

EFFECTS OF FOREST FRAGMENTATION ON AMAZONIAN UNDERSTORY BIRD COMMUNITIES.

Richard O. Bierregaard, Jr. (*)

Thomas E. Lovejoy (**)

SUMMARY

Data from an intensive mist-netting mark-recapture program in the central Amazon demonstrate significant changes in the understory avian community in isolated patches of 1 and 10 ha of terra firme forest. Following isolation, capture rates increase significantly as birds fleeing the felled forest entered the newly formed forest fragments. Movement to and from the reserve is restricted, as witnessed by an increase in recapture percentages following isolation. Species of birds that are obligate army ant followers disappeared at the time the surrounding habitat was removed from 1- and 10-ha areas. The complex mixed-species insectivorous flocks typical of Amazonian forests deteriorated within 2 years of isolation of 1- and 10-ha forest fragments. Several species of mid-story insectivores changed their foraging behavior after isolation of small forest reserves.

INTRODUCTION

The Biological Dynamics of Forest Fragments project (Minimum Critical Size of Ecosystems) is a multidisciplinary attempt to understand the effects of fragmentation of Amazonian tropical rainforest. Through systematic surveys of a broad range of organisms in different sized tracts of forest before and after isolation by deforestation of surrounding areas for cattle pastures, we are studying the ecological changes associated with the fragmentation of tropical forests. Insights gained may lead to methods of managing reserves that maximize species carrying capacity in areas scheduled for deforestation.

The principal question addressed by the project is not whether or not there will be ecosystem decay associated with forest fragmentation (which we take as given), but rather, to what extent does the decay depend on interspecific relationships, on specific autecological requirements or on microhabitat requirements. The importance of stochastic events, including sampling effects at the moment of isolation and the vagaries attendant on small populations (Soule, 1980; Franklin, 1980; Lovejoy & Oren, 1981) will also be assessed.

There is general agreement that in order to maintain viable populations of species

(*) World Wildlife Fund 1250 24 th St. NW, Washington, DC 20037 - EUA.

(**) Smithsonian Institution, Washington, DC 20560.

with large territorial requirements (principally large predators), Amazonian forest reserves should be on the order of hundreds of thousands of hectares (Terborgh, 1975). However, there is little doubt that much of the remaining forests will be fragmented into areas much smaller.

This study is the first to quantitatively sample the avian community in small forest tracts before and after fragmentation from surrounding virgin forest. Although the data are from very small reserves (1 and 10 ha), it is hoped that our analyses will provide insights into processes which might otherwise be obscured or might be much longer in becoming apparent in studies of larger tracts. Future analyses of post-isolation data from 100- and 1000-ha reserves will show the extent to which the phenomena documented in smaller reserves may apply to larger areas.

A program of periodic sampling in the project's study tracts before and after their isolation provides the quantitative basis for an assessment of the effects of isolation on this part of the ecosystem. Data from mist-net captures of understory birds from isolated forest reserves were compared to pre-isolation data from the same reserves to investigate changes related to isolation of the former virgin forest tracts. Birds of the forest understory probably are particularly susceptible to the effects of fragmentation of virgin forest because physiological and behavioral constraints limit or preclude their movement through areas where no forest cover is available. The large number of understory birds whose ranges are delimited by rivers (Meyer de Schauensee, 1966; Sick, 1967) reflects this tendency.

Comparisons were made of isolated forest reserves of different sizes (1 and 10 ha) to test the effect of size on the resultant avian community composition. As well as comparisons of pre- and post-isolation data from the isolated patches themselves, post-isolation data were compared to near-by, non-isolated forest plots studied simultaneously to control for the effects of temporal variation in avian community structure.

METHODS

The study areas are situated on nutrient poor, clayey or sandy yellow latosols (Chauvel, 1982) 70 km north of Manaus, Brazil (Fig. 1). The average annual rainfall is approximately 2200 mm and is strongly seasonal, with the dry season extending from June through October and the peak of the rainy season in February and March (Anon., 1978).

The forest canopy is about 30-40 m high, with a few emergent trees towering up to 55 m above the forest floor. The canopy is even and closed, permitting little sunlight to penetrate to the rather open understory, which is characterized by many stemless palms (Guillaumet & Kahn, 1982). The woody plant community is diverse as many as 250; woody species have been recorded in a single 10 ha plot (Rankin *et al.*, 1988). The predominant woody plant families are Burseraceae, Sapotaceae, Lecythidaceae, and Leguminosae.

The isolation of the reserves was the result of deforestation for cattle pastures

by three large firms investing in the Manaus free trade zone. The first step in the process was the clearing of the understory so that chain sawyers had access to canopy trees. Understory clearing began in May or June, with the chain saws arriving about a month later. Depending on the area being cleared, felling continued into August and sometimes into October. The felled area was burned as late as possible in the dry season, usually in the end of October.

Six isolated reserves were studied, varying in size and the time at which they were isolated from the surrounding forest. One 1-ha and one 10-ha reserve were isolated in 1980, while two 1-ha and two 10-ha reserves were isolated in 1983. Fourteen sites in undisturbed forest provided control data.

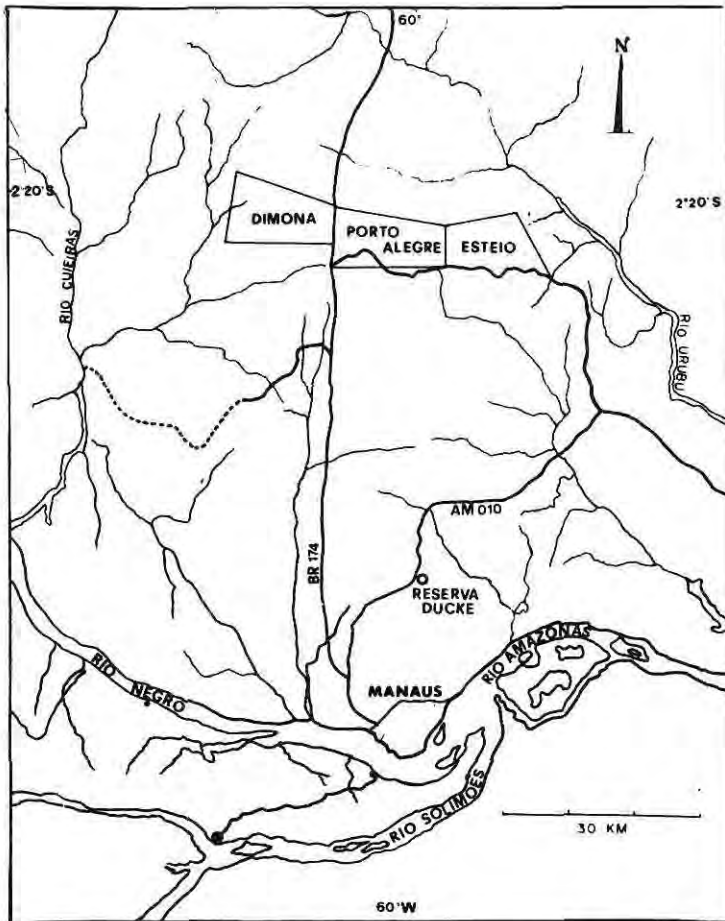


Fig. 1. The location of the three cattle ranches (fazendas) in the agricultural development area north of Manaus, Brazil, where the majority of the study sites are located.

Distance to continuous forest varied from reserve to reserve. The 1980 10-ha isolate at its closest point is slightly less than 100 m from a narrow peninsula of stream forest, itself less than 100 m wide. On all other sides it is more than 500 m to the nearest continuous forest. Similarly, the 1980 1-ha isolate is roughly 80m from continuous forest on its west side and hundreds of meters to virgin forest on the other sides. One of the 1983 10-ha isolated, reserve 1207, is isolated on the south by a 500 ha clearing and on the remaining three sides by only 100 m from virgin forest. All other reserves isolated in 1983 are isolated by at least 200 m.

All reserves were sampled with transects of tethered mist-nets (EBBA type ATX, 12 m x 2 m, 36 mm mesh) once every three or four weeks, with occasional breaks in the routine of up to six months. Post-isolation reserves were sampled with high priority, so that few long gaps exist in post-isolation data. One-ha reserves were sampled with an 8 net line and 10-ha reserves with a line of 16 nets.

Nets were opened from dawn (about 0600 h) until 1400 h. All birds captured, except hummingbirds, were banded with uniquely numbered aluminum bands and released at the point of capture. Hummingbirds were marked by cutting the tips of tail feathers in unique combinations. In addition, all birds seen or heard by the banders in the reserve on each banding day were recorded.

The percentage of captures on a given day of birds already banded were calculated for all non-isolated reserve net-lines. An asymptotic regression (Snedecor & Cochran, 1967; Patterson, 1960) was fit to these "pre-isolation" data to obtain the best fit curve describing the relation between the number of days a given reserve had been sampled and the expected proportion of recaptures on that sample day. Recapture percentages were analyzed from the 1980 isolates and compared to values predicted by pre-isolation data.

Capture rates from both 1980 and 1983 isolated reserves were compared before and after isolation to measure the effect of isolation on population size and/or avian activity in the recently isolated reserves.

The relative abundances of a group of 25 of the more abundant species in the 1980 isolates (1 and 10 ha) were compared to pre-isolation values from the same reserves to determine what ecological guilds were most susceptible to the effects of isolation. The species selected were the most abundant representatives of the following guilds; obligate army ant followers (Willis, 1967), mixed-species flock species, frugivores, tree-fall specialists, hummingbirds and a general category of abundant insectivorous species occupying small territories throughout the study area.

Capture rates were also calculated for each species from non-isolated reserves and in each size class of isolated reserves (both 1980 and 1983 isolates) beginning approximately 6 months after isolation (1 Jan. of the year following isolation). For the species in the guilds mentioned above, these rates were compared to the capture rates from undisturbed forest samples.

RESULTS

From October 1979 through 5 January 1985, 19,494 captures of 10,918 individuals of 141 species were recorded in non-isolated reserves (see App. 1). In isolated reserves an additional 2,673 captures were recorded in isolated forest fragments of 1 and 10 ha. Four species not encountered in the non-isolated reserves were captured in the isolates (see App. 1).

