growth dominated by *Vismia*, closed circles represent fragments surrounded by *Cecropia*. The values at 0 yr after isolation represent the entire pre-isolation sample.

We selected the 35 most commonly netted insectivores for more detailed analysis (Table 3). These species were all captured at least 14 times, at a minimum rate of 1.25. This group can be further subdivided into three categories based on their sociality and foraging associations: three species that forage only at army ant swarms ("ant followers"); 13 species generally found in mixed-species flocks ("flock species"); and 19 species that occur as territorial pairs independent of flocks ("solitary species"). The solitary species can be further subdivided into 7 terrestrial species and 12 arboreal species. This separation reflects differences in where the birds forage and how they move as they forage. Although some of the "arboreal" species perch and forage within 10 cm of the ground, and in some cases descend to the ground, they may be distinguished from the "terrestrial" species by the fact that they fly rather than walk or hop as they forage. Morphology also sep-

arates the arboreal and terrestrial species; the terrestrial species are generally stout-bodied with short wings and tails. Although this dichotomous classification works well for certain species, such as comparing antthrushes to spadebills, some species are intermediate.

#### Postisolation

In times 2–4, 1900 captures of 81 insectivorous species were recorded in the nine fragments. This represents a capture rate of 65.4,  $\approx$ 41% of the pre-isolation rate. For all insectivores combined, capture rate declined between isolation and time 2 (Wilcoxon signed-ranks test,  $P < 0.003$ ).

#### Ant followers

By time 2, ant followers had disappeared or almost disappeared from all fragments (Fig. 1). These three species were quite commonly captured before isolation, so the decrease in abundance between time 0 and time 2 was significant (Wilcoxon signed-ranks test,  $P < 0.003$ ). After their initial decline, ant followers began to return to fragments surrounded by *Cecropia*. Repeated-measures ANOVA for times 2–4 indicated significant effects of time, second growth, and time  $\times$  second growth (all  $P < 0.04$ ), but no main or interactive effect of fragment size (both  $P > 0.39$ ). Thus fragment size was not important for recolonization, but development of *Cecropia* second growth facilitated use of fragments by ant followers. All three species of ant follower returned to fragments (Table 4).

#### Mixed-species flocks

The response of the 13 flock species to isolation was more variable across species than the response of ant followers; some species persisted in fragments, others did not. Overall, capture rate declined significantly from pre-isolation to time 2 (Wilcoxon signed-ranks test,  $P < 0.003$ ). In general, flock species stopped moving as a unit immediately after isolation in 1-ha fragments, and in the 2nd yr in 10-ha fragments (R. O. Bierregaard, *personal observation*).

Although flocks disintegrated after isolation, three

TABLE 4. Species richness in time 4 (6–9 yr after isolation) for each fragment. Pre-isolation total is the number of species in the group in pre-isolation samples, Time 4 total is the species richness in time 4 for all fragments combined.

Group	Pre-isolation total	Vismia secondary growth					Cecropia secondary growth				Time 4 total
		1 ha			10 ha		1 ha		10 ha		
		1V-1	1V-2	1V-3	10V-1	10V-2	1C-1	1C-2	10C-1	10C-2	
Ants	3	0	0	0	0	2	2	3	3	1	3
Flock											
Dropouts	3	2	1	1	3	3	3	3	3	3	3
Nondropouts	10	0	0	0	0	2	1	0	8	8	9
Solitary											
Gap	2	2	2	2	2	2	2	2	0	2	2
Arboreal	10	0	2	2	2	4	4	3	6	4	10
Terrestrial	7	1	1	0	0	0	0	1	2	0	4

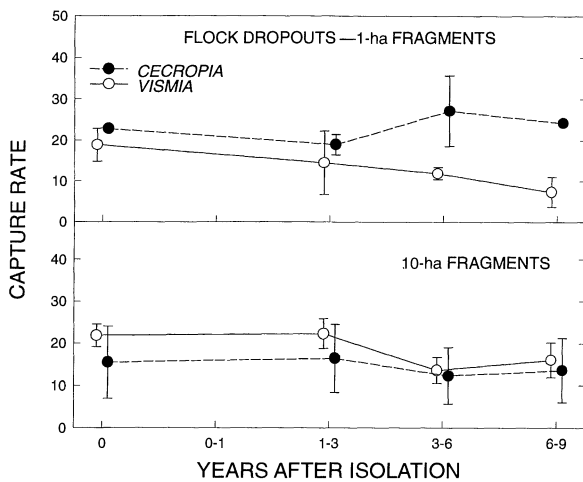


FIG. 2. Capture rates (mean  $\pm$  1 SE) of three species that drop out of mixed-species flocks in fragments, as in Fig. 1.

species stopped participating in flocks and maintained relatively stable capture rates in some fragments (Fig. 2). These "flock dropouts," the woodcreepers *Glyphorhynchus spirurus* and *Xiphorhynchus pardalotus*, and the antbird *Myrmotherula axillaris*, showed no change in abundance between pre-isolation and time 2 (Wilcoxon signed-ranks test,  $P > 0.10$ ). Repeated-measures analysis of times 0-4 and times 2-4 showed no significant effect of time, fragment size, type of second growth, or any of their interactions (all  $P > 0.22$ ).

Excluding flock dropouts, the other 10 flock species showed a significant decline between pre-isolation and time 2 in all fragments (Fig. 3; Wilcoxon signed-ranks test,  $P < 0.003$ ). This initial increase continued in 1-ha fragments and 10-ha fragments surrounded by *Vismia*, but capture rate increased beginning 3-6 yr after isolation in 10-ha fragments surrounded by *Cecropia*. Repeated-measures analysis of times 0-4 showed significant effects of fragment size, type of second growth, and time (all  $P < 0.009$ ). Capture rates were highest in fragments surrounded by *Cecropia* and in 10-ha fragments. Our observations indicate that flocks had reassembled in the two 10-ha fragments surrounded by *Cecropia* by 1991, where they moved in and out of the fragments through second growth.

In addition to higher capture rates for all non-dropouts, 10-ha fragments surrounded by *Cecropia* also had higher species richness in time 4 than other fragments (Table 4). Obligate flock species *Deconychura stictolaema*, *Automolus infuscatus*, *Thamnomanes ardesiacus*, *Myrmotherula longipennis*, *Myrmotherula menetriesii*, *Myiobius barbatus*, and *Hylophilus ochraceiceps* were captured only in fragments 10C-1 and/or 10C-2. *Thamnomanes caesi*, the nuclear species for understory flocks, may have been less affected by fragmentation; it was captured in four fragments in time 4.

