Local Extinctions of Terrestrial Insectivorous Birds in a Fragmented Landscape near Manaus, Brazil

JEFFREY A. STRATFORD* AND PHILIP C. STOUFFER

Department of Biological Sciences, Southeastern Louisiana University, Hammond, LA 70402–0736, U.S.A., and Biological Dynamics of Forest Fragments Project, Instituto Nacional de Pesquisas de Amazonia, CP478, Manaus, AM 69011, Brazil

Abstract: We examined the distributions of nine species of terrestrial insectivorous birds in 4- to 14-year-old rainforest fragments north of Manaus, Brazil. We surveyed 11 fragments of 1, 10, and 100 ha, 95 ha of secondary vegetation, and nine continuous forest plots (controls) of 1–100 ha. We augmented standard spot-mapping with extensive playback surveys. The fragments had been sampled with mist nets before isolation, so our results could be compared with the pre-isolation distribution. For the nine species, there were 55 cases of local extinction in the 11 fragments between about 1 year after isolation and the time of our surveys. This corresponds to 74% extinction of the local populations in fragments. These extinctions occurred despite the second-growth connection of some fragments to continuous forest as little as 70 m away. Three apparent colonization events by species not detected before isolation also occurred, but these may also reflect inadequate sampling before isolation. Our comparison of fragments and similar-sized control plots in continuous forest showed an area effect on species richness in both fragments and control plots, but fragments had fewer species than control plots of equal size. In a fragmented Amazonian landscape, the full suite of terrestrial insectivores would persist in the short term only in large fragments (>100 ha), although much larger areas are probably necessary for the long-term persistence of their populations.

Extinciones Locales de Aves Insectívoras Terrestres en un Paisaje Fragmentado Cercano a Manaus, Brazil

Resumen: Examinamos las distribuciones de nueve especies de aves de insectívoros terrestres en fragmentos de bosque lluvioso de 4 a 14 años cercanos a Manaus, Brazil. Muestreamos once fragmentos de 1, 10 y 100 ha de vegetación secundaria y nueve áreas de bosque continuo (control) de 1–100 ha. Aumentamos el mapeo de puntos convencionales con muestreos extensivos. Los fragmentos fueron muestreados con redes antes del aislamiento, por lo que nuestros resultados pueden ser comparados con distribuciones pre-aislamiento. Para las nueve especies hubieron 55 casos de extinción local en los 11 fragmentos entre cerca de 1 año posterior al aislamiento y el tiempo del muestreo. Esto corresponde a una extinción de un 74% de las poblaciones locales en los fragmentos. Estas extinciones ocurrieron a pesar de conexiones de segundo grado de algunos fragmentos con bosques continuos a tan solo 70 m de distancia. Tres eventos aparentes de colonización por especies no detectadas antes del aislamiento también ocurrieron, pero esto puede ser reflejo de un inadequate muestreo antes del aislamiento. Nuestra comparación de fragmentos y áreas control de similar tamaño en bosques continuos muestra un efecto de área en la riqueza de especies tanto en sitios fragmentados como controles, pero los fragmentos tuvieron menos especies que los sitios control de similar tamaño. En un paisaje Amazónico fragmentado la totalidad de insectívoros terrestres persistirá en un corto plazo únicamente en los fragmentos grandes (>100 ha), aunque probablemente se necesitarán áreas mucho más grandes para la persistencia de sus poblaciones a largo plazo.

*Current address: Department of Zoology and Wildlife, 331 Funchess Hall, Auburn University, Auburn, AL 36849–5414, U.S.A., email antbirds@hotmail.com
Paper submitted October 15, 1998; revised manuscript accepted April 28, 1999.
**Introduction**

The effects of habitat fragmentation on avian communities are well documented in various parts of the temperate zone. For forest-interior species, fragmentation reduces abundance and richness (e.g., Saunders 1989; Askins et al. 1990). If habitats are fragmented throughout the landscape, population characteristics such as dispersal (Matthysen et al. 1995), philopatric returns of migrants (Villard et al. 1995), and demography (Verboom et al. 1991) will be affected. Isolated and reduced populations may also have reduced genetic variation (Frankham 1996). Forest fragmentation has effects on fitness through increased egg predation (Yahner & Scott 1988), increased brood parasitism (S. K. Robinson et al. 1995), and reduced pairing success (Van Horn et al. 1995). Forest-interior species may also be excluded by species associated with disturbance (Ambuel & Temple 1983; Grey et al. 1998). Fragmentation may have more direct consequences by affecting microclimate (Saunders et al. 1991).