The log-transformed rank abundance distribution from undisturbed forest (Fig. 2b) was linear, with only the most common species, the White-plumed Antbird, *Pithys albifrons*, (7.66% of individuals banded, see Fig. 2a, App. 1) deviating slightly from the linear trend seen among the other 140 species. This linear distribution indicates the

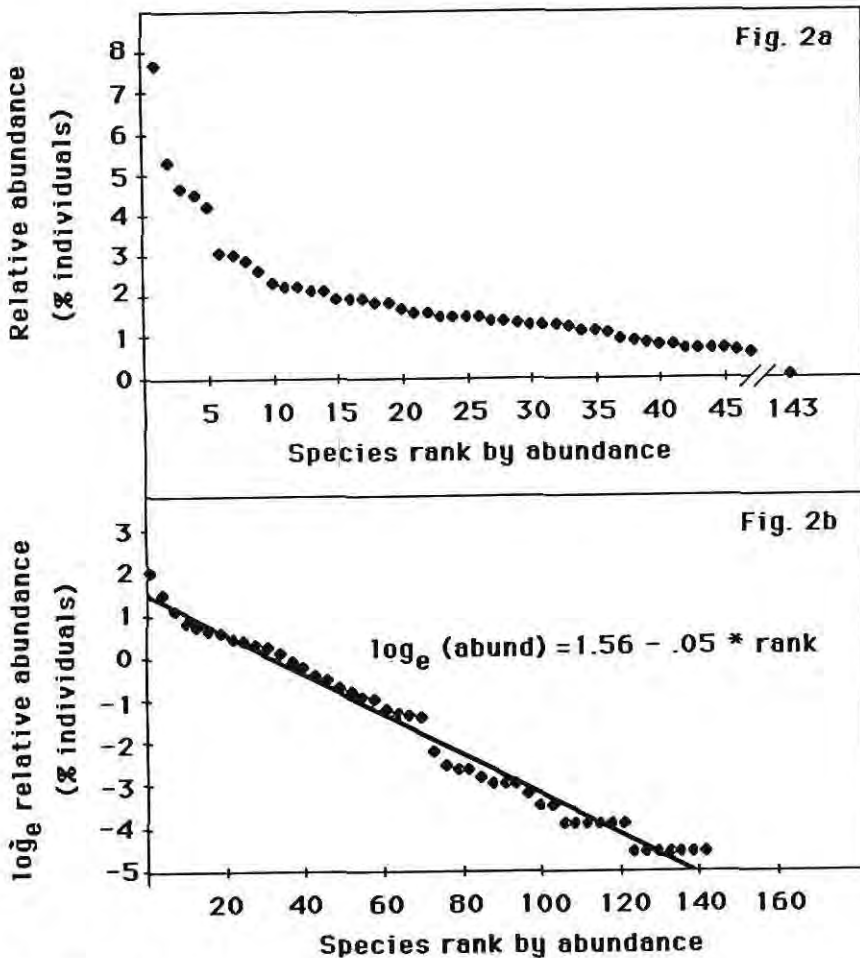


Fig. 2. The rank abundance distribution of birds netted in the understory of undisturbed terra firme forest north of Manaus, Brazil. 2a) The relative abundance of each species, as represented by individuals banded, plotted in decreasing order for the 143 species encountered in the netting sample. 2b) A semi-log representation of the rank abundance distribution presented in Fig. 2a.

absence of a single dominant species or group of species and a long tail of very rare species. Following Karr (1971), if we define as rare any species represented by less than of 2% of individuals banded, 127 species, or 90% of the community, are rare. The large number of rare species is typical of tropical forests (Karr, 1971; Lovejoy, 1975; Pearson, 1977; Wong, 1986).

In the non-isolated control sites the 25 most abundant species represented 71.7% of all captures and 67.3% of all birds banded. The 25th most abundant species represented only 1.47% of all birds banded. Of the remaining 116 species, 18 were recorded from a single capture.

The understory avian community in the Manaus area is predominantly insectivorous; 79.2 of the individuals banded (67.96% by biomass) and 83.33% of all captures are strictly or predominantly insectivorous (Table 1). Obligate army ant followers and regular mixed species flock followers comprise 37.43% of the individuals captured (32.13% by biomass) and 41.06% of captures in non-isolated reserves (Table 1).

Frugivores accounted for only 14.7% of the individuals banded, and 12.7% of captures in undisturbed forest. However, because of the large size of several species in the guild, biomass the group represented 23.4% of the total biomass (Table 1).

The most common frugivore, the White-crowned Manakin (*Pipra pipra*), was the fourth most commonly banded species (4.49% of all individuals, 2.1% by biomass). The Ruddy Quail-dove (*Geotrygon montana*), although not numerically dominant in the sample (the 26th most abundant species, representing 1.47% of bandings), was by biomass the most important species in our sample from undisturbed forest, slightly ahead of the White-plumed Antbird (6.53% vs. 6.17%) (App. 1).

Capture rates from undisturbed, virgin forest net lines decline gradually over time according to the relation $y = .227 - .06x$ where y is the capture rate/net-hour and x is the number of days since the first sample in the course of a monthly sampling regime (Bierregaard & Lovejoy in press). While capture rate declined slowly, the percent recapture on a given sample day approaches an asymptote of 42.7% according to the equation $y = .427 - .429(.364)^x$ where y is the recapture percentage and x is the days since first sample as above (Bierregaard & Lovejoy in press).

Capture rates and recapture percentages in isolated reserves differed markedly from those in undisturbed forest. As deforestation proceeded around the 1980 isolates, the most dramatic effect witnessed in the understory avian community was a dramatic increase in avian activity, as reflected quantitatively by increased capture rates (see Fig. 3), and in the amount of avian vocalizations heard by the banding crews working in the reserves. The mean capture rate during the 7 capture days before isolation was not significantly different between the 1- and 10-ha reserves isolated in 1980, but was significantly higher on the 7 capture days following isolation in both reserves (Student's t-test for paired observations, 1-ha, $p < .05$; 10-ha $p < .01$, Table 2). The increase in activity in the smaller, 1-ha reserve was greater than in the 10-ha ($p < .05$, Table 2).

After six months, capture rates declined precipitously to below pre-isolation rates in the 1-ha area and roughly to pre-isolation levels in the 10-ha reserve.

Replication of this pattern was seen in all but one of the 1983 isolates (Fig. 3). The one exception to the general tendency was reserve 1207, which was surrounded on three sides by continuous forest only 100 m away. As in 1980, the 1 ha reserve isolated in 1983 showed greater increases in capture rates than the 10 ha reserves.

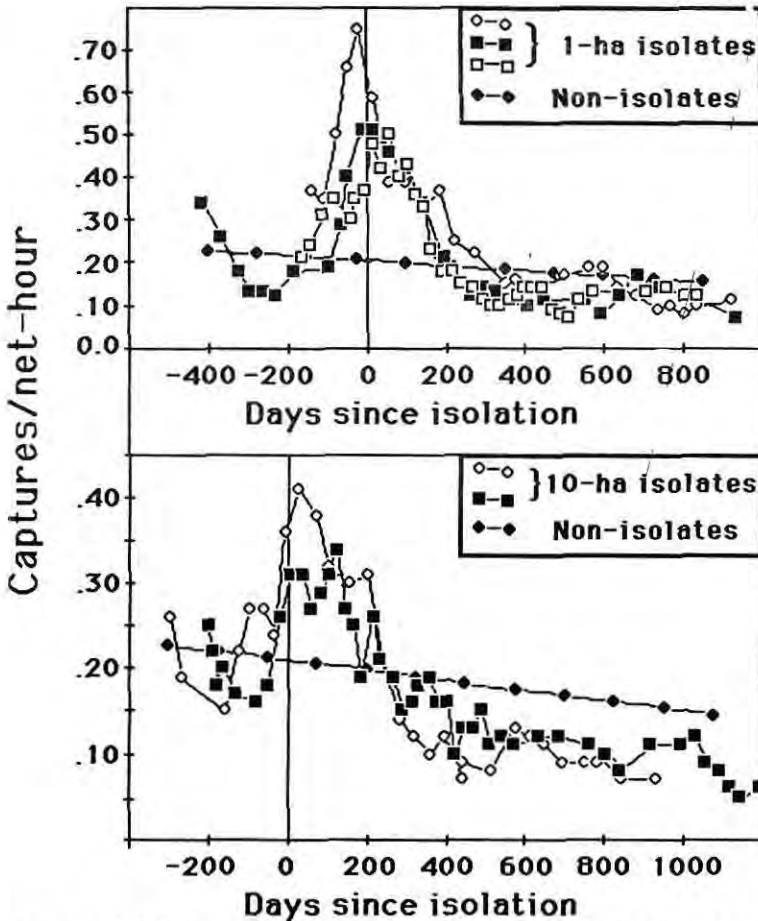


Fig. 3. Capture rate (birds/net-hour) as a function of time in three 1-ha reserves (above) and in two 10-ha reserves (below) before and after isolation (indicated by the vertical line). Expected values are shown as calculated from net-lines in continuous forest. Points are three-point running means.

Recapture rates also changed after the isolation of a small (1- or 10-ha) reserve (Fig. 4). Coincidental with the increased capture rates, the percentage of previously banded birds captured on a given day decreased for about three months after isolation began (Fig. 4). Following this decrease, recapture rates climbed rapidly to somewhere between 60 and 90%, considerably above the asymptote of 43% in non-isolated reserves.