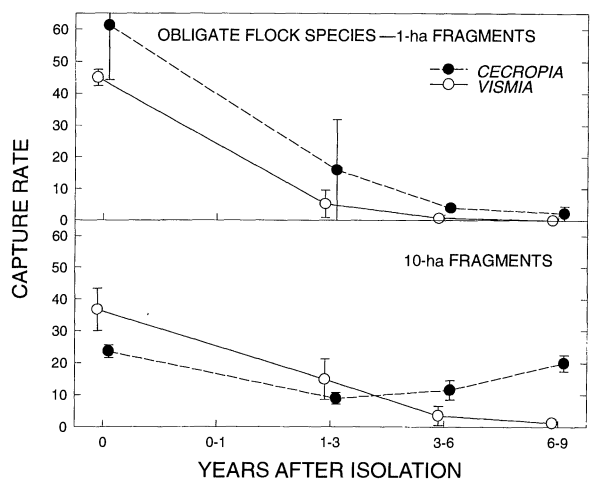


FIG. 3. Capture rates (mean  $\pm$  1 SE) of 10 species that forage together in mixed-species flocks, as in Fig. 1.

#### Solitary arboreal species

Solitary arboreal species exhibited two responses to isolation. Capture rate of most species declined after isolation, but two species typically found around gaps in continuous forest, *Percnostola rufifrons* and *Hypocnemis cantator*, were captured in all fragments in time 2 (Fig. 4). Capture rates of these species increased over time in 1-ha fragments, but remained relatively constant in 10-ha fragments. Repeated-measures ANOVA of times 0-4 showed significant main effects of fragment size ( $P = 0.002$ ) and type of second growth ( $P = 0.024$ ), as well as a significant interaction between fragment size and time ( $P = 0.003$ ).

The other group of arboreal species showed declines in capture rate between pre-isolation and time 2 (Fig. 5; Wilcoxon signed-ranks test,  $P < 0.003$ ). This decline continued in all fragments, and time was a significant effect by repeated-measures ANOVA ( $P = 0.002$ ). No

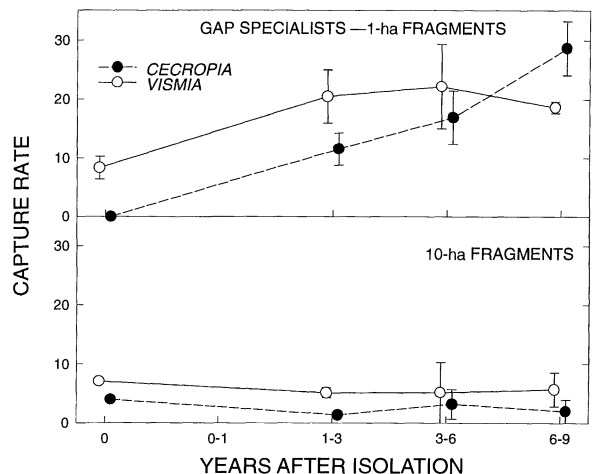


FIG. 4. Capture rates (mean  $\pm$  1 SE) of two species of edge specialists, as in Fig. 1.

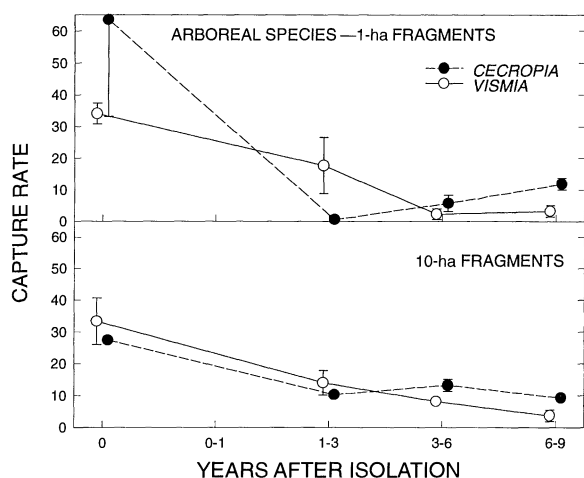


FIG. 5. Capture rates (mean  $\pm$  1 SE) of 10 solitary arboreal species, as in Fig. 1.

other main or interactive effects were significant in this analysis, although fragment size ( $P = 0.093$ ) and time  $\times$  type of second growth ( $P = 0.067$ ) approached significance. Despite the overall reduction in capture rate, at least one individual of all of these species was present in a fragment at time 4, and the most species were captured in 10-ha fragments surrounded by *Cecropia* (Table 4). We analyzed species richness at time 4 with a  $2 \times 2$  ANOVA with fragment size and type of secondary growth as main effects. Despite a sample size of only the nine fragments, the analysis showed marginally significant effects of fragment size ( $P = 0.049$ ) and type of secondary growth ( $P = 0.075$ ).

Although we classified them as arboreal species because they fly rather than walk or hop as they forage, five species in this group are almost never observed  $>2$  m off the ground (*Hylophylax poecilinota*, *Microbates collaris*, *Microcerculus bambla*, *Myrmotherula guttata*, and *Hylophylax naevia*). For these species, the substantial decline in capture rate after isolation (Fig. 5, Appendix) was almost certainly not due to changes in foraging height. *Myrmotherula guttata* and *Hylophylax naevia* may be especially vulnerable to fragmentation; both were captured only once in time 4. The other solitary arboreal species are sometimes observed above the level of nets (*Dendrocincla fuliginosa*, *Automolus rubiginosus*, *Automolus ochrolaemus*, *Platyrinchus coronatus*, and *Platyrinchus saturatus*). For these species, change in foraging height may be related to their reduced capture rates after isolation.

