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# LOSS OF INSECTIVOROUS BIRDS ALONG A GRADIENT OF HUMAN IMPACT IN AMAZONIA

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**Abstract**

*Birds were surveyed within four zones defined along a gradient of decreasing impact by the petroleum industry and small-scale agriculture in the moist tropical forest of the Cuyabeno Wildlife Production Reserve in northeastern Ecuador. A total of 12 3-day surveys were conducted at nine sites, divided among the four zones, which consisted of a coffee plantation on the edge of a large deforested area, and three primary forest zones at approximately 0, 1500, and 3200 m from the deforested area (0, 200, and 1000 m from small clearings; 200, 2000, and > 3500 m from roads). All sites were located on the same types of soil and terrain, and the vegetation of all forested sites was physiognomically similar. The most outstanding difference in bird species composition across zones was the reduced number of insectivores in areas of greater human impact* ($p=0\cdot03$)*. Interior forest insectivore species were significantly more likely to be absent from impacted forests (and non-forest habitats) than were non-insectivores* ($p=0\cdot000004$)*, and this tendency was also present in the results of other studies of tropical forest birds. These results underscore the need to take insectivores, as well as other particularly sensitive groups, into special consideration within conservation strategies if intact faunas are to be preserved. Copyright © 1996 Elsevier Science Ltd*

*Keywords*: Ecuador, edge effect, Furnarioidea, insectivory, rain forest, sensitivity.

## INTRODUCTION

Tropical forest ecosystems are deteriorating rapidly due to human activities, and in order to conserve the rich biological diversity found in them we must understand this process of deterioration. It is particularly important to know which sorts of species are most affected and how far the effects reach into the forest (Willis, 1984).

The question of some species being more sensitive than others to the continuing and rapid loss of tropical forests has received much discussion (e.g. Terborgh, 1974), but there has been little empirical testing in landscapes representative of ongoing deforestation. Effects of habitat fragmentation on neotropical forest birds have been examined in a few cases (Leck, 1979; Willis, 1979; Lovejoy *et al.*, 1986), as well as those of habitat alteration (Johns, 1991; Thiollay, 1992). A number of other studies have used forested tropical landbridge islands as surrogates for tropical forest parks surrounded by deforestation (Terborgh, 1974; Faaborg, 1979; Terborgh & Winter, 1980; Karr, 1982; Gotelli & Graves, 1990). Although the islands studied experienced drastic reductions in habitat size, application of the results of these studies to protected area planning and management on the mainland is limited by the fact that the areas surrounding continental nature reserves (e.g. coffee plantations around a forest reserve, in the present study) are not as forbidding to, or devoid of, terrestrial fauna as is the water surrounding true islands (Janzen, 1983). In none of the bird studies mentioned above has the effect of distance from disturbance been examined as a determinant of species composition.

The suitability of uncut Amazonian forest as habitat for the native fauna is not as uniformly high as one may assume. Superimposed on the spatial heterogeneity of lowland tropical forest (Gentry, 1990) and little-known effects of past occupation by native peoples (Posey *et al.*, 1984; Balée, 1989; Roosevelt, 1989; Canaday, 1990, 1991; Redford, 1990), the impacts of present-day people vary with their ease of access to these forests. The principal human impacts on the fauna of Amazonia result from (a) agricultural colonization, (b) petroleum and mining operations, (c) the hunting and capture of wild animals (Redford, 1992), and (d) timber extraction (Thiollay, 1992). All of these activities are concentrated along roads (which are constructed for one or another of these activities) and navigable rivers. The impacts of these human activities extend variable distances into the forest, depending on the strength of various, inter-related physical, biological, sociological and economic factors. Nevertheless, all of these impacts undoubtedly attenuate with

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increasing distance from roads or other forms of access.

Birds represent an excellent segment of the fauna for the study of human impacts on Amazonian ecosystems. Within Amazonia, birds are the class of animals most fully understood in terms of their ecology and taxonomy (e.g. Hilty & Brown, 1986; Karr *et al.*, 1990). The ecological niches of birds are quite varied, and birds are also more readily detected than most other types of animals, due to their often loud vocalizations, sometimes bright coloration, and generally diurnal behavior. Finally, Amazonian birds are highly diverse, with the greatest concentration of species located in western Amazonia (Haffer, 1990).

In this study, I examine the species richness of broad ecological guilds of birds found in four zones along a gradient of human impact. Proximity to roads and clearings is used as an index of the degree of human impact present within the different zones. If the species richness of a guild is shown to be affected by the degree of human impact, I also examine whether its member species are more likely to be limited to undisturbed forest than those of other guilds, both in the context of the present study and in reviewing other studies of tropical forest birds. The goal of this work is to shed light on the relative sensitivity of different guilds to the environmental changes taking place in Amazonia. The results should be applicable to the determination of conservation priorities and monitoring methodologies.