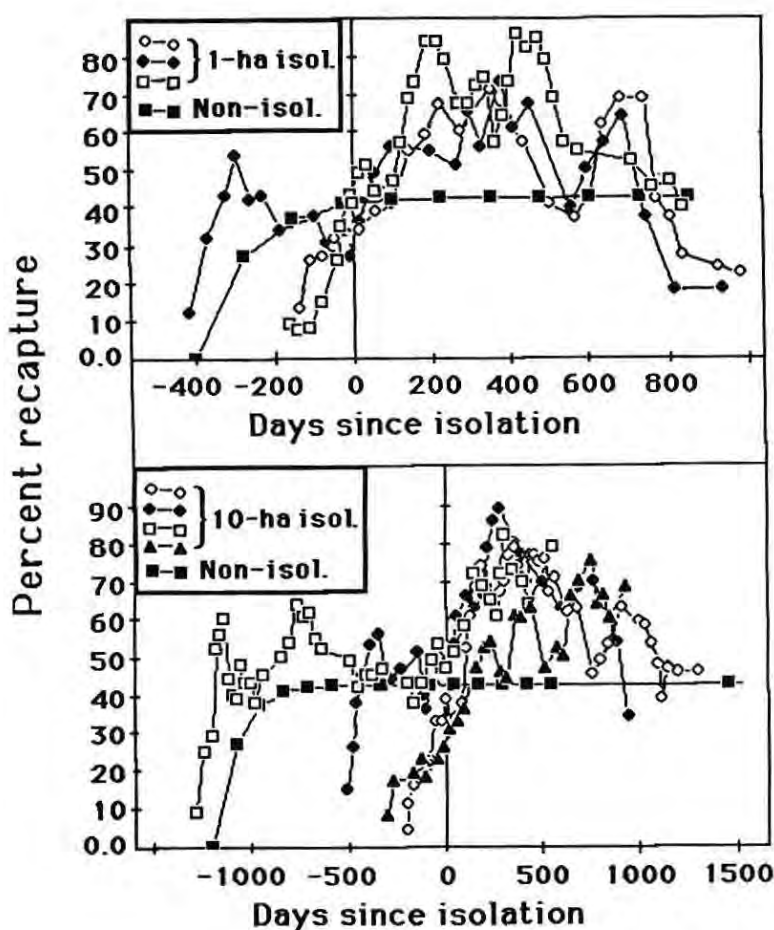


Fig. 4. Recapture rates as a function of time in 1- and 10-ha isolated reserves. The vertical lines marks the time of isolation for the two sets of reserves. The expected values, calculated from net-lines in undisturbed forest, approaches an asymptote of slightly over 40%. Points are three-point running means.

Subsequent to isolation of the reserves, resprouting from felled trees and an exuberant flush of second growth species connected the reserves to the adjacent extensive forest. Two years after isolation, capture rates in the two 1980 isolates increased somewhat and recapture rates dropped sharply. These changes in avian activity were witnessed when the second growth attained a height sufficient to have a heavily shaded understory (approx. 3-4 m). Individuals of understory species that had disappeared, such as the Ferruginous-backed Antbird (*Myrmeciza ferruginea*), or had decreased in frequency in the nets, such as the White-crowned Manakin, began entering the reserves. In the case of the Ferruginous-backed Antbird, the recolonization of the reserve was by the last individual of the species caught in the reserve over 18 months previously.

Different ecological guilds responded differently to the isolation of the 1980 reserves (Fig. 5). In addition, species within guilds responded differently to isolation. The fastest and most dramatic change was the disappearance of the obligate army ant following species. This group virtually disappeared within two capture days of isolation. The disappearance of the Formicariid members of the guild, the White-plumed Antbird and the Rufous-throated Antbird (*Gymnopithys rufigula*) was virtually complete and permanent. Since isolation, only 2 individuals of the Rufous-throated Antbird have been netted in isolated reserves, and these only in the 10-ha reserve isolated in three sides by only 100 m. In contrast, other species that follow army ant swarms, the White-chinned Woodcreeper (*Dendrocincila merula*) and 3 much rarer, large Dendrocolaptids, the Plain-brown (*Dendrocincila fuliginosa*), the Barred (*Dendrocolaptes certhia*) and the Black-banded (*D. picumnus*) woodcreepers, have been netted more than 25 times (17 for the more generalist Plain-brown Woodcreeper) in both 10 and 1-ha reserves, in most cases over army ant swarms. Ant swarms have been observed to invade the reserves through as much as 250 m of pasture and low second growth.

More slowly, but no less definitively, the mixed species flocks gradually lost species in the 1980 isolates (Fig. 5). Two species, the Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*) and the Chestnut-rumped Woodcreeper (*Xiphorhynchus pardalotus*) became relatively more abundant in both 1980 isolates over the course of time. Capture rates for the Chestnut-rumped Woodcreeper were, in fact higher in 1-ha than in 10-ha isolates and higher in both than in undisturbed forest (Fig. 6). Capture rates for the Wedge-billed Woodcreeper were higher in 10-ha isolates than in undisturbed forest while in 1-ha isolates the capture rate was virtually identical to that recorded in non-isolated samples.

In the 1980 isolates, tree-fall and edge specialists increased in relative abundance, while understory frugivores declined initially but seemed to recover later on (Fig. 5). The largest Piprid, (ca. 30 g.), the Thrush-like Manakin (*Schiffornis turdinus*), more insectivorous than its confamilials, persisted only in the 10 ha reserve (Fig. 5).

For most common frugivores, capture rates in 1-ha reserves were much lower than in 10-ha reserves or the non-isolated samples (Fig. 7). The Thrush-like Manakin and the White-fronted Manakin (*Pipra serena*) disappeared completely from 1-ha isolates, while capture rates for the White-crowned Manakin and the White-throated thrush, *Turdus albicollis*, were similar in undisturbed forest and in 10-ha isolates but much lower in 1-ha tracts.

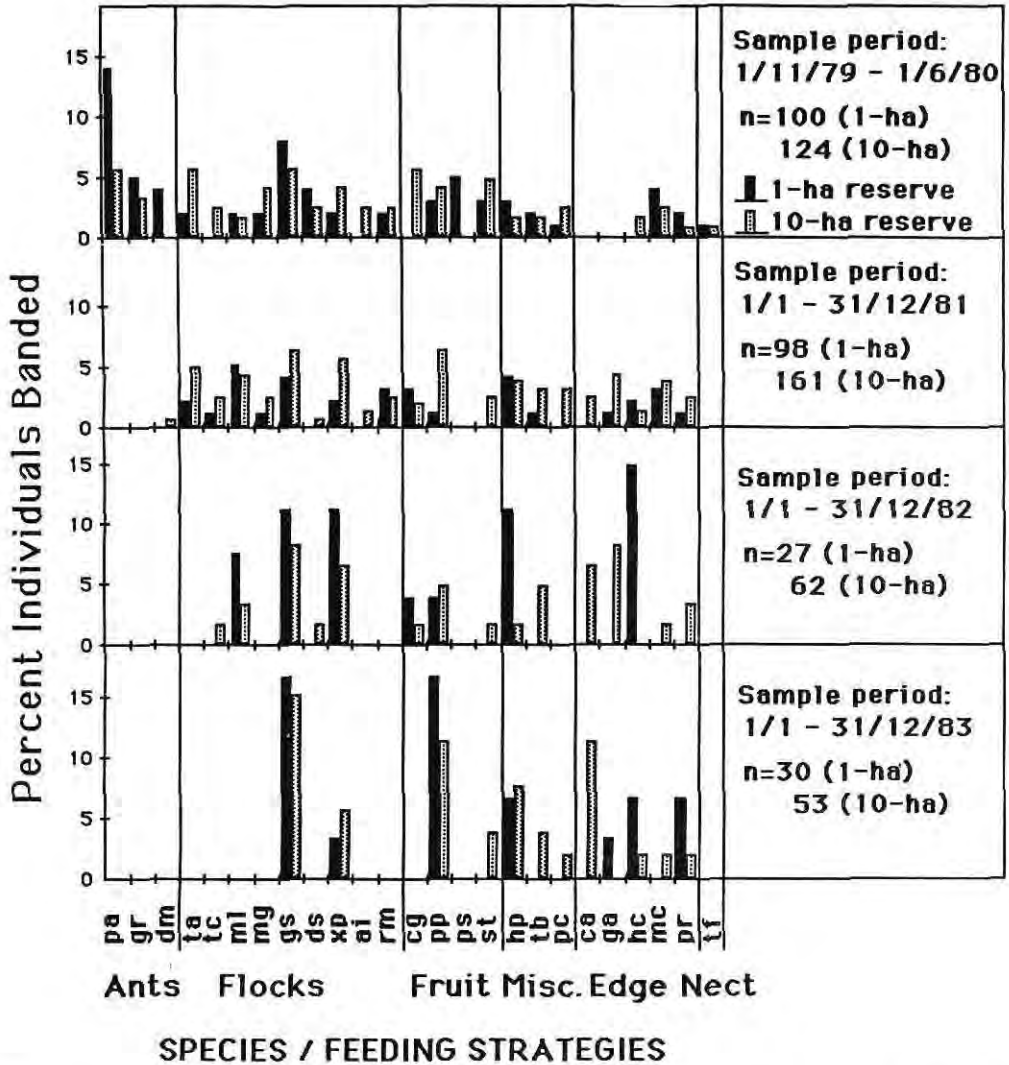


Fig. 5. Relative abundances of a representative group of 25 species before and the subsequent periods following isolation of the 1980 isolates. The ecological guilds represented are: Ants - Obligatory army ant followers; Flock - Mixed species, understory insectivorous flocks; Fruit - Understory frugivores; Misc - Common insectivores and one frugivore/insectivore; Edge - Tree-fall and forest edge specialists; Nect - Nectivores. Species abbreviations: pa - *Pithys albifrons*; gr - *Gymnopithys rufigula*; dm - *Dendrocincla merula*; ta - *Thamnomanes aredesiacus*; tc - *Thamnomanes caesius*; ml - *Myrmotherula longipennis*; mg - *Myrmotherula gutturalis*; gs - *Glyphorhynchus spirurus*; ds - *Deconychura stictolaema*; xp - *Xiphorhynchus pardalotus*; ai - *Automolus infuscatus*; mb - *Myiobius barbatus*; cg - *Corapipo gutturalis*; pp - *Pipra pipra*; ps - *Pipra serena*; st - *Schiffornis turdinus*; hp - *Hylophylax poecilinota*; ta - *Turdus albicollis*; pc - *Platyrinchus coronatus*; ca - *Cyphorhinus arada*; ga - *Galbula albigularis*; hc - *Hypocnemis cantator*; mc - *Microbates collaris*; pr - *Pernostola rufifrons*; tf - *Thalurania furcata*.