Human settlement patterns in the Amazon tend to leave forest remnants amid deforested areas, as is the case in the temperate zone (Dale et al. 1994; Skole et al. 1994), but the effects of forest fragmentation on Neotropical birds are not as well understood. Local extinction has been suggested from indirect evidence or documented for unreplicated sites (e.g., Willis 1974, 1979; Leck 1979; Karr 1982; Thiollay 1996; W. D. Robinson 1999), but there is less direct evidence of extinction caused by forest fragmentation from replicated fragments.

The most complete study of the effects of fragmentation on a tropical avian community has been the long-term mist-netting program of the Biological Dynamics of Forest Fragments Project (BDFFP) near Manaus, Brazil. Some of the results of this study are reported by Stouffer and Bierregaard (1995a, 1995b), Bierregaard and Stouffer (1997), and Stouffer and Borges (2000). The BDFFP data are unique because replicated treatments (fragments) were sampled before they were isolated from the continuous forest surrounding them. Long-term data of the BDFFP show that terrestrial insectivores are particularly sensitive to fragmentation. Abundance, measured by mist-net captures, declined with decreasing fragment size and over the 9 years of study (Stouffer & Bierregaard 1995a). Other studies of fragmentation and habitat alteration in the Neotropics also suggest negative effects on terrestrial insectivores (Willis 1974, 1979; Leck 1979; Karr 1982; Canaday 1996). Borges (1995) found terrestrial insectivores rare or absent in the secondary forest at the BDFFP site.

We examined the distribution of nine species of terrestrial insectivores in forest fragments, second growth, and continuous forest at the BDFFP site. The data from fragments can be compared to results from the same areas before they were isolated. Although some of the study species were probably overlooked in the pre-isolation surveys, we designed our sampling to minimize the chance of overlooking birds.

**Methods**

**Study Site and Species**

The study was conducted approximately 80 km north of Manaus in the Brazilian state of Amazonas (lat 2°30′ S, long 60° W; Fig. 1). The area is a mosaic of terra firme forest, cattle ranches, secondary areas, and fragments of primary forest. Lovejoy and Bierregaard (1990) provide a detailed account of the study site. In continuous forest, canopy height averages 30–37 m, with occasional emergents up to 55 m. The understory is open and dominated by palms. The area has relatively pronounced wet and dry seasons. Rainfall at Reserva Ducke, approximately 50 km south of the study site, averaged 2500 mm per year from 1966 to 1990, with the greatest amount of rainfall from January to April and a dry season from June to September (Stouffer & Bierregaard 1993). There are several small streams in the forest, some of which have flowing water only during the wet season.

We collected data from 11 fragments: five 1 ha, four 10 ha, and two 100 ha in size (for individual descriptions of the fragments, see Lovejoy et al. 1986). The fragments were created between 1980 and 1990 by cattle ranchers working in collaboration with the BDFFP (10 of the 11 fragments were isolated by 1984; reviews in Lovejoy & Bierregaard 1990; Bierregaard et al. 1992). Distances of 70–650 m separated fragments from the nearest continuous forest; 6 of the 11 fragments were separated by 100–200 m. At 6 fragments, the surrounding vegetation was burned, and cattle were allowed to graze around the fragments. After several years, plant growth emerged, dominated by trees in the genera *Visnia* (Clusiaceae) and *Bellucia* (Melastomataceae). At 5 other fragments, the felled vegetation was not burned, and *Cecropia scidophylla* (Cecropiaceae) quickly dominated. Apart from the cattle ranches, the sites were embedded in continuous forest unbroken for hundreds of kilometers.