#### Solitary terrestrial species

Capture rate of solitary terrestrial species declined between pre-isolation and time 2 (Fig. 6; Wilcoxon signed-ranks test,  $P = 0.0039$ ). This trend continued, and repeated-measures ANOVA showed a highly significant effect of time ( $P < 0.001$ ), but no interactive or main effects of fragment size or type of secondary

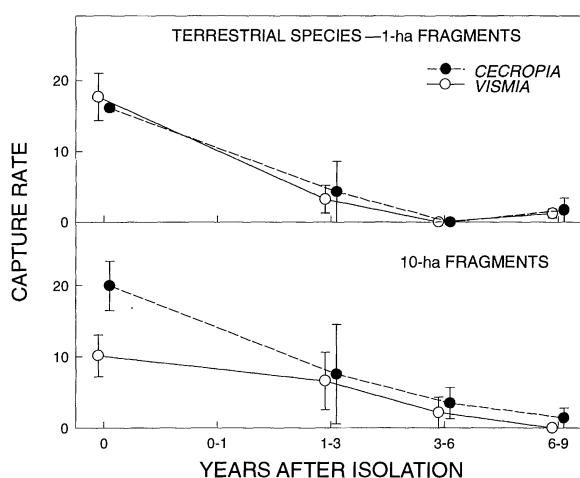


FIG. 6. Capture rates (mean  $\pm$  1 SE) of seven solitary terrestrial species, as in Fig. 1.

growth (all  $P > 0.16$ ). Although no solitary terrestrial species persisted at pre-isolation levels, several species appeared especially vulnerable to fragmentation. *Scelerurus caudacutus*, the least common species before isolation, was captured only once after isolation. *Myrmornis torquata* was not captured after time 2, and *Corythopsis torquata* was captured only once after time 2. Richness of these species was especially low at time 4 (Table 4). Only in 10C-1 was more than one species captured, and only *Formicarius colma* was captured in more than one fragment.

#### Nonforest and uncommon species

In general, the pronounced decline in capture rates of common forest insectivores after isolation was not matched by an increase in capture rates of previously uncommon species (Fig. 7). For all insectivores not

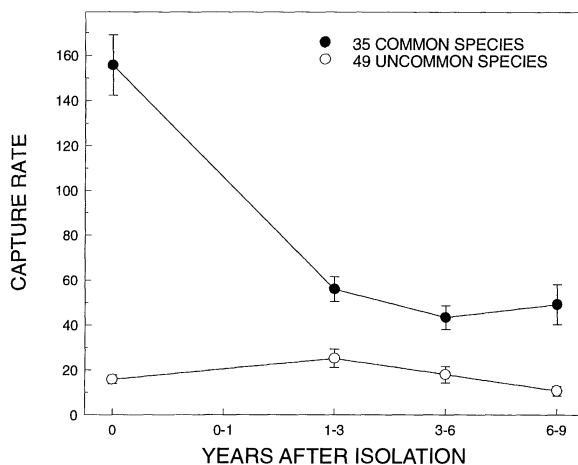


FIG. 7. Capture rates (mean  $\pm$  1 SE) across fragments for the 35 most common insectivores in the pre-isolation sample (those listed in Table 3) and 49 uncommon species (those not listed in Table 3; see Appendix).



discussed above (i.e., the 49 species not listed in Table 3, see Appendix), capture rate increased significantly between isolation and time 2 (Wilcoxon signed-ranks test,  $P < 0.003$ ). The magnitude of this increase,  $\approx 7$  captures/1000 nh, was relatively small. In comparison, *Pithys albifrons* declined by over 14 captures/1000 nh (Appendix). Several species that were uncommon before isolation were netted more frequently after isolation in some reserves, but only one species, the jacamar *Galbula albirostris*, reached the abundance of the top 35 insectivores before isolation (Appendix). This increase for *G. albirostris* was significant between pre-isolation and time 2 (Wilcoxon signed-ranks test,  $P = 0.0391$ ).

Twenty-one species of insectivores that were not captured before isolation were captured after isolation (Appendix). Most of these are canopy or edge species that are found in continuous forest, and most were only netted a few times. Four species, however, are very rare in continuous forest but more common in second growth. These species, the antbird *Cercomacra tyrannina*, the migrant flycatcher *Contopus virens*, and the wrens *Thryothorus coraya* and *Troglodytes aedon*, were probably not present before isolation. These species were not netted frequently in fragments; only *T. coraya* had a capture rate over 0.5. Despite the low capture rate, both wrens colonized several fragments; *T. coraya* was captured in all five 1-ha fragments and one 10-ha fragment, and *T. aedon* was captured in four 1-ha fragments and two 10-ha fragments. Neither wren was captured in the two 10-ha fragments surrounded by *Cecropia*.

#### Community-level patterns

Ordination of sites by DCA showed substantial temporal variation in samples from the same fragment (Fig. 8). Pre-isolation samples were relatively similar among all fragments, but later samples diverged, especially in 1-ha fragments. Axis 1, with an eigenvalue of 0.485, separates sites by presence of forest species (low scores) or edge and secondary growth species (high scores). Axis 2, with an eigenvalue of 0.161, is more difficult to interpret. Typical forest insectivores have intermediate scores, resulting in high similarity of sites before isolation. Low scores indicate presence of birds associated with fragments surrounded by *Vismia*; high scores indicate birds most common in 1-ha fragments surrounded by *Cecropia*. Fig. 8 includes all insectivores, but we also performed the analysis without 15 species that were captured  $< 4$  times. Eigenvalues for the first two axes changed to 0.470 and 0.201, indicating slightly greater explanatory power by the second axis. Gradients represented by the two axes did not change, however, and the patterns of sites were very nearly identical. Thus the DCA was not strongly affected by rare species.

In 1-ha fragments, the loss of forest insectivores soon after isolation led to large changes along axis 1 between

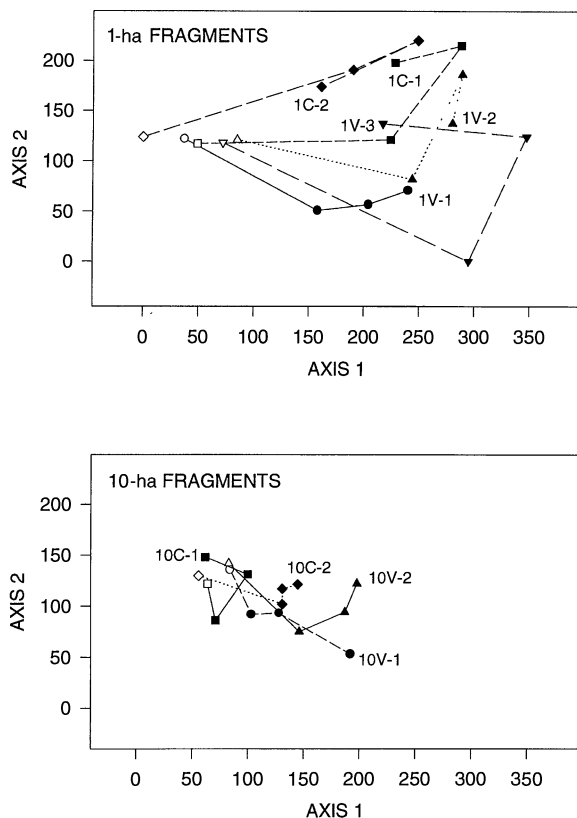


FIG. 8. Detrended correspondence analysis from DECORANA of insectivore assemblages in each fragment for each time period. The top figure shows 1-ha fragments, the bottom shows 10-ha fragments from the same analysis. Lines connect successive samples from the same fragment. For each fragment, the hollow symbol indicates the pre-isolation sample. See Results: Community-level patterns for an explanation of the axes.