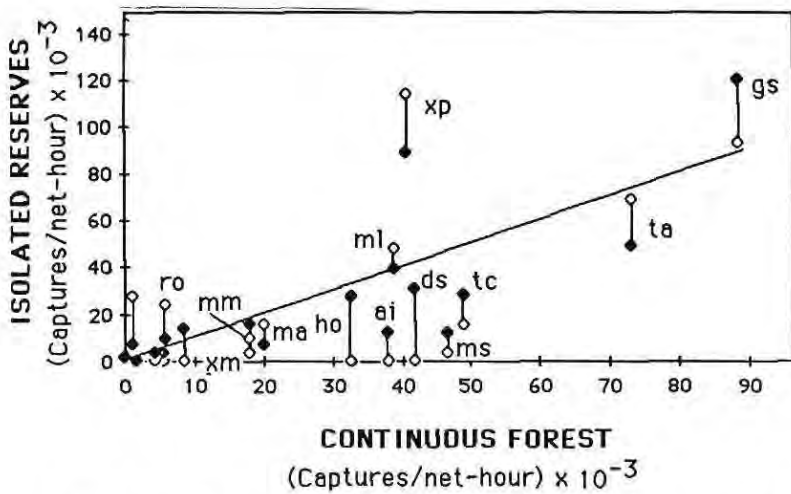


Fig. 6. Capture rates for Mixed species flock species comparing rates in isolated reserves to those in continuous forests. For each species, the average capture rates in both 1- and 10-ha isolates are plotted against the average capture rates in continuous forest. The open diamond represents the capture rate in 1-ha isolates and the dark diamond that from 10-ha reserves. Species abbreviations as in Fig. 6, with the inclusion of: ro - *Rhynchocyclus olivaceus*; xm - *Xenops minutus*; mm - *Myrmotherula menetriesii*; ma - *Myrmotherula axillaris*; ho - *Hylophilus ochraceiceps*; ms - *Myrmotherula gutturalis*. Species whose points lie on or near the diagonal line show equal capture rates in isolated and non-isolated reserves.

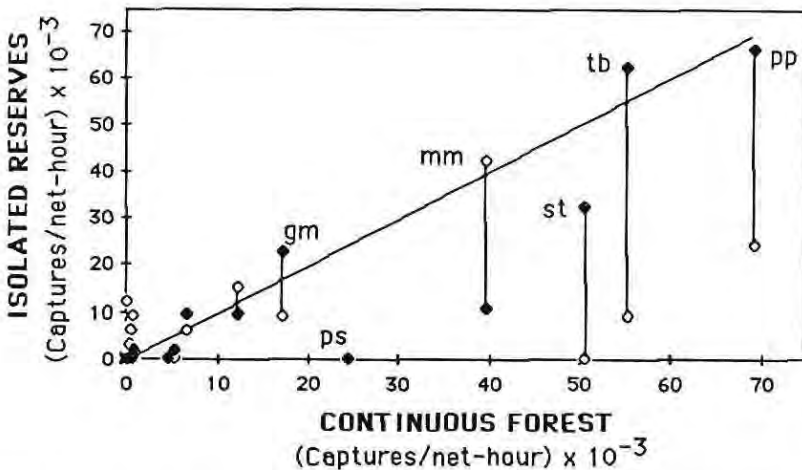


Fig. 7. Capture rates for frugivorous species comparing rates in isolated reserves to those in continuous forests. For each species, the average capture rates in both 1- and 10-ha isolates are plotted against the average capture rates in continuous forest. Symbols as in Fig. 7, abbreviations as in Fig. 6 with the inclusion of: gm - *Geotrygon montana*; mm - *Mionectes macconnelli*.

Five of the 6 most commonly captured edge and tree-fall specialists had higher capture rates in 1-ha isolates than in 10-ha isolates, and 2 of these, the Yellow-billed Jacamar, *Galbula albirostris*, and the Ferruginous-backed Antbird had greatly elevated capture rates in 1-ha reserves when compared to both 10-ha isolates and undisturbed forest (Fig. 8).

Hummingbirds, particularly the Long-tailed Hermit (*Phaethornis superciliosus*) increased in relative abundance in the 1980 isolated 1-ha reserve (Fig. 5). Capture rates from all 1- and 10-ha isolates for the Fork-tailed Woodnymph (*Thalurania furcata*) were indistinguishable from those in undisturbed forest (Fig. 9). The two other common, and congeneric understory hummingbirds reacted oppositely to forest fragmentation. The Long-tailed Hermit was captured more frequently in 1-ha isolates than in 10-ha fragments or in undisturbed forest, while the Straight-billed Hermit (*Phaethornis bourcierii*) showed a very slight decrease in capture rates when compared to 10-ha isolates or undisturbed forest. Capture rates for both species in 10-ha isolates were very similar to those in non-isolated forest samples (Fig. 9).

Comparing capture rates from undisturbed forest with those after 6 months of isolation of 1- and 10-ha reserves, we see that the trends witnessed in the 1980 isolates seem to be general (Figs. 6 - 9). These data show that species are not simply becoming more or less important in relative abundance, but also are showing dramatic changes in their levels of activity in the reserves, as measured by capture rates.

Soon after isolation of 1- and 10-ha reserves capture rates of several species of the middle story of the forest increased dramatically, suggesting an increase in abundance or activity levels. Sneathlague's Tody-tyrant (*Hemitriccus minor*), the Olivaceous Flatbill (*Rhynchocyclus olivaceus*), the Olivaceous Woodcreeper (*Sittasomus griseicapillus*), and the Black-throated Trogon (*Trogon rufus*), in particular, were relatively common in virgin forest, but were rarely captured in mist-nets because they normally foraged above the 2 m that the nets sample. Sneathlague's Tody-tyrant, for example, is heard calling on roughly 50% of all capture days, yet it is extremely rare in the nets in undisturbed forest (Table 3). The capture rate for isolated 10-ha reserves was more than 10 times that in undisturbed forest and nearly 30 times the undisturbed forest rate in 1-ha reserves (Table 3).

Capture rates for all these mid-story species were higher in isolated reserves than in the undisturbed forest and in general tended to be higher in the 1-ha isolates than in the 10-ha tracts, despite the higher capture rates for all species combined in the 10-ha isolates (356.87 vs. 233.41 captures/10000 net-hours) (see App. 1).

This pattern was not pervasive throughout the mid-story insectivores, however. At least two common flycatchers of the mid-stories of undisturbed forest, the Forest Elaenia (*Myiopagis gaimardi*) and the Yellow-margined Flycatcher (*Tolmomyias assimilis*) did not show similar changes in foraging height.

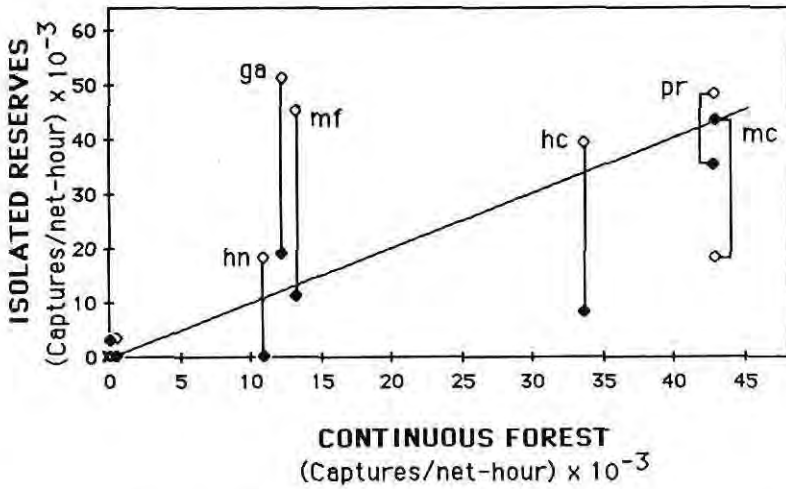


Fig. 8. Capture rates for tree-fall and forest edge specialists, comparing rates in isolated reserves to those in continuous forests. For each species, the average capture rates in both 1- and 10-ha isolates are plotted against the average capture rates in continuous forest. Symbols as in Fig. 7, with the inclusion of: hn - *Hylophylax naevia*; mf - *Myrmeciza ferruginea*.

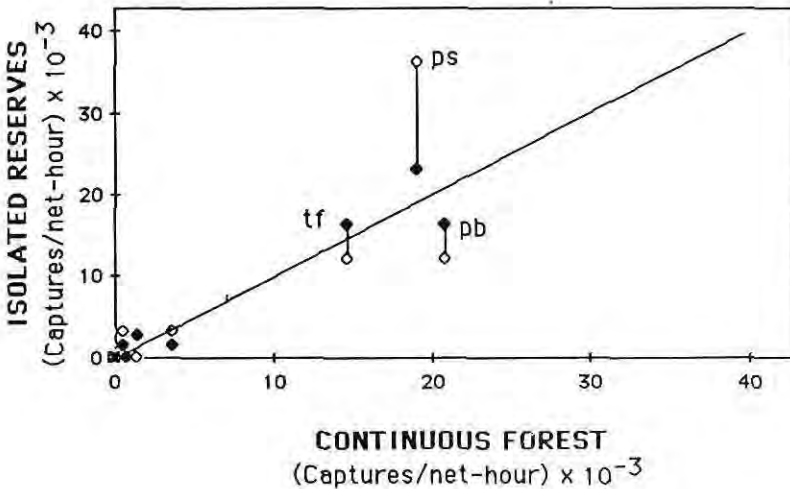


Fig. 9. Capture rates for hummingbirds, comparing rates in isolated reserves to those in continuous forests. For each species, the average capture rates in both 1- and 10-ha isolates are plotted against the average capture rates in continuous forest. Symbols as in Fig. 7, with the inclusion of: pb - *Phaethornis bourcierii*; ps - *Phaethornis superciliosus*.