We also sampled nine control plots in nearby continuous forest. Three 1-ha control plots were chosen a priori based on topography to match the 1-ha fragments, which were all relatively flat and without streams. We also sampled four 10-ha plots, a 50-ha plot, and a 100-ha plot. For our analyses, we consider the 50-ha continuous forest plot to be a replicate of the 100-ha plot because it contained all the possible species. All control plots were at least 500 m apart. Secondary growth available for surveying was found around fragments or in pastures that were either abandoned or used infrequently for grazing.
We surveyed nine species of birds: Myrmeciza ferruginea (Ferruginous-backed Antbird), Formicarius colma (Rufous-capped Anthrush), Formicarius analis (Black-faced Anthrush), Myrmornis torquata (Wing-banded Antbird), Hylopezus macularius (Spotted Antpitta), Myrmothera campanisona (Thrush-like Antpitta), Grallaria varia (Variegated Antpitta), Conopophaga aurita (Chestnut-belted Gnateater), and Corythopis torquata (Ringed Antpiper). All have stout bodies and short wings, although they vary in mass from 15 g (Corythopis torquata) to 120 g (Grallaria varia; Bierregaard 1988). Our observations and published accounts suggest that most of these species forage almost exclusively on the ground. Conopophaga aurita, a difficult bird to observe, may be an exception. We have seen it on the ground, but we have not observed it foraging. It was reported as terrestrial by Sick (1993:422), although Ridgely and Tudor (1994) imply that Conopophaga feed in low vegetation. Corythopis torquata forages both in the litter and by stretching or jumping from the ground to remove invertebrates from the underside of leaves. Marra and Remsen (1997) and Stratford (1997) describe the habitat used by some of these species. There are other species of terrestrial insectivores at the site, but we chose a subset that could be accurately sampled with spot-mapping and tape playback (for a complete description of the BDFFP avifauna, see Cohn-Haft et al. 1997).

Survey Methods

We sampled birds from July 1994 through July 1995. Surveys were conducted from 0530 to 0900 hours for 3 days in plots of 1–10 ha and for 6 days in larger plots. Most plots were surveyed on consecutive days. The observer walked around the perimeter of the plot and on trails through the interior, noting the location of any study species seen or heard. Peak singing for the study species is within about 30 minutes of sunrise (approximately 0530 to 0630 hours all year), although some species sing or call later in the day, especially around sundown. Surveys in the secondary growth were conducted from trails, roads, and around fragments. Only birds within 100 m of the trail were counted in second-growth surveys.

For species that were not detected by 0630 hours, we used playback to elicit a species-specific response. Playback has been recommended to survey secretive birds and has been used successfully to census birds in North America (Johnson et al. 1981; Marion et al. 1981) and for experimental purposes in the Neotropics (S. K. Robinson & Terborgh 1995; Stouffer 1997). Tapes were played at...
the center and at the perimeter of each of the study plots with using either a Sony TC-D5 Pro II or a Marantz PMD222 with an Archer external speaker. All tapes included songs and calls recorded at the BDFFP sites.

After testing for normality, we used the results from these surveys in a two-way analysis of variance to test for the effects of plot size and fragmentation on species richness. We tested for specific differences among the 1-, 10-, and 100-ha plots using a post-hoc GT2 comparison, a recommended comparison for means from unequal sample sizes (Sokal & Rohlf 1981).

We compared mist-netting data from fragments before isolation with the presence-absence data from our surveys. We included 1 year of the post-isolation period with the pre-isolation period because several fragments had little pre-isolation sampling effort. Captures confirmed presence, but the lack of a capture does not confirm an absence, especially for species like the antpittas, which seldom fall into mist nets (e.g., Stouffer & Bierregaard 1995a). Because all the study species respond to playback, we doubt we overlooked any birds in our surveys. Thus we are more likely to assume falsely that a species was absent before isolation than after isolation.

Results

The fragments had zero to seven of the nine species at the time of our surveys (Table 1; Fig. 2). The two 100-ha fragments had six and seven species. Missing from both 100-ha fragments was Myrmornis torquata, which was also absent from all the smaller fragments. Formicarius analis and Myrmeciza ferruginea were also missing from one 100-ha fragment, and Conopophaga aurita was missing from the other 100-ha fragment. The 10-ha fragments contained one to four species. Missing from all 10-ha fragments were Myrmothera campanisona, Corythopis torquata, Formicarius analis, Hylopezus macularius, and Myrmornis torquata. A single 1-ha fragment had a terrestrial insectivore (Myrmothera campanisona).

Two to nine species were found in the control plots (Table 2; Fig. 2). The 100- and 50-ha control plots each contained all of the terrestrial insectivores. The 10-ha control plots had four to six species. The 1-ha control plots had two to three species. Formicarius colma was found in all of the control plots. Conopophaga aurita and Myrmeciza ferruginea were found in the three 10-ha control plots. Formicarius analis was not detected in any of the 1- or 10-ha plots. Myrmothera campanisona, Grallaria varia, and Conopophaga aurita were not detected in any of the 1-ha plots.