times 0 and 2. Not only did these communities diverge from pre-isolation samples, they also diverged greatly from each other, reflecting the heterogeneity of post-isolation communities. On both axes, successive samples of 1-ha fragments showed that understory communities continued to change substantially during the postisolation period, although the time 4 samples from 1C-1, 1C-2, and 1V-3 show these communities becoming more like the pre-isolation communities, at least as measured by axis 1. For these fragments, this change is probably due to recolonization of forest species.

In 10-ha fragments, the divergence from pre-isolation along both axes was much less than in 1-ha fragments. These fragments lost species more gradually than 1-ha fragments, so the change between time 0 and time 2 was not pronounced. Divergence along axis 1 continued through time 4 in 10V-2, 10C-2, and especially in 10V-1. These fragments are continuing to lose species, and few are recolonizing, especially to 10V-1. In contrast, 10C-1 changed little, and by time 4 was within the range of pre-isolation samples on axis

1. For this fragment, fluctuation along axis 2 was as pronounced as changes along axis 1, perhaps reflecting relatively little change in a core group of relatively common forest species, but temporal variation in abundance for a group of less common species.

## DISCUSSION

### *Loss of species after isolation*

All fragments showed striking reduction in abundance of understory insectivores after isolation, both in number of individuals and in number of species (Fig. 7, Table 4). Patterns of species loss were predictable among fragments, and were related to fragment size and behavioral differences among the species. It should be pointed out that although some variation in abundance over time is expected based on chance and population processes (Karr 1982a, Karr et al. 1982), the fragments were isolated in different years. Thus the declines we measured were due to isolation, not to the unlikely event of a regional decline, independent of fragmentation, such as disease.

Ant followers were the first group to be lost (Fig. 1; see also Harper 1987, Bierregaard and Lovejoy 1989). These birds forage over large areas of forest, but are very reluctant to cross open areas (Willis and Oniki 1978, Willis 1979b, Harper 1987). Harper's studies suggest that these species were lost from fragments because the fragments were too small to contain enough active ant swarms to support them. Obligate ant followers must track several swarms simultaneously to be able to continue foraging when swarms enter inactive periods. Moving between swarms is especially important for *Pithys albifrons*, which is socially subordinate at swarms (Willis and Oniki 1978). These movements also make *Pithys* especially common in mist net samples.

Other species were lost more gradually than the ant followers. Flocks disintegrated after isolation, first in 1-ha fragments, then, after  $\approx 2$  yr, in 10-ha fragments (Fig. 3; see also Bierregaard and Lovejoy 1989, Bierregaard 1990a). Fragments of 1 ha are far too small for flocks, which use group territories of slightly more than 10 ha in continuous forest at our site (Powell 1989). Although 10-ha fragments are only slightly smaller than flock territories in continuous forest, flocks did not persist in these fragments. Our observations suggest that understory flocks avoid edges, so the effective area for flock territories was much reduced after isolation of 10-ha fragments. Because of the social cohesion of flocks, loss of a few species, especially *Thamnomanes caesi*, leads to disintegration of the rest of the flock. Changes in the resource base or physical structure of the fragments after isolation may have contributed to the demise of flocks. However, flocks eventually reassembled in 10-ha fragments surrounded by *Cecropia*, suggesting that structural changes after isolation did not make fragments unsuitable.

Flock dropouts persisted in fragments because they have the behavioral plasticity to forage outside of flocks, where they persist in fragments as small as 1 ha (Fig. 2). In addition, flock dropouts foraging alone appear to be more likely to use edges and secondary growth than when they are with flocks (P. C. Stouffer, *personal observation*). Territory size may have been reduced for these species outside of flocks because they did not need to partition food resources with other flock species (Powell 1985, 1989). Presumably this effect was especially important for *Myrmotherula axillaris*, which is one of four species of *Myrmotherula* in understory flocks (Powell 1989). Foraging outside of flocks was not unexpected for *Glyphorhynchus spirurus* and *Xiphorhynchus pardalotus*, since they are often observed alone or in pairs in the continuous forest. Indeed, *Glyphorhynchus* may be more appropriately described as a facultative flock member, with several pairs holding territories within the territory of one flock, and each pair joining the flock only as it passes through its territory. *Glyphorhynchus* also commonly uses second growth (Loiselle and Blake 1994, S. H. Borges and P. C. Stouffer, *unpublished data*). Dropping out of flocks was more surprising for *Myrmotherula axillaris*, which is seldom seen outside of flocks in continuous forest at our site (Powell 1989). Abundance of *Myrmotherula axillaris* may be stable in fragments; it has bred in a 1-ha fragment (P. C. Stouffer, *personal observation*), and is common in *Cecropia*-dominated second growth (S. H. Borges, *unpublished data*). Apparently, persistence outside of flocks in continuous forest is not sufficient to insure persistence in fragments, however. *Myiobius barbatus* may also be a facultative flock member (Meyer de Schauensee and Phelps 1978, Stiles and Skutch 1989), but it did not persist in fragments.

Solitary terrestrial species such as antthrushes and leafscrapers declined gradually in fragments, but the cause of their decline is not clear (Fig. 6). These birds were also found to be adversely affected by forest perturbation in Ecuador (Canaday 1991) and French Guiana (Thiollay 1992). Several factors may make these species unlikely to persist in fragments of 1 or 10 ha. First, 1- and 10-ha fragments may simply be much too small for them to meet their energy requirements. Based on data for some of the same species and some congeners in Peru, 10 ha should be large enough for a normal-sized territory for most of these species, although 1-ha fragments are certainly too small (Terborgh et al. 1990). Second, the structure or microclimate of the ground level may have been altered sufficiently to reduce the availability of prey or the ability of these species to procure it. Treefalls on borders make the ground level much more crowded and alter the composition of litter. These effects extend at least 40 m into the fragment, and are associated with a hotter, drier microclimate (Kapos 1989), which may affect litter arthropod abundance, microhabitat selection by birds, or

physiological performance of birds (Karr and Freemark 1983, Levings and Windsor 1984).