DISCUSSION

The most immediate and dramatic effect of forest fragmentation was the near doubling of capture rates in 1- and 10-ha reserves (Fig. 3). The increased capture rates may in part reflect greater foraging activity of the birds in a reserve whose area is smaller than their normal home range. The drop in recapture percentages coincidental with the increase in capture rates (Fig. 4) showed that an influx of displaced individuals fleeing the felled forest is certainly an important factor. More detailed analyses of the trends in capture and recapture rates are presented by Bierregaard & Lovejoy (in press).

The influx of birds witnessed in the 1980 isolates after the surrounding capoeira (second growth) reached a height sufficient to have a shaded understory suggests the presence in undisturbed forest of a floating population of birds looking for suitable territory. The recolonization of the reserves by birds that had disappeared from the isolates emphasizes the importance suitable habitat connecting a potential colonizing source and the forest tract in question. Recolonization was first witnessed in the 1-ha reserve, as expected, given its greater proximity to undisturbed forest (the recolonization source) than the 10-ha reserve.

Clearly, the avian understory community undergoes drastic changes in its species composition following fragmentation into 1- and 10-ha reserves surrounded by pasture and low second growth. Other studies by Willis (1979) in the State of São Paulo, Brazil, Leck (1979) in Ecuador, and Terborgh (1974), Willis (1974), Willis & Eisenmann (1979) and Karr (1982) on Barro Colorado Island in Panama have also reported the disappearance of various species of birds following fragmentation or insularization of once continuous tropical forest into areas of up to 1,500 ha.

Willis (1979) has shown that avian communities in remnant woodlots of 21, 250, and 1,400 ha in the Atlantic forest regions of the State of São Paulo are depauperate when compared to a hypothetical list of the avifauna that should have been present at the moment of isolation of the woodlots. What cannot be determined from his data is exactly how many species have been lost from each size woodlot. It is certain, for instance, that the 10-ha remnant did not have the full complement of 230 species when it was isolated, but rather some sub-sample, whose composition would have depended on both a random sampling effect and on the micro-habitat the remnant prior to isolation. Willis' (1979) calculations of percentage species lost in each woodlot size are consequently difficult to interpret.

Analyses of species loss from the 1,500-ha Barro Colorado Island (Willis & Eisenmann, 1979; Karr, 1982), are based on species lists compiled from the hilltop that became Barro Colorado Island when the Chagres River was dammed in 1912. However, since systematic surveys were not conducted prior to insularization, Karr (1982) suggested the most appropriate method to analyze changes in the ecosystem was to compare the avifauna with that extant on the adjacent mainland. This approach is usually the only one available to biogeographers concerned with questions of species loss from islands (Brown, 1977; Soule et al., 1979; Terborgh & Winter, 1980) and suffers the same lack of quantitative pre-iso

lation data as Willis' (1979) analyses mentioned above.

The most drastic result of forest fragmentation studied here was the reduction of continuous forest to patches smaller than the home range of a given individual. The disappearance of the obligate army ant following species from our isolated study plots was predictable on the basis of knowledge of their home range requirements. Willis & Oniki (1979) states that individual White-plumed Antbirds use an area 3-5 km across at Reserva Ducke, while Harper (1988) and Bierregaard (unpubl. data) have shown that individual birds of this species use an area of between 1 to 2 km in diameter, with little evidence of movements more than 2 kms through the forest. Regardless of this small difference, it is not surprising that individuals of the obligate army ant following species did not persist in a 10-ha forest fragment (ca. 350 m across). Army ant swarms themselves use an area larger than 10 ha (Harper, unpubl. data; Franks, 1982).

The disappearance of the mixed species flock from the 10-ha 1980 isolate was not predictable purely on the basis of known home range information. These flocks typically use an area of about 5 ha in western Amazonia (Munn & Terborgh, 1979) and about 12 ha in the Manaus area (Powell, unpubl. data) and use the same area over a period of years (Munn & Terborgh, 1979; Powell, unpubl. data).

It is tempting to suggest a relation between the disappearance of the flock and the greatly increased levels of avian activity immediately following isolation. Were individuals of flock species so busy defending their home range from invaders that they suffered higher mortality? There was an obvious increase in vocalizations of flock species in the reserves after isolation. Were resources depleted to such low levels that even the residents could not find enough food? Our data are currently insufficient to answer these questions. However, observations in a 10-ha reserve (1207) isolated without any noticeable post-isolation crowding (see Fig. 3) show that the mixed species flock there "shed" species in roughly the same order as from the 1980 isolate where crowding was pronounced (D. Stotz, pers. comm.).

Capture rate data from all isolates show that only certain flock species disappeared from the reserves. However, one of the species that disappears from the reserves, the Cinereous Antshrike (*Thamnomanes caesius*) is one of the more important nuclear species (sensu Winterbottom, 1949) of the flocks (Powell, pers. comm.). After the loss of the Cinereous Antshrike, the species that do persist in the isolates no longer traveled as coherent flocks. It is particularly interesting that the Dusky-throated Antshrike (*Thamnomanes ardesiacus*) shows higher capture rates in both 1- and 10-ha isolates than its extremely similar congener, the Cinereous Antshrike. This may reflect the extent to which the Cinereous Antshrike depends on traveling within a cohesive flock. As much as 50% of its prey may be insects that have been flushed by other species traveling with the flock (Powell, 1985). As certain species are lost from the flock due to some modification in the habitat occasioned by isolation, the flock may become too small to sustain the Cinereous Antshrike.

Several flocking species seem little affected by isolation. The Long-winged and the White-flanked Antwrens (*Myrmotherula longipennis* and *M. axillaris*) are captured more

frequently in 1-ha than in 10-ha isolates, although the differences are very slight, and at approximately the same rates in isolates as in undisturbed forest (Fig. 6). Powell (1985) has suggested that the co-occurrence of up to 7 species of antwrens in the genus *Myrmotherula* may be due to the flocking species foraging along with birds 2 to 3 times heavier than they are, through an area much larger than would be necessary to support a pair of antwrens. This, Powell argues, may result in a density of antwrens below the carrying capacity of the ecosystem, which in turn would ameliorate the effect of inter-specific competition. Were this the case, it would not be surprising to find pairs persisting in 1-ha isolates. Gradwohl & Greenberg (1980) report territory sizes of slightly over 2 ha for mixed species flocks in Panama whose nuclear species are the Checkered-throated Anteren (*Myrmotherula fulviventris*) and the Dot-winged Antwren (*Microrhopias quixensis*), birds of similar weight to the antwrens in the Manaus flocks. It would be interesting to study the foraging behavior and success rates of antwren pairs feeding independently from flocks to assess the value of flock membership to these species. This in turn might permit us to predict whether or not antwrens in small isolates will persist.

The Chestnut-rumped Woodcreeper (*Xiphorhynchus pardalotus*) is the largest (ca. 36 g.) of the common understory species to persist in 1-ha isolates and seems to do so by way of a very diverse array of foraging strategies, including foraging with canopy flocks. The elevated capture rates recorded for the species in isolates (Fig. 6) may reflect a high level of activity necessary to procure sufficient food in a small forest fragment.

Mist-netting captures of the Wedge-billed Woodcreeper with no other mixed-species flock members near-by suggests that the species is not a permanent member of the flocks. Powell's (pers. comm.) observations of the species in the project reserves suggested that it used a home range roughly one-half the size of that used by the mixed-species flocks, and that each pair will join a flock when there is one foraging in its territory. Thus there is almost always a pair of Wedge-billed Woodcreepers with every flock, but each pair of Wedge-billed Woodcreepers spends a substantial amount of time foraging away from flocks. Given this independence from the flocks, it is not surprising that the Wedge-bills persist in 10-ha isolates.

The persistence of hummingbirds in the isolated reserves is interesting in light of Willis' (1979) observations that this group was under-represented in the smallest (20 ha) woodlot he studied in Sao Paulo. Perhaps because the reserves are separated from continuous forest by 100 to several hundred meters, individuals can move to the adjacent forest on a daily or seasonal basis when resources are lacking. As well, there may be plants in the connecting second growth that serve as food sources. This will be tested in the future, as further felling will increase the isolation of these and other reserves from continuous forest to at least 1 km, and maintenance by fazenda personnel will replace the second growth with pasture. We can offer no explanation for the intriguing difference in response to isolation shown by the Long-tailed and Straight-billed Hermits. Detailed field observations of the species will be necessary to understand this difference.

If all bird species were equally likely to be captured by mist nets, capture data from mist nets would reflect actual relative abundances of the species under study. However, species are disproportionately represented in mist net data because of morphological or behavioral factors (Bierregaard, unpubl. data). Birds that are either too small (hummingbirds) or too large (tinamous) for the mesh of the net size used will be less likely to be caught than other species. Birds that move through the forest primarily by walking also have a reduced probability of becoming entangled in the nets. It is assumed in this study that these biases will be the same in virgin forest and isolated reserves, such that differences in the mist net data reflect some real difference in the two habitats (virgin forest vs. isolated forest remnants), either in behavior or in real population densities. However, the significance of such differences can only be interpreted based on an understanding of the biology of the birds under study, an understanding that can only be gained by direct field observations.

The appearance of common mid-story birds (see Table 3) in understory nets in isolated reserves could easily have been misinterpreted as the result of an increase in the population sizes of these species were it not for our observational data on their abundance and foraging behavior in the undisturbed forest. Based on these data, we know that the increases in post-isolation relative abundance for these is due principally to behavioral, rather than populational (immigration) changes.

The behavioral shifts in foraging height that bring these species into the nets in isolated reserves suggest that birds need a given volume of forest through which to forage, rather than just an given area, per se. They seem to be increasing their vertical foraging range to compensate for the reduction in horizontal space. Such species may be more persistent than species of the lowest stratum in smaller reserves because they can adjust their foraging volume vertically and horizontally, while ground foraging species can only increase the three dimensional space, or home range volume, horizontally. If this is insufficient to compensate for lost foraging territory, they may be forced to increase the rate of foraging in the available volume, perhaps preventing adequate replenishment of food resources.

Three alternative explanations could account for the observed shifts in foraging heights; competitive release, physiological restraints attendant on the changes in microclimate in newly isolated reserves (Karr, pers. comm.), and changes in the distribution of food resources (Malcolm, pers. comm.). The latter 2 explanations might be linked, as micro-climatological changes could cause changes in insect activity attracting birds to lower levels of the forest.