A two-way analysis of variance of area and fragmentation (fragments vs. control plots; Fig. 2) revealed significant area effects and significant effects of fragmentation but no significant interaction (area: $F = 71.15$, df = 1,14, $p < 0.0001$; fragmentation: $F = 62.59$, df = 1,12, $p < 0.0001$; interaction: $F = 0.81$, df = 1,14, $p = 0.464$). Not surprisingly, 100-ha fragments and control plots had more species than 1-ha fragments and control plots. Fragments and control plots of 10 ha were intermediate.

Before isolation, five to nine species were recorded in the plots that later became fragments (Table 1). Local extinction occurred in all fragments, with the proportion of local populations that went extinct varying from 100% in 1-ha fragments to 31% in 100-ha fragments. The most extinction-prone species were those that occurred in the most plots before isolation—Myrmornis torquata, Corythopis torquata, Formicarius colma, and Myrmeciza ferruginea—all of which went extinct in at least 7 of the 11 fragments. Our results show three possible colonizations (two by Myrmothera campanisona and one by Formicarius analis), although

Table 1. Distribution of terrestrial insectivorous birds in Amazonian forest fragments before and after isolation.

<table>
<thead>
<tr>
<th>Species</th>
<th>100</th>
<th>100</th>
<th>10</th>
<th>10</th>
<th>10</th>
<th>10</th>
<th>1</th>
<th>1</th>
<th>1</th>
<th>Extinctions/colonizations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Myrmornis torquata</td>
<td>–</td>
<td>P</td>
<td>P</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>P</td>
<td>P</td>
<td>–</td>
<td>11/0</td>
</tr>
<tr>
<td>Corythopis torquata</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>A</td>
<td>P</td>
<td>9/0</td>
</tr>
<tr>
<td>Formicarius colma</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>A</td>
<td>7/0</td>
</tr>
<tr>
<td>Myrmeciza ferruginea</td>
<td>P</td>
<td>–</td>
<td>P</td>
<td>–</td>
<td>–</td>
<td>A</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>7/0</td>
</tr>
<tr>
<td>Conopophaga aurita</td>
<td>–</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>P</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>7/0</td>
</tr>
<tr>
<td>Hyllopezus macularius</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>–</td>
<td>A</td>
<td>–</td>
<td>A</td>
<td>A</td>
<td>–</td>
<td>5/0</td>
</tr>
<tr>
<td>Formicarius analis</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>A</td>
<td>A</td>
<td>–</td>
<td>A</td>
<td>A</td>
<td>–</td>
<td>5/1</td>
</tr>
<tr>
<td>Grallaria varia</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>–</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>–</td>
<td>4/0</td>
</tr>
<tr>
<td>Myrmothera campanisona</td>
<td>+</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>0/2</td>
</tr>
<tr>
<td>Extinctions/colonizations</td>
<td>2/2</td>
<td>3/0</td>
<td>3/0</td>
<td>5/0</td>
<td>6/0</td>
<td>6/1</td>
<td>6/0</td>
<td>6/0</td>
<td>7/0</td>
<td>8/0</td>
</tr>
<tr>
<td>Location code</td>
<td>3304</td>
<td>2303</td>
<td>3209</td>
<td>1207</td>
<td>1202</td>
<td>2206</td>
<td>3114</td>
<td>2107</td>
<td>1104</td>
<td>1112</td>
</tr>
</tbody>
</table>

Notes: +, present before isolation, absent after isolation (i.e., local extinction); *, absent before isolation, present after isolation (i.e., colonization); P, present before and after isolation; A, absent before and after isolation.

See Fig. 1.
these species could have been overlooked in the pre-isolation survey.

Fifty-three ha of Cecropia-dominated vegetation was sampled. Formicarius colma (two individuals or pairs), Myrmothera campanisona (two individuals or pairs), and Myrmeciza ferruginea (one pair) were found in Cecropia forests. In 42 ha of Vismia-dominated vegetation, only a single F. colma was detected.

**Discussion**

Three approaches have been used to study the effects of fragmentation on forest taxa. One is to analyze patterns of species richness in fragments of various sizes (e.g., Blake & Karr 1987). The drawback to this method is that it is difficult to eliminate the effect of sampling area; both fragmentation and decreasing sampling area should result in decreasing species richness. Another method is to sample fragments and similarly sized plots in continuous forest to test the hypothesis that fewer species are found in fragments (e.g., Karr 1982). A weakness with this and the first method is that the pre-isolation species richness is unknown, so local extinction or colonization after isolation cannot be shown directly. The third method, sampling fragments before and after isolation, can explicitly show changes after isolation (e.g., Stouffer & Bierregaard 1995a).