Solitary arboreal species also declined after isolation, especially in 1-ha fragments, but less dramatically than terrestrial species (Fig. 5). Determining why these species were lost would require intensive study of individual species, as this group is quite heterogeneous morphologically and behaviorally. In general, the factors described above for solitary terrestrial species also apply to these birds, although the arboreal species are more vagile and probably more likely to recolonize (see *Recolonization of fragments* below). For the solitary arboreal species that forage on or near the ground (*Microbatas collaris*, *Microcerculus bambla*, *Myrmotherula guttata*, and *Hylophylax naevia*), the causes of decline after isolation may have been most like those for the solitary terrestrial species. These species are smaller than the solitary terrestrial species, so they probably need smaller territories and could persist longer in fragments.

Habitat preferences of two solitary species allowed them to persist after isolation. Treefall/edge specialists *Pernostola rufifrons* and *Hypocnemis cantator* thrived in 1-ha fragments (Fig. 4). These species also persisted in French Guianan forests damaged by logging (Thiollay 1992), which are probably structurally similar to 1-ha fragments. *Pernostola rufifrons* may receive an additional benefit in fragments without other species that forage at ant swarms, as it can feed at swarms without interference from larger, more dominant species (Willis 1982b).

Other solitary arboreal species include a woodcreeper (*Dendrocincla fuliginosa*), two foliage-gleaners (*Automolus rubiginosus* and *A. ochrolaemus*), and two flycatchers (*Platyrinchus coronatus* and *P. saturatus*). These species all sometimes travel and forage above the level of nets in continuous forest, so mist net data could be an inaccurate measure of abundance for any species that showed a systematic change in height preference after isolation. *Dendrocincla fuliginosa* was not strongly affected by fragmentation, possibly because it is flexible in its foraging behavior (Willis 1972) and readily uses edges and secondary growth (Willis 1972, Loiselle and Blake 1994, S. H. Borges and P. C. Stouffer, unpublished data). This behavioral plasticity may have allowed it to take advantage of the absence of other woodcreepers, such as *Deconychura* spp., *Hylexetastes perrotii*, and *Dendrocolaptes picumnus*. The two foliage-gleaners commonly forage in dead leaves and tangles and seem to prefer dense undergrowth (Hilty and Brown 1986). For them, it is not clear what caused their decline in fragments, since physical changes in fragments probably increased the availability of their foraging areas. For *Automolus ochrolaemus*, netting data may be an underestimate. This species is occasionally found along the edges of fragments, and readily uses second growth (S. H. Borges, unpublished data). The two *Platyrinchus* flycatchers,

unlike the foliage-gleaners, seem to prefer areas with open understory but complete canopy (Hilty and Brown 1986, Stiles and Skutch 1989). Even though their territories are probably among the smallest of any birds at the site (Terborgh et al. 1990), isolation of fragments likely had a negative effect on their preferred microhabitat.

#### Community patterns from ordination

The heterogeneity among bird communities after isolation was far greater than the heterogeneity among the pre-isolation samples (Fig. 8). This indicates that any difference among sites was far less important in determining the understory community than the effects of isolation. Ordination showed that 1-ha fragments changed most dramatically from pre-isolation, and that their communities continued to change markedly over time. Some of the difference among 1-ha fragments revealed by ordination may reflect variation in physical structure. For example, the 1-ha fragment that diverged least from pre-isolation to time 2 was 1V-1. This fragment has a band of  $\approx 10$  m of standing forest trees on two sides, and has been less damaged by treefalls than the other 1-ha fragments. The most divergent fragment was 1V-3, the most damaged by treefalls. The 10-ha fragments were more clustered than the 1-ha fragments at time 2, and were closer to the original communities. By time 4, only 10V-1 continued to diverge from pre-isolation along axis 1, the axis based on presence of forest species. This fragment continued to lose forest species through time 4, but had little recolonization. In contrast, 10C-1 was recolonized by ant followers and flock species, and was within the pre-isolation values on axis 1 by time 4, although it differed slightly along axis 2.

#### Recolonization of fragments

When use of fragments is viewed over the 9 yr of postisolation data, it becomes apparent that fragment size alone is a poor predictor of which species were present, especially in the last sampling period, when some birds had recolonized. The time since isolation affected local extinction and the development of secondary growth. Older second growth provides more cover and more resources for birds passing through it. Cover is probably especially important for many of the understory birds we studied, which are generally considered to be poor colonizers and unwilling to cross open areas (Terborgh and Weske 1969, Karr 1982b). *Cecropia*-dominated secondary growth grows very rapidly, so fragments surrounded by this vegetation were part of a much different landscape than fragments surrounded by slower growing regeneration in cattle pastures. Similar interactions of fragment size, type of secondary growth, and time since isolation were found to be important influences on abundance of nonvolant small mammals in the fragments (Malcolm 1991). For understory hummingbirds, however, neither fragmen-

tation nor succession around fragments led to pronounced changes in abundance (Stouffer and Bierregaard, *in press*).

Ant followers were not influenced by fragment size, but only used fragments surrounded by *Cecropia* at least 6 yr old (Fig. 1). These species cannot be said to "persist" in the fragments surrounded by *Cecropia*, as they only pass through as they follow ant swarms or move from swarm to swarm. In this respect they are certainly the most mobile of the species we considered, and exhibit behavior patterns more like temperate birds that move among small woodlots (Howe 1984). Thus, although they are extremely vulnerable to deforestation, they cannot be considered species restricted to undisturbed forest. For ant followers, the most important feature of developing second growth is probably just the cover it provides. We doubt that more complicated aspects of vegetation structure or prey availability have much effect on these birds, since they used 1-ha fragments that are very heavily disturbed, such as 1C-1. They also move through old *Vismia*-dominated second growth in some areas (S. H. Borges, *unpublished data*). Thiollay (1992) reported declines of the ant followers *Pithys albifrons* and *Gymnopathys rufigula* after 8–12 yr in selectively logged sites, but this may have been due to the difficulty in detecting these species by point counts in dense undergrowth. Canaday (1991) and Andrade and Rubio-Torgler (1994) reported *P. albifrons* in mist net surveys in secondary habitats.