The competitive release explanation would suggest that rather than being forced to expand vertical foraging behavior, mid-story species may be changing their foraging downwards to use a volume of forest vacated by understory species which did not persist in the reserve for some other reason. Although it is not always clear what species might be competitively excluding the mid-story species which moved down to net levels after isolation (particularly the Black-throated Trogon), the speed with which they do suggests that such an interspecific interaction is not the causative factor. The mid-story birds

are appearing in the nets long before all but the obligate army ant followers have begun to disappear from the reserves. For the Olivaceous Woodcreeper, which shows the most pronounced increase in activity at net level, several other similar sized Dendrocolaptids, such as the Wedge-billed and Spot-throated (*Deconychura stictolaema*) Woodcreepers, continue to be caught in the nets well after the Olivaceous appears in the samples. In fact, the competitive effect may be just the reverse, with increased resource use by invading (descending) mid-story species mitigating against the persistence of the understory species. The Spot-throated Woodcreeper does, indeed, disappear completely from 1-ha isg lates.

The extent to which mid-story species are fleeing unfavorable microclimatic conditions in the isolated reserves will be difficult if not impossible to determine and must be considered a viable alternative explanation to the observed phenomenon. However, in this regard, the lack of such vertical displacement in the Forest Elaenia and the Yellow margined Flycatcher (Stotz, pers. comm.), two of the most common mid-story insectivores in the undisturbed forest is particularly intriguing. The elucidation of the ecological or physiological differences leading to this asymmetry will require more detailed aut-ecological studies of the species involved. Perhaps these species tend to compensate for restricted home ranges by shifting their foraging up into the canopy rather than down into the understory, or perhaps their home ranges are so small that they need not expand their foraging volume at all.

ACKNOWLEDGMENTS

A. McGrath, L. van der Tok, D. Graham, F. Joyce, P. Oyens, D. Walczak, B. Winn, E. Perkins, C. Strang, T. Tesche, G. Brandão, M. Magalhães, M. Berte, P. Polshek, D. Stotz, C. Quintela, R. Downer, J. Bates, and N. Belfiore most energetically and capably ran the net lines and assisted in data management since the beginning of the project. The current manuscript has benefitted greatly from discussions with and suggestions made by B. Zimmerman, L. Harper, J. Bates, B. Klein, J. Karr, and especially D. Stotz, J. Malcolm, M. Wong, and an anonymous reviewer.

This study was supported by the World Wildlife Fund-US, the Instituto Nacional de Pesquisas da Amazônia (INPA), the Instituto Brasileiro de Desenvolvimento Floresta' (IBDF), a grant from the National Park Service, Cooperative Agreement CX-0001-9-0041, the Man and the Biosphere program of US-AID, and represents publication number 31 in the Minimum Critical Size of Ecosystems Project (Dinâmica Biológica de Fragmentos Florestais) Technical Series.

RESUMO

Análises de mais de 19.000 capturas em cinco anos de um programa de marcação e recaptura (captura em rede e anilhamento) foram feitas para comparar a estrutura da comunidade de aves entre uma floresta virgem de terra firme e as reservas florestais isoladas de 1 a 10 ha localizadas em 3 fazendas do Distrito Agropecuário da SUFRAMA. Pela primeira vez, dados sobre a perda de espécies em fragmentos florestais, ou "ilhas de habitat", podem ser comparados com recenseamentos quantitativos feitos nos próprios locais em estudo, antes da insularização. A comunidade de aves em sua condição original é muito diversificada; 141 espécies de aves foram anilhadas em redes de nylon do sub-bosque. Nenhuma espécie representou mais de 8% de todos os indivíduos anilhados ou 10% de todas as capturas. A comunidade é principalmente insetívora; mais de que 80% dos indivíduos anilhados são principalmente insetívoros, dos quais, 37% são seguidores obrigatórios de formigas de correição ou membros de bandos muito evoluídos de espécies mistas. Um pequeno Píprideo está entre as 4 espécies mais anilhadas, mas a maior parte das atividades dos frugívoros e beija-flores ocorre no dossel. Análises destas comunidades em reservas isoladas de 1 a 10 ha mostram que os seguidores obrigatórios de formigas são os mais sensíveis a fragmentação da floresta. Bandos de espécies mistas deterioram-se também, perdendo espécies antes de dois anos de isolamento. Espécies cujo habitat preferencial são clareiras formadas por queda de árvores aumentam em importância relativa e em nível de atividade nas amostras pós-isolamento. Com o isolamento, os passáros residentes enfrentam um influxo de passáros oriundos da floresta derrubada. Esta tendência é refletida no aumento do número de capturas e o decréscimo da proporção de passáros já anilhados nas amostras de cada dia. Diversas espécies de insetívoros dos estratos intermediários aumentam o alcance vertical de seus hábitos alimentares diante da restrição horizontal de seus territórios nas reservas isoladas de 1 e 10 ha. Isto sugere que territórios devem ser considerados em termos de volume do habitat em vez de área.

Table 1. Percent of 10,918 individuals employing various feeding strategies, number of species, percent of individuals corrected by biomass, and number of captures.

Diet	No. of species	% Individuals	% Biomass	% Captures
Nectar feeders	8	4.85	0.95	3.05
Fruits, seeds	36	14.6	22.96	12.7
Fruits, vertebrates	3	0.05	0.43	0.03
Insects (over army ants)	3	14.43	15.93	18.86
Insects	64	41.34	34.07	41.98
Insects, fruits	4	0.04	0.03	0.02
Insects, vertebrates	1	0.38	1.74	0.27
Mixed-species flocks	21	23.0	16.19	22.2
Fish, insects	2	0.14	0.22	0.09
Vertebrates	6	1.16	7.48	0.8
Total	143	100.0	100.0	100.0

Table 2. Comparisons of mean capture rates (number of birds/net-hour) in a 1-ha and a 10-ha forest reserve before and after isolation. Means are shown for each case from 7 capture days. The results of Student-T statistic for paired means are indicated. NS = no difference between the means was detected. * = null hypothesis of equal means rejected at $P \leq 0.05$. *** = null hypothesis rejected at $P = .001$.

	Pre-isolation		Post-isolation
1-ha	0.26	*	0.45
	NS		*
10-ha	0.19	***	0.31

APPENDIX

Species of birds captured in continuous forest and isolated reserves of 1 and 10ha. Diet categories are: f - fruit, i - insects, n - nectar, p - fish, msf - forage for insects in mixed-species flocks, v - vertebrates. In the "band" column is listed the number of individuals of each species banded in continuous forest. One individual flycatcher and Emberizid were not identified to species and have been excluded from this appendix, bringing the actual total of birds banded in continuous forest to 10,918 of 143 species. Columns labelled "prnh", "prnh 1" and "prnh 10" indicate capture rates (captures per 1000 net-hours) in continuous forest, 1-ha isolates and 10-ha isolates, respectively. The column labelled "biom" indicates for each species the total biomass represented by the individuals banded for that species. Weights were estimated for species indicated with an *. For all other species, weights are based on our own capture data.

Species	Diet	Band	Prnh	Prnh 1	Prnh 10	Biom
TINAMIDAE						
<i>Tinamus major</i> *	f	1	0.10	0.00	0.00	500.0
<i>Tinamus guttatus</i> *	f	2	0.21	0.00	0.00	1000.0
<i>Crypturellus variegatus</i>	f	8	0.93	0.00	1.35	3072.0
ACCIPITRIDAE						
<i>Accipiter superciliosus</i>	v	2	0.21	0.00	0.00	160.0
FALCONIDAE						
<i>Micrastur ruficollis</i>	v	6	0.82	0.00	1.35	1202.6
<i>Micrastur gilvicolis</i>	v	44	5.55	0.00	4.06	9284.0
CRACIDAE						
<i>Penelope jacuacu</i> *	f	1	0.10	0.00	0.00	1000.0
PHASIANIDAE						
<i>Odontophorus gujanensis</i>	f	1	0.10	0.00	0.00	255.0
PSOPHIIDAE						
<i>Psophia crepitans</i> *	f	5	0.51	0.00	0.00	5000.0
COLUMBIDAE						
<i>Columba subvinacea</i>	f	2	0.21	0.00	0.00	256.0
<i>Geotrygon montana</i>	f	160	17.37	9.05	23.00	18000.0
STRIGIDAE						
<i>Otus watsoni</i>	v	2	0.21	0.00	5.41	295.2
<i>Glaucidium minutissimum</i>	v	2	0.21	6.03	2.71	110.5
TROCHILIDAE						
<i>Phaethornis superciliosus</i>	n	163	19.02	36.19	23.00	896.5
<i>Phaethornis bourcierii</i>	n	171	20.87	12.06	16.23	721.6
<i>Campylopterus largipennis</i>	n	30	3.60	3.02	1.35	256.2
<i>Florisuga mellivora</i>	n	13	1.44	0.00	2.71	79.7
<i>Thalurania furcata</i>	n	141	14.70	12.06	16.23	566.8
<i>Hylocharis sapphirina</i> *	n	2	0.21	0.00	0.00	10.0
<i>Topaza pela</i>	n	5	0.72	0.00	0.00	50.5
<i>Heliothryx aurita</i>	n	5	0.51	3.02	1.35	25.0
TROGONIDAE						
<i>Trogon viridis</i>	f	0	0.00	0.00	0.00	0.0
<i>Trogon rufus</i>	f	8	0.82	9.05	1.35	399.0
ALCEDINIDAE						
<i>Chloroceryle inda</i>	p	10	1.23	0.00	0.00	511.7
<i>Chloroceryle aena</i>	p/i	5	0.62	0.00	0.00	69.5