We used all three methods to analyze terrestrial insectivorous bird distribution in Amazonian forest fragments. Both area effects and fragmentation effects were significant; species richness increased with area, but continuous forest plots always had more species than did fragments of the same size (Fig. 2). More important, comparing our surveys of the fragments with data collected in the same fragments before they were isolated directly showed local extinction of most terrestrial insectivores in most of the fragments (Table 1).

We documented 55 cases of local extinction in the fragments out of a possible maximum of 74 (74%). Our extinction result is a minimum estimate because species were more likely to be overlooked in the pre-isolation mist-net surveys than in our intensive playback surveys.

---

**Table 2. Distribution of terrestrial insectivorous birds in plots within continuous Amazonian forest.**

<table>
<thead>
<tr>
<th>Species</th>
<th>100</th>
<th>50</th>
<th>10</th>
<th>10</th>
<th>10</th>
<th>10</th>
<th>1</th>
<th>1</th>
<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Formicarius colma</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td>Myrmeciza ferruginea</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Conopophaga aurita</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Myrmornis torquata</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Grallaria varia</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Hylotezus macularius</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>P</td>
</tr>
<tr>
<td>Corythopis torquata</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Myrmothera campanisona</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Formicarius analis</td>
<td>P</td>
<td>P</td>
<td>A</td>
<td>P</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>Total ssp.</td>
<td>9</td>
<td>9</td>
<td>6</td>
<td>6</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Location code</th>
<th>1501a</th>
<th>1501b</th>
<th>1204</th>
<th>1501c</th>
<th>1205</th>
<th>1201</th>
<th>1501d</th>
<th>1501e</th>
<th>1501f</th>
</tr>
</thead>
</table>

---

*P, present; A, absent.*

*See Fig. 1.*
The most extinction-prone species in our sample was *Myrmornis torquata*, which was captured in all of the fragments before isolation but was not recorded by us in any fragments (Table 2). This species was regularly present in control plots, so its loss from fragments seems directly related to the fragmentation process. Not all species were found in all fragments before isolation, so we also consider colonization. We found only three colonizations for the 25 possible vacancies (12%) based on the pre-isolation surveys. Two of these colonizations were by *Myrmothera campanisona*, a species that prefers treefall gaps and edges (Stratford 1997).

The most dramatic effect of fragmentation was in the 1-ha fragments. All terrestrial insectivores recorded in these fragments before isolation were later absent in our surveys. The single terrestrial insectivore found in a 1-ha fragment was an individual *Myrmothera campanisona* that colonized after isolation. Terrestrial insectivores fared only slightly better in 10-ha fragments, with 68% of the original 16 occurrences resulting in extinctions. The 100-ha fragments lost 31% of the original 16 occurrences of terrestrial insectivores, although both of the possible empty sites were colonized.

Our descriptive studies do not reveal the mechanisms responsible for species loss in this system, although we have evidence that the combination of large territory sizes, sedentary lifestyles, and strong preference for old-growth forest makes terrestrial insectivores vulnerable to local extinction in small fragments (see also Mac Nally & Bennett 1997). These species all use territories of at least 5 ha, with territories of >20 ha sometimes found for *Myrmornis torquata* and *Formicarius analis* (Stouffer 1997 and unpublished data; see also Terborgh et al. 1990). Thus, no terrestrial insectivore can maintain even 20% of a normal territory in 1-ha fragments, and 10-ha fragments may be too small for even a single territory of some species. In 100-ha fragments the local populations comprise a maximum of about 10 pairs, and this would apply only to *Myrmeciza ferruginea* and *Formicarius colma*, the two most common species (Stouffer 1997 and unpublished data).

Small populations in fragments make these species vulnerable to local extinction through demographic stochasticity, even if conditions are suitable for reproduction and survival (Bolger et al. 1991). In fact, we suspect that fragmentation leads to decreased survival or reproductive success. Stratford (1997) showed that several species of terrestrial insectivores use microhabitats that are more common in continuous forest than in the fragments we studied. Some leaf-litter arthropods are less abundant in these fragments than in continuous forest (Didham 1997). We do not know if these are important resources for our study species, but there is evidence from a temperate system of reduced food affecting breeding of a terrestrial insectivore (Burke & Nol 1998). Increased stress or reduced food may also be related to reduced rates of feather growth in fragments for two common species at our site (J.A.S. and P.C.S., unpublished data).