The response to fragmentation of *Hylophylax peocilinota*, the most common solitary arboreal species in the pre-isolation sample, may be related to its foraging at ant swarms. This species is common in mist net samples in *Cecropia* and old *Vismia* (S. H. Borges and P. C. Stouffer, *unpublished data*). It has also been recorded in all 10-ha fragments in time 4, although in no 1-ha fragments. Willis (1982a) suggested that immature *H. peocilinota* may wander widely following ants. Apparently, like the professional ant followers, this vagility allows them to recolonize 10-ha fragments. Unlike the professional ant followers, they eschew 1-ha fragments, so their habitat requirements may be slightly more specific.

For mixed-species flocks, fragment size and secondary growth affected the suitability of fragments for recolonization for nondropouts (Fig. 3). Flocks reassembled in 10-ha fragments surrounded by *Cecropia* at least 6 yr old. Since these birds often use territories slightly larger than 10 ha in continuous forest (Powell 1989), foraging in secondary growth around the fragment probably allows them to hold a territory of typical size. Also, flocks use the edges of fragments surrounded by tall *Cecropia*, although they avoid edges that are more exposed (P. C. Stouffer, *personal observation*). Our data indicate that all commonly netted flock species returned to 10-ha fragments surrounded by *Cecropia*. *Xenops minutus* has not been netted, but has been observed in 10C-1, as has *Deconychura longicauda*, a

flock species that rarely descends to net level. For flock species, use of *Cecropia*-dominated second growth is probably related to its physiognomy. Understory flocks spread out over a vertical range of 10–20 m, so only older *Cecropia* is tall enough to provide the substrates necessary for flock birds (including vines, hanging dead leaves, snags, and live trees of various sizes). Ironically, some second growth may be more suitable for these birds than small, damaged fragments; flocks move through the second growth around 1C-1, but do not use the fragment, which has few standing tall trees (P. C. Stouffer, *personal observation*).

Solitary arboreal and terrestrial species showed little sign of recolonizing fragments (Figs. 5 and 6). For these species, several factors may account for their inability to recolonize. First, secondary growth may be inadequate habitat for these species, avoided because of its physiognomy or floristics (e.g. Wiens and Rotenberry 1981), or because of reduced prey availability. *Vismia*-dominated secondary growth is more crowded, and appears to be hotter and drier than continuous forest or fragments. Because it has a closed canopy, *Cecropia* secondary growth is microclimatically more like fragments, but the litter layer is dominated by the enormous leaves of *Cecropia*, which may be too big to be manipulated by birds that forage by actively moving litter, such as most terrestrial insectivores. It is unlikely that insect abundance or diversity is reduced appreciably in secondary areas (Janzen 1973), but a detailed study of diet would be required to determine prey availability in fragments and secondary areas. Second, low vagility probably makes many solitary species unlikely to recolonize (see also Terborgh and Weske 1969, Karr 1982b). This factor is probably also most pronounced for the large-bodied terrestrial insectivores.

Although terrestrial species as a whole appear unlikely to use fragments, species differed somewhat in their vulnerability. *Formicarius colma* and *Myrmeciza ferruginea* have been regularly recorded in *Cecropia* secondary growth and 10-ha fragments (S. H. Borges, M. Cohn-Haft, P. C. Stouffer, and J. A. Stratford, *unpublished data*). Most of the other terrestrial species have not been netted in fragments or secondary growth, nor have we heard or seen them there. Our observations suggest that other terrestrial birds not netted frequently enough to analyze separately also declined in fragments. This group includes the antpittas *Grallaria varia* and *Hylopezus macularius*, two of the largest terrestrial insectivores, as well as the leafscraper *Sclerurus mexicanus*. Another antpitta, *Myrmothera campanisona*, is sometimes heard around the edges of gaps in continuous forest and may be more able to cope with habitat disturbance caused by fragmentation (but see Thiollay 1992). The terrestrial frugivore *Geotrygon montana* also avoids 1-ha fragments (Stouffer and Bierregaard 1993).

### *Invasion of fragments by nonforest species*

The wrens *Thryothorus coraya* and *Troglodytes aedon* had a strong, but temporary, peak in abundance in the fragments, although they did not compensate numerically for the species lost after isolation. Our data show that clearings remain suitable for only a few years, after which the wrens must once again move. *Troglodytes aedon* was also found in small woodlots in North America (Galli et al. 1976, Howe 1984), although it may be less restricted to successional or disturbed habitats in the temperate zone (Askins et al. 1987, Blake and Karr 1987).

Negative interactions with nonforest birds, rather than structural changes or degree of isolation, has been proposed as a factor that limits use of edges and fragments by forest-interior birds in North America (e.g., Ambuel and Temple 1983). Since fragments in our study became essentially devoid of forest insectivores after isolation, and were colonized by few nonforest species, this conclusion is not supported at our site for insectivores. Migrant songbirds are common in some disturbed Neotropical forests (e.g., Hutto 1980). Neither insectivorous nor omnivorous migrants are common at our site, however, even though several of the more regularly occurring species, such as *Contopus borealis*, *C. virens*, and *Vireo olivaceus*, appear to prefer edges and fragments (Stotz et al. 1992). Willis (1979a) also concluded that density compensation did not occur in fragments in southern Brazil.

Many forest species were netted for the first time or increased in abundance after isolation, although these species, even in aggregate, were a small part of the postisolation sample (Fig. 7). In some cases, increased abundance may reflect a shift in foraging height of common midstory birds that makes them more prone to capture (Bierregaard and Lovejoy 1989, Bierregaard 1990a). Some canopy and edge species may forage lower in fragments because canopy vegetation is reduced and treefalls are more common (Malcolm 1991). Birds that forage at the top of the canopy will follow this contour to lower heights along edges and in gaps (Stiles 1983). Midstory and canopy insectivores probably move more readily between fragments and continuous forest than do understory species (Willis 1974, Karr 1982b), and may forage lower in fragments because their typical competitors in that stratum are absent. In some cases, however, these new captures may have been simply an artifact of increased sample effort after isolation.