Species	Diet	Band	Prnh	Prnh 1	Prnh 10	Biom
TINAMIDAE						
<i>Tinamus major</i> *	f	1	0.10	0.00	0.00	500.0
<i>Tinamus guttatus</i> *	f	2	0.21	0.00	0.00	1000.0
<i>Crypturellus variegatus</i>	f	8	0.93	0.00	1.35	3072.0
ACCIPITRIDAE						
<i>Accipiter superciliosus</i>	v	2	0.21	0.00	0.00	160.0
FALCONIDAE						
<i>Micrastur ruficollis</i>	v	6	0.82	0.00	1.35	1202.6
<i>Micrastur gilvicollis</i>	v	44	5.55	0.00	4.06	9284.0
CRACIDAE						
<i>Penelope jacuacu</i> *	f	1	0.10	0.00	0.00	1000.0
PHASIANIDAE						
<i>Odontophorus gujanensis</i>	f	1	0.10	0.00	0.00	255.0
PSOPHIIDAE						
<i>Psophia crepitans</i> *	f	5	0.51	0.00	0.00	5000.0
COLUMBIDAE						
<i>Columba subvinacea</i>	f	2	0.21	0.00	0.00	256.0
<i>Geotrygon montana</i>	f	160	17.37	9.05	23.00	18000.0
STRIGIDAE						
<i>Otus watsoni</i>	v	2	0.21	0.00	5.41	295.2
<i>Glaucidium minutissimum</i>	v	2	0.21	6.03	2.71	110.5
TROCHILIDAE						
<i>Phaethornis superciliosus</i>	n	163	19.02	36.19	23.00	896.5
<i>Phaethornis bourcierii</i>	n	171	20.87	12.06	16.23	721.6
<i>Campylopterus largipennis</i>	n	30	3.60	3.02	1.35	256.2
<i>Florisuga mellivora</i>	n	13	1.44	0.00	2.71	79.7
<i>Thalurania furcata</i>	n	141	14.70	12.06	16.23	566.8
<i>Hylocharis sapphirina</i> *	n	2	0.21	0.00	0.00	10.0
<i>Topaza pela</i>	n	5	0.72	0.00	0.00	50.5
<i>Heliothryx aurita</i>	n	5	0.51	3.02	1.35	25.0
TROGONIDAE						
<i>Trogon viridis</i>	f	0	0.00	0.00	0.00	0.0
<i>Trogon rufus</i>	f	8	0.82	9.05	1.35	399.0
ALCEDINIDAE						
<i>Chloroceryle inda</i>	p	10	1.23	0.00	0.00	511.7
<i>Chloroceryle aena</i>	p/i	5	0.62	0.00	0.00	69.5

continuation (Appendix).

Species	Diet	Band	Prnh	Prnh 1	Prnh 10	Biom
MOMOTIDAE						
<i>Momotus momota</i>	v	71	8.94	0.00	16.23	9573.6
GALBULIDAE						
<i>Galbula albirostris</i>	i	95	12.33	51.27	18.94	1735.7
<i>Jacamerops aurea</i>	i	3	0.31	0.00	0.00	183.8
BUCCONIDAE						
<i>Bucco tamatia</i>	i	3	0.31	15.08	0.00	108.0
<i>Bucco capensis</i>	i	7	0.72	15.08	4.06	378.0
<i>Malacoptila fusca</i>	i	51	7.81	27.14	27.06	2254.7
<i>Nonnula rubecola</i>	i	1	0.10	0.00	0.00	20.3
<i>Monasa atra</i>	i	3	0.31	0.00	1.35	266.0
RAMPHASTIDAE						
<i>Pteroglossus viridis</i>	f/v	1	0.10	0.00	0.00	140.0
<i>Selinedera culik</i>	f/v	3	0.31	0.00	0.00	447.0
<i>Ramphastos vitellinus*</i>	f/v	2	0.21	0.00	0.00	600.0
PICIDAE						
<i>Venilliornis cassini</i>	i	5	0.51	0.00	0.00	167.5
<i>Piculus flavigula</i>	msf	0	0.00	3.02	0.00	0.0
<i>Celeus elegans</i>	i	5	0.51	0.00	1.35	690.5
<i>Campephilus rubricollis</i>	i	2	0.21	0.00	0.00	432.0
DENDROCOLAPTIDAE						
<i>Dendrocinclia fuliginosa</i>	i	73	10.69	18.09	23.00	2936.8
<i>Dendrocinclia merula</i>	i	230	47.08	0.00	4.06	12088.8
<i>Deconychura longicauda</i>	msf	44	5.45	0.00	2.71	1283.9
<i>Deconychura stictolaema</i>	msf	180	42.04	0.00	31.11	3042.0
<i>Sittasomus griseicapillus</i>	msf	9	1.03	27.14	6.76	123.7
<i>Glyphorhynchus spirurus</i>	i	458	88.50	93.49	120.40	6274.6
<i>Hylexetastes perrotii</i>	i/v	42	5.35	0.00	9.47	4809.0
<i>Dendrocolaptes certhia</i>	i	27	2.88	9.05	2.71	1792.8
<i>Dendrocolaptes picumnus</i>	i	7	0.93	0.00	2.71	550.0
<i>Xiphorhynchus pardalotus</i>	msf	244	40.81	114.60	89.29	9211.0
<i>Campylorhamphus trochilirostris</i>	msf	33	4.42	0.00	2.71	1135.2
FURNARIIDAE						
<i>Synallaxis rutilans</i>	i	31	6.58	0.00	0.00	527.0
<i>Philydor erythrocercus</i>	msf	68	8.63	0.00	13.53	1571.5
<i>Philydor pyrrhodes</i>	i	27	3.29	0.00	1.35	831.6

continuation (Appendix).

Species	Diet	Band	Prnh	Prnh 1	Prnh 10	Biom
<i>Automolus ochrolaemus</i>	i	28	5.35	0.00	2.71	980.3
<i>Automolus infuscatus</i>	msf	195	38.03	0.00	12.18	6107.4
<i>Automolus rubiginosus</i>	i	71	13.88	0.00	6.76	2592.9
<i>Sclerurus mexicanus</i>	i	30	7.20	0.00	0.00	751.2
<i>Sclerurus rufigularis</i>	i	122	28.68	0.00	0.00	2581.5
<i>Sclerurus caudacutus</i>	i	71	12.03	0.00	4.06	2762.6
<i>Xenops milleri</i>	msf	1	0.10	0.00	0.00	11.3
<i>Xenops minutus</i>	msf	116	17.99	3.02	14.88	1415.2
FORMICARIIDAE						
<i>Cymbilaimus lineatus</i>	i	2	0.21	0.00	0.00	70.7
<i>Frederickena viridis</i>	i	34	4.73	3.02	1.35	2315.7
<i>Thamnophilus murinus</i>	i	50	5.96	9.05	0.00	888.0
<i>Thamnomanes ardesiacus</i>	msf	333	73.29	69.36	48.70	6097.2
<i>Thamnomanes caesius</i>	msf	330	49.03	15.08	28.41	5765.1
<i>Myrmotherula guttata</i>	i	123	22.72	3.02	20.29	1264.4
<i>Myrmotherula gutturalis</i>	msf	250	46.56	3.02	12.18	2175.0
<i>Myrmotherula axillaris</i>	msf	140	20.04	15.08	6.76	1082.2
<i>Myrmotherula longipennis</i>	msf	230	39.06	48.25	39.23	1920.5
<i>Myrmotherula menetriesii</i>	msf	135	17.99	9.05	14.88	1081.4
<i>Cercomacra tyrannina</i>	i	1	0.10	0.00	0.00	18.3
<i>Hypocnemis cantator</i>	i	209	33.72	39.20	8.12	2464.1
<i>Sclateria naevia</i>	i	1	0.10	0.00	0.00	21.5
<i>Percnostola rufifrons</i>	i	239	42.86	48.25	35.17	6883.2
<i>Percnostola leucostigma</i>	i	57	9.05	0.00	0.00	1384.0
<i>Myrmeciza ferruginea</i>	i	86	13.26	45.24	10.82	2125.1
<i>Myrmeciza atrothorax</i>	i	1	0.10	0.00	0.00	18.5
<i>Pithys albifrons</i>	i	836	210.82	0.00	6.76	17021.0
<i>Gymnopithus rufigula</i>	i	509	120.06	0.00	25.70	14832.3
<i>Hylophylax naevia</i>	i	53	11.00	18.09	0.00	672.6
<i>Hylophylax poecilinota</i>	i	577	159.63	144.75	91.99	9687.8
<i>Formicarius colma</i>	i	163	24.77	15.08	31.11	7504.5
<i>Formicarius analis</i>	i	28	3.60	0.00	5.41	1742.7
<i>Myrmornis torquata</i>	i	91	18.91	15.08	20.29	4062.2
<i>Grallaria varia</i>	i	8	1.03	0.00	0.00	975.0
<i>Hylopezus macularius</i>	i	26	3.49	0.00	1.35	1099.8
<i>Myrmothera campanisona</i>	i	2	0.21	0.00	0.00	95.3

continuation (Appendix)