Interactions with invasive birds from nonforested habitats probably do not threaten the species we studied, although the influence of invasive predators remains unknown. The parasitic cowbirds *Molothrus bonariensis* and *Scaphidura oryzivora* were present at our sites, but we have no evidence that cowbird parasitism is a significant effect here, especially compared to some temperate systems (e.g., Robinson et al. 1995). In addition to being uncommon at our sites (Cohn-Haft et al. 1997), these cowbirds are unlikely to parasitize forest species (Sick 1993). Neither interspecific aggression nor resource exploitation from invasive birds (Ambuel & Temple 1983; Grey et al. 1998) is likely to be a contributor to loss of terrestrial insectivores at our sites because the forest understory is largely unused by birds after fragmentation (Stouffer & Bierregaard 1995a; Stouffer & Borges 2000). We have no data on predation on nests or adults, but other Neotropical work suggests that predation is likely higher in fragments than in continuous forest (Loiselle & Hoppes 1983; Sieving 1992; Sieving & Karr 1997).

Our data also show that terrestrial insectivores generally avoid second growth (Borges 1995; Stouffer & Borges 2000). Like most other understory birds at our site, they are more likely to be found in *Cecropia*- than in *Visnia*-dominated growth (Stouffer & Bierregaard 1995a). Second-growth avoidance has two negative effects on persistence in fragments. First, birds in fragments cannot augment their territories by using multiple fragments or adjacent second growth (e.g., Howe 1984). Second, it reduces colonization of fragments from nearby continuous forest. Results of long-term mist-net surveys show that the abundance of terrestrial insectivores declines gradually in fragments, even when rapidly growing second growth provides a link to continuous forest as little as 75 m away (Stouffer & Bierregaard 1995a). This link allows recolonization by some forest birds, suggesting that other taxa are less specific in the habitats they will cross. Most Amazonian forest understory species have probably had little need to cross open or nonforested areas in their evolutionary history, so unwillingness to leave old-growth forest cover may be an innate behavioral response (Greenberg 1989; see Sieving et al. 1996). Because these species do not migrate, there is no mechanism for recolonization of truly isolated fragments, a phenomenon that occurs annually in some temperate-zone systems (Blake & Karr 1987). In addition to direct avoidance, some species may be unable to use secondary growth areas because of constraints of morphology or behavior (Winkler & Leisler 1985). For example, *Myrmornis torquata*, a bird that forages by tossing leaves, is probably unable to manipulate the large fallen leaves of *Cecropia* that dominate the litter of some secondary forests at our site.
If allowed to grow, second growth from logged areas or abandoned cattle pastures will eventually converge on the old-growth forest in our continuous forest sites, but we predict that terrestrial insectivores will be among the last birds to be able to use regenerated forest (see also Loiselle & Blake 1994; Borges 1995). At the moment, we cannot tell how long it will take for the study species to use second growth; we have seen little use of second growth that has been growing for 15 years. Regardless of how these areas take to become suitable, throughout the regrowth period terrestrial insectivores will have little demographic linkage among fragments, so subpopulations will remain isolated, small, and vulnerable to local extinction. Those subpopulations that do persist also may be vulnerable to the genetic effects of inbreeding (Frankham 1996), although we know too little about demography to estimate this effect.

Our results demonstrated a rapid and pronounced loss of ground-foraging, insect-eating birds after isolation of Amazonian forest fragments. This augments a growing body of evidence suggesting that terrestrial insectivores are exceptionally vulnerable to forest fragmentation (e.g., Karr 1982; Recher & Lim 1990; Stouffer & Bierregaard 1995a; Canaday 1996). In the landscape we studied, the fragments where birds went extinct were demographically isolated from the vast adjacent areas of continuous forest where the birds persisted (Table 2; Fig. 1). From this observation, we conclude that fragments of 1–100 ha will contribute little to the long-term persistence of populations of these species, even in a minimally fragmented landscape.

Acknowledgments

We thank R. Bierregaard and the banders and mateiros who collected the mist-net data. C. Gascon and the Associação de Levantamento de Amazónias staff facilitated our fieldwork. Reviews by D. Saunders and two anonymous reviewers improved the manuscript. Financial support for our surveys was provided by the Biological Dynamics of Forest Fragments Project and Southeastern Louisiana University. This is publication number 233 in the BDFFP Technical Series.

Literature Cited