### *Distance effects*

Isolation of fragments from continuous forest by as little as 100 m led to rapid loss of species. Part of the reason Amazonian fragments are so insularized is because there is no pattern of seasonal migration that brings insectivores to the fragments, giving birds the

chance to evaluate fragments as possible breeding locations. For understory insectivores, it appears that isolated fragments without surrounding secondary growth are analogous to true islands, with some individuals trapped by isolation, and new individuals only rarely colonizing (Willis 1979a, Karr 1982b). This contrasts dramatically with temperate fragments, which, although well isolated, may be used every year by migratory species (e.g., Blake and Karr 1987, Winker et al. 1992).

Based on ordination, the fragment closest to continuous forest, 10C-1, was most similar to continuous forest at time 4 (Fig. 8). Despite a separation of only 70–100 m, even this fragment lost species after isolation, and at time 2 had a community distinct from pre-isolation. Also, solitary terrestrial species continued to decline through 9 yr postisolation. Recovery of 10C-1, especially for ant followers and flocks, may have been enhanced by its proximity to the forest, since it recovered more quickly than 10C-2, which was 650 m from continuous forest. Even a short separation from continuous forest by *Vismia* impeded recolonization; 10V-1 remained divergent from pre-isolation through time 4, despite isolation by only  $\approx 100$  m.

### *Implications for conservation and recommendations for further study*

Results from the landscape at our site may be generally applicable to much of the terra firme rain forest of the Amazon basin as it is presently developed. As at our site, patterns of land use throughout Amazonia often lead to fragments of forest in the 1–100 ha size range (Leite and Furley 1985, Skole and Tucker 1993, Dale et al. 1994). In many cases, fragments are within  $\approx 1$  km of larger pieces of forest, since most development initially occurs in a narrow band along roads (e.g., Buschbacher 1986). Present land use patterns are likely to lead to deforestation of more and more areas adjacent to existing development, leading to increased distances between smaller and smaller fragments (e.g., Dale et al. 1994). *Cecropia* dominates early succession in areas that are not heavily disturbed (Uhl et al. 1981, Uhl and Jordan 1984). Cattle pastures and farm plots are often abandoned, and in the early years of regeneration are dominated by *Vismia* spp. and several other pioneer species (Uhl and Jordan 1984, Uhl 1987).

Our data indicate that some forest birds can persist in a matrix of forest fragments and *Cecropia*-dominated secondary growth. The important questions for conservation are how far birds will move through second growth, and whether their use of second growth and fragments means that they can maintain populations in those areas without continued colonization from larger areas of forest. We have evidence of breeding for many species in fragments, but successful breeding is not sufficient for habitat patches to serve as sources of future breeders. Indeed, fragments and secondary areas may serve only as sinks for wandering individuals ex-

cluded from breeding in more appropriate habitat (e.g., Robinson 1992). Nest predation may limit reproductive success in fragments, as has been suggested for temperate habitat islands (Gates and Gysel 1978, Wilcove 1985, Andrén and Angelstam 1988) and for Barro Colorado Island, Panama (Sieving 1992). One important difference from the temperate zone, however, is that birds in Amazonian fragments are not heavily victimized by brood parasites. Although it is uncommon at our site, the parasitic cowbird *Molothrus bonariensis* is found in disturbed areas throughout South America (Ridgely and Tudor 1989). *Molothrus bonariensis* may become a more significant problem as disturbance increases, as did *M. ater* in eastern North America (e.g., Brittingham and Temple 1983).

As a group, the terrestrial species were the most vulnerable to fragmentation (see also Karr 1982b, Canaday 1991, Thiollay 1992). Presumably, at some point the secondary growth will be sufficiently developed to permit them first to move through it and later persist in it, but this has not happened in secondary growth up to 9 yr old. Because of the ongoing structural decay of fragments, especially 1-ha fragments, fragments may no longer provide suitable habitat for these species should they recolonize. For species that are poor colonizers, persistence in fragments will probably prove to be more dependent on fragment size (i.e., delaying extinction) than on the matrix of second growth around the fragment (i.e., facilitating colonization). Presently, basic information on territory size, density, and microhabitat requirements are unknown; this information is necessary to predict which birds can use a fragment of a given size or second growth of a given structure. Fragments and secondary areas may lack important resources for these species, but the birds also may avoid "new" areas simply because of behavioral inflexibility (e.g., Greenberg 1989).

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## APPENDIX

All insectivores captured, with pre- and postisolation abundance (captures/1000 net hours).