Species	Diet	Band	Prnh	Prnh 1	Prnh 10	Biom
CONOPOPHAGIDAE						
<i>Conopophaga aurita</i>	i	60	10.07	9.05	16.23	1422.6
COTINGIDAE						
<i>Phoenicercus carnifex</i>	f	5	0.51	0.00	0.00	472.5
<i>Lipaugus vociferans</i>	f	7	0.72	0.00	0.00	511.4
PIPRIDAE						
<i>Pipra erythrocephala</i>	f	43	4.63	0.00	0.00	529.8
<i>Pipra pipra</i>	f	490	69.49	24.13	66.29	5786.9
<i>Pipra serena</i>	f	150	24.57	0.00	0.00	1597.5
<i>Corapipo gutturalis</i>	f	55	6.68	6.03	9.47	451.0
<i>Neopipo cinnamomea</i>	f, i?	1	0.10	0.00	0.00	7.0
<i>Tyrannetes virescens</i>	f, i?	2	0.21	0.00	1.35	17.3
<i>Piprites chloris</i>	f, i	1	0.10	0.00	0.00	17.0
<i>Schiffornis turdinus</i>	f, i	196	50.57	0.00	32.47	6573.8
TYRANNIDAE						
<i>Terenotriccus erythrurus</i>	i	43	5.04	30.16	6.76	289.0
<i>Attila spadiceus</i>	i	2	0.21	0.00	0.00	63.8
<i>Rhytipterna simplex</i>	i	8	0.93	0.00	0.00	275.7
<i>Laniocera hypopyrrha</i>	i?	4	0.41	0.00	0.00	196.0
<i>Myiobius barbatus</i>	i	209	33.61	18.09	16.23	2205.0
<i>Onychorhynchus coronatus</i>	i	44	8.74	0.00	0.00	647.2
<i>Platyrinchus platyrhynchos</i>	i	9	0.93	0.00	4.06	110.2
<i>Platyrinchus coronatus</i>	i	138	21.38	0.00	28.41	1184.0
<i>Platyrinchus saturatus</i>	i	146	31.86	6.03	1.35	1522.8
<i>Tolmomyias assimilis</i>	msf	1	0.10	3.02	0.00	13.5
<i>Rhynchocyclus olivaceus</i>	msf	40	5.86	24.13	9.47	780.0
<i>Ramphotrigon ruficauda</i>	i	12	1.54	0.00	0.00	224.6
<i>Hemitriccus minor</i>	i	9	0.93	6.03	1.35	76.8
<i>Lophotriccus galeatus</i>	i	2	0.21	0.00	1.35	16.0
<i>Mionectes macconnelli</i>	i	310	39.78	42.22	10.82	3822.3
<i>Corythopsis torquata</i>	i	161	34.43	3.02	9.47	2403.7
TROGLODYTIDAE						
<i>Thryothorus coraya</i>	i	3	0.51	3.02	0.00	49.5
<i>Thryothorus leucotis</i>	i	1	0.10	0.00	0.00	15.0
<i>Troglodytes aedon</i>	i	1	0.10	0.00	2.71	11.5
<i>Microcerculus bambla</i>	i	85	16.45	0.00	1.35	1428.9
<i>Cyphorhinus arada</i>	i	171	30.12	3.02	58.17	3452.5

continuation (Appendix).

Species	Diet	Band	Prnh	Prnh I	Prnh 10	Biom
TURDIDAE						
<i>Catharus fuscescens</i>	f, i	7	0.72	0.00	0.00	193.1
<i>Catharus minimus</i>	f, i	7	0.72	0.00	0.00	208.3
<i>Turdus albicollis</i>	f, i	285	55.40	9.05	62.23	14096.1
SYLVIIDAE						
<i>Microbates collaris</i>	i	210	43.07	18.09	43.29	2244.9
<i>Ramphocaenus melanurus</i>	i	1	0.10	9.05	0.00	9.0
EMBERIZIDAE						
<i>Oryzoborus angolensis</i>	f	2	0.21	0.00	0.00	25.6
<i>Arremon taciturnus</i>	i, f	4	0.41	0.00	0.00	89.5
<i>Pitylus grossus</i>	f	4	0.41	6.03	0.00	174.0
<i>Cyanopcompsa cyanoides</i>	f	33	5.24	0.00	1.35	847.8
THRAUPIDAE						
<i>Hemithraupis flavicollis</i>	f	0	0.00	0.00	0.00	0.0
<i>Lanio fulvus</i>	msf	12	1.54	0.00	0.00	300.0
<i>Tachyphonus cristatus</i>	f, i	5	0.51	6.03	0.00	91.8
<i>Tachyphonus surinamus</i>	f, i	102	12.33	15.08	9.47	2094.1
<i>Ramphocelus carbo</i>	f	1	0.10	12.06	0.00	24.2
<i>Tangara chilensis</i>	f	2	0.21	0.00	0.00	29.5
<i>Tangara punctata</i>	f	1	0.10	0.00	0.00	14.3
COEREBIDAE						
<i>Dacnis cayana</i>	f	1	0.10	0.00	0.00	13.0
<i>Chlorophanes spiza</i>	f	2	0.21	6.03	0.00	31.8
<i>Coerba flaveola</i>	f	3	0.31	3.02	0.00	26.6
PARULIDAE						
<i>Phaeothlypis rivularis</i>	i	13	2.06	0.00	0.00	169.0
VIREONIDAE						
<i>Hylophilus muscicapinus</i>	msf	0	0.00	0.00	1.35	0.0
<i>Hylophilus ochraceiceps</i>	msf	150	32.79	0.00	27.06	1518.0
Total:			10916			

Referências bibliográficas

- Projeto RadamBrasil - 1978. Folha SA 20 Manaus. Rio de Janeiro. Ministério de Minas e Energia: Departamento Nacional de Produção Mineral. p. 261.
- Bierregaard Jr., R. O. & Lovejoy, T. E. - In press. Birds in Amazonian Forest fragments: Effects of insularization. *Proc. XIX Int. Ornith. Cong.*
- Brown, J. H. - 1971. Mammals on mountaintops: non equilibrium insular biogeography. *Am. Nat.*, 105:467-478.
- Chauvel, A. - 1983. Os latossolos amarelos, álicos, argilosos dentro dos ecossistemas das bacias experimentais do INPA e da região vizinha. *Acta Amazonica*, Supl., 12(4): 47-60.
- Franklin, I. R. - 1980. Evolutionary change in small populations. In: Soule, M. E. & Wilcox, B. A. eds. *Conservation Biology: An Evolutionary-ecological Perspective*. Sinauer Assoc. Inc. Sunderland, MA. p. 135-149.
- Franks, N. - 1982. Ecology and population regulation in the army ant *Eciton burchelli*. In: Leigh, E. G. Jr.; Rand, A. S.; Windsor, D. M. eds. *The ecology of a tropical forest: Seasonal rhythms and long-term changes*. Smithsonian Institution. Washington, DC. p. 389-395.
- Gradwohl, J. & Greenber, R. - 1980. The formation of antwren flocks on Barro Colorado Island, Panama. *Auk*, 97:385-395.
- Guillaumet, J. & Kahn, F. - 1982. Estrutura e dinamismo da floresta. *Acta Amazonica*, Supl., 12(4):61-77.
- Harper, L. H. - 1988. The persistence of ant-following birds in small Amazonian forest fragments. *Acta Amazonica*, 18(3-4):
- Karr, J. - 1971. Structure of avian communities in selected Panama and Illinois habitats. *Ecol. Monogr.*, 41:207-231.
- - 1982. Avian extinction on Barro Colorado Island. Panama: a reassessment. *Am. Nat.*, 119:220-239.
- Leck, C. F. - 1979. Avian extinctions in an isolated tropical wet-forest preserve. Ecuador. *Auk*, 96:343-352.
- Lovejoy, T. E. - 1975. Bird diversity and abundance in Amazon forest communities. *Living Bird*, 13:127-191.
- Lovejoy, T. E. & Oren, D. C. - 1981. The minimum critical size of ecosystems. In: Burgess, R. L. & Sharpe, D. M. eds. *Forest Island Dynamics in Man Dominated Landscapes*. New York, Springer-Verlag. p. 7-12.
- Meyer de Schauensee, R. - 1966. *The species of birds of South America and their distribution*. Narbeth, Pa. Livingston. 577 p.
- Munn, C. A. & Terborgh, J. W. - 1979. Multi-species territoriality in neotropical foraging flocks. *Condor*, 81:338-347.
- Patterson, H. D. - 1960. A further note on a simple method for fitting an exponential curve. *Biometrika*, 47:177-180.
- Pearson, D. - 1977. A pantropical comparison of bird community structure on six lowland rain forest sites. *Condor*, 79:232-244.
- Powell, G. V. N. - 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the neotropics. *Ornith. Monogr.*, 36:713-732.

- Rankin, J. M.; Prance, G. T.; Silva, M. F.; Rodrigues, W. A.; Uehling, M. E. -
Resultados preliminares de um levantamento florestal de 31 ha de terra firme na Amazônia Central. Descrição geral da vegetação e dados taxonômicos. (em preparação).
- Sick, H. - 1967. Rios e enchentes na Amazônia como obstáculo para a avifauna. **Atas Simp. Biota Amazonica.**, 5:495-520.
- Snedecor, G. W. & Cochran, W. G. - 1967. **Statistical Methods.** Ames, Iowa, Iowa State University Press. p. 467-471.
- Soule, M. E. - 1980. Thresholds for survival: maintaining fitness and evolutionary potential. **In: Soule, M. E. & Wilcox, B. A. eds. Conservation Biology an Evolutionary-ecological Perspective.** Sunderland, MA. Sinauer Assoc., Inc. p. 151-169.
- Soule, M. E.; Wilcox, B. A.; Holtby, C. - 1979. Benign neglect: a model of faunal collapse in the game reserves of East Africa. **Biol. Conserv.**, 15:259-272.
- Terborgh, J. W. - 1974. Preservation of natural diversity: the problem of extinction prone species. **BioScience**, 24:715-722.
- - 1975. Faunal equilibria and the desing of wildlife preserves. **In: Colley, F. B. & Medina, E. eds. Tropical Ecology.** New York, Springer-verlag. p. 369-380.
- Terborgh, J. W. and Winter, B. - 1980. Some causes of extinction. **In: Soule, M. E. & Wilcox, B. A. eds. Conservation biology: an evolutionary-ecological perspective.** Sunderland, Mass. Sinauer. p. 119-133.
- Willis, E. O. - 1967. The behavior of Bicolored Antbirds. **Univ. Calif. Publ. Zool.**, 79:1-132.
- - 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. **Ecol. Monogr.**, 44:153-169.
- - 1979. The composition of avian communities in remanescent woodlots in southern Brasil. **Papéis Avulsos, Zoologia**, São Paulo, 33:1-25.
- Willis, E. O. & Eisenmann, E. - 1979. A revised list of birds on Barro Colorado Island, Panama. **Smithson. Contrib. Zool.**, 291:1-31.
- Willis, E. O. & Oniki, Y. - 1978. Birds and army ants. **Ann. Rev. Ecol. Syst.**, 9:243-263.
- Winterbottom, J. M. - 1949. Mixed bird parties in the tropics, with special reference to northern Rhodesia. **Auk**, 66:258-263.
- Wong, M. A. - 1986. Trophic organization of understory birds in a Malaysian dipterocarp forest. **Auk**, 103:100-116.

(Aceito para publicação em 22.01.1989)