Species	Common name	Pre-isolation abundance	Postisolation abundance
<b>Galbulidae</b>			
<i>Galbula albirostris</i>	Yellow-billed Jacamar	0.80	1.48
<i>Jacamerops aurea</i>	Great Jacamar	0.09	
<b>Bucconidae</b>			
<i>Notharchus tectus</i>	Pied Puffbird	0.00	0.10
<i>Bucco tamatia</i>	Spotted Puffbird	0.00	0.27
<i>Bucco capensis</i>	Collared Puffbird	0.00	0.14
<i>Malacoptila fusca</i>	White-chested Puffbird	0.54	1.03
<i>Monasa atra</i>	Black Nunbird	0.00	0.41
<b>Picidae</b>			
<i>Picumnus exilis</i>	Golden-spangled Piculet	0.00	0.04
<i>Piculus flavigula</i>	Yellow-throated Woodpecker	0.00	0.04
<i>Celeus elegans</i>	Chestnut Woodpecker	0.00	0.04
<b>Dendrocolaptidae</b>			
<i>Dendrocincla fuliginosa</i>	Plain-brown Woodcreeper	1.52	1.14
<i>Dendrocincla merula</i>	White-chinned Woodcreeper	4.19	0.21
<i>Deconychura longicauda</i>	Long-tailed Woodcreeper	0.89	0.14
<i>Deconychura stictolaema</i>	Spot-throated Woodcreeper	4.55	0.52
<i>Sittasomus griseicapillus</i>	Olivaceous Woodcreeper	0.09	0.55
<i>Glyphorhynchus spirurus</i>	Wedge-billed Woodcreeper	9.73	7.92
<i>Hylexetastes perrotii</i>	Red-billed Woodcreeper	1.07	0.48
<i>Dendrocolaptes certhia</i>	Barred Woodcreeper	0.54	0.69
<i>Dendrocolaptes picumnus</i>	Black-banded Woodcreeper	0.18	0.04
<i>Xiphorhynchus pardalotus</i>	Chestnut-rumped Woodcreeper	5.17	5.79
<i>Campylorhamphus procurvoides</i>	Curve-billed Scythebill	0.80	0.04
<b>Furnariidae</b>			
<i>Synallaxis rutilans</i>	Ruddy Spinetail	1.16	0.59
<i>Philydor erythrocercus</i>	Rufous-rumped Foliage-gleaner	0.62	0.21
<i>Philydor pyrrhodes</i>	Cinnamon-rumped Foliage-gleaner	0.18	0.10
<i>Automolus infuscatus</i>	Olive-backed Foliage-gleaner	2.86	0.59
<i>Automolus rubiginosus</i>	Ruddy Foliage-gleaner	2.23	0.41
<i>Automolus ochrolaemus</i>	Buff-throated Foliage-gleaner	1.34	0.27
<i>Xenops minutus</i>	Plain Xenops	1.25	0.38
<i>Sclerurus mexicanus</i>	Tawny-throated Leafscraper	1.16	0.00
<i>Sclerurus rufigularis</i>	Short-billed Leafscraper	2.77	0.14
<i>Sclerurus caudacutus</i>	Black-tailed Leafscraper	1.43	0.04
<b>Formicariidae</b>			
<i>Cymbilaimus lineatus</i>	Fasciated Antshrike	0.34	0.34
<i>Frederickena viridis</i>	Black-throated Antshrike	0.62	0.45
<i>Thamnophilus murinus</i>	Mouse-colored Antshrike	0.54	0.79
<i>Thamnomanes ardesiacus</i>	Dusky-throated Antshrike	6.33	2.24
<i>Thamnomanes caesi</i>	Cinereous Antshrike	4.64	1.24
<i>Myrmotherula guttata</i>	Rufous-bellied Antwren	2.77	0.41
<i>Myrmotherula gutturalis</i>	Brown-bellied Antwren	5.26	0.72
<i>Myrmotherula axillaris</i>	White-flanked Antwren	2.59	2.72
<i>Myrmotherula longipennis</i>	Long-winged Antwren	4.01	0.96
<i>Myrmotherula menetriesii</i>	Gray Antwren	2.41	0.65
<i>Cercomacra tyrannina</i>	Dusky Antbird	0.00	0.10
<i>Hypocnemis cantator</i>	Warbling Antbird	2.77	3.03
<i>Percnostola rufifrons</i>	Black-headed Antbird	4.10	6.47
<i>Percnostola leucostigma</i>	Spot-winged Antbird	1.07	0.07
<i>Myrmeciza ferruginea</i>	Ferruginous-backed Antbird	0.89	1.00
<i>Myrmeciza atrothorax</i>	Black-throated Antbird	0.09	0.10
<i>Pithys albifrons</i>	White-plumed Antbird	16.28	1.38
<i>Gymnophithys rufigula</i>	Rufous-throated Antbird	9.28	1.14
<i>Hylophylax naevia</i>	Spot-backed Antbird	2.50	0.04
<i>Hylophylax poecilinota</i> *	Scale-backed Antbird	12.40	4.03
<i>Formicarius colma</i>	Rufous-capped Antthrush	2.77	1.07
<i>Formicarius analis</i>	Black-faced Antthrush	0.27	0.48
<i>Myrmornis torquata</i>	Wing-banded Antbird	2.86	0.45
<i>Hylopezus macularius</i>	Spotted Antpitta	0.54	0.17
<i>Grallaria varia</i>	Variegated Antpitta	0.09	0.10
<i>Conopophaga aurita</i>	Chestnut-belted Gnatcatcher	1.87	0.24

\* According to Ridgely and Tudor (1994), the correct spelling is *poecilinota*, contrary to most recent publications.

## APPENDIX. Continued.

Species	Common name	Pre-isolation abundance	Postisolation abundance
<b>Tyrannidae</b>			
<i>Corythopsis torquata</i>	Ringed Antpiper	2.05	0.17
<i>Lophotriccus vitioides</i>	Double-banded Pygmy-Tyrant	0.24	0.24
<i>Hemitriccus zosterops</i>	White-eyed Tody-Tyrant	0.09	0.14
<i>Rhynchocyclus olivaceus</i>	Olivaceous Flatbill	0.80	0.65
<i>Tolmomyias assimilis</i>	Yellow-margined Flycatcher	0.09	0.27
<i>Tolmomyias poliocephalus</i>	Gray-crowned Flycatcher	0.00	0.07
<i>Platyrinchus saturatus</i>	Cinnamon-crested Spadebill	3.03	0.48
<i>Platyrinchus coronatus</i>	Golden-crowned Spadebill	1.78	0.69
<i>Platyrinchus platyrhynchos</i>	White-crested Spadebill	0.18	0.17
<i>Onychorhynchus coronatus</i>	Royal Flycatcher	0.27	0.10
<i>Terenotriccus erythrurus</i>	Ruddy-tailed Flycatcher	0.71	0.79
<i>Myiobius barbatus</i>	Sulphur-rumped Flycatcher	3.03	0.72
<i>Contopus virens</i>	Eastern Wood-Pewee	0.00	0.04
<i>Attila spadiceus</i>	Bright-rumped Attila	0.00	0.27
<i>Rhytipterna simplex</i>	Grayish Mourner	0.09	0.00
<i>Laniocera hypopyrrha</i>	Cinereous Mourner	0.00	0.04
<i>Pachyramphus minor</i>	Pink-throated Becard	0.00	0.10
<b>Troglodytidae</b>			
<i>Thryothorus coraya</i>	Coraya Wren	0.00	2.38
<i>Troglodytes aedon</i>	House Wren	0.00	0.45
<i>Microcerculus bambla</i>	Wing-banded Wren	3.03	0.34
<i>Cyphorhinus arada</i>	Musician Wren	2.41	0.86
<b>Muscicapidae</b>			
<i>Microbates collaris</i>	Collared Gnatwren	4.64	1.24
<i>Ramphocaenus melanurus</i>	Long-billed Gnatwren	0.24	0.24
<b>Vireonidae</b>			
<i>Cyclarhis gujanensis</i>	Rufous-browed Peppershrike	0.00	0.10
<i>Hylophilus muscicapinus</i>	Buff-cheeked Greenlet	0.00	0.10
<i>Hylophilus ochraceiceps</i>	Tawny-crowned Greenlet	2.14	0.55
<b>Emberizidae</b>			
<i>Phaeothlypis rivularis</i>	River Warbler	0.00	0.04