## STUDY AREA

Field work was conducted in humid tropical forest of the Reserva de Producción Faunística Cuyabeno from August through December 1989. This protected area, located in the northeast corner of Ecuador (250 m elevation, 0°5'S Lat, 76°20'W. Long.; Fig. 1), includes a petroleum company road that was constructed in the 1970s. Before this time, the area was very isolated and inhabited only by widely-scattered groups of Siona, Tetete, and Cofán Indians. Farmers from elsewhere in the country have since claimed land along the petroleum company's road, planting coffee, subsistence crops, and pasture. Palms are often left standing in clearings, and such fruit trees as *Inga* and *Psidium* (guava) are planted to shade the coffee. Rainfall, which averages 3400 mm per year, is heaviest from April through July, and lightest in January and February. The history and pattern of human habitat disturbance in the Reserve are described in more detail elsewhere (Canaday, 1991). The study area is located within the Napo Region, which is considered to be among the nine greatest concentrations of biodiversity within the world's tropical forests (Myers, 1988).

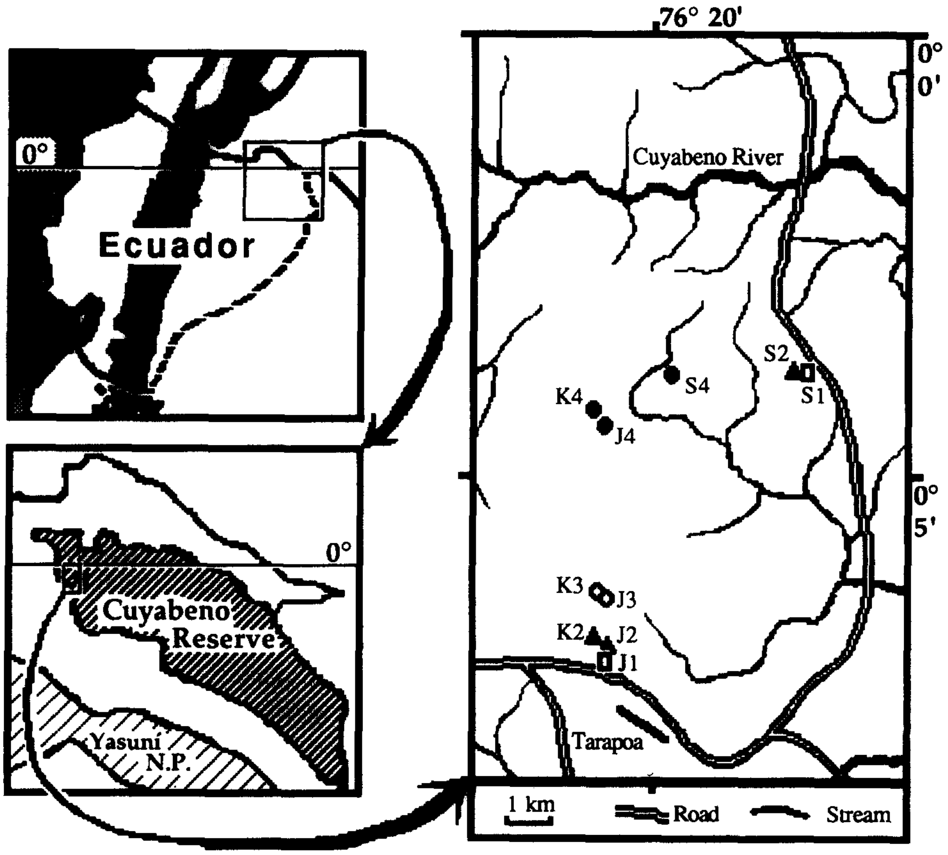

**Fig. 1.** Aproximate location of survey sites within the Cuyabeno Reserve and the country of Ecuador. Zones are indicated as follows: □-coffee plantations, ▲-edge forest, ○-intermediate forest, ●-interior forest. J, K, and S refer to the three replicate sets of sites. The line near Tarapoa represents an airplane runway. The limits of the Cuyabeno Reserve reflect considerable enlargement in 1991 and small dismemberment in 1994. Black areas on the map of Ecuador indicate areas over 1000 m elevation in the Andes.

## METHODS

### Study design

Birds were surveyed at sites within four zones: (1) coffee plantations less than 100 m from uncut forest; (2) 'edge forest' – uncut forest <300 m from roads and <100 m from the contiguous clearings bordering the roads of the region; (3) 'intermediate forest' – uncut forest 2 km from roads and about 200 m from small clearings; and (4) 'interior forest' – uncut forest at least 3·5 km from roads and 1 km from any clearings. Sampling was conducted at selected sites in each zone using standardized methods. At each site, ten 10-m mist nets (8 of 37 mm mesh, 2 of 60 mm) were set up along approximately two-thirds of a loop trail encompassing about 1 ha. Nets were operated from dawn to 1400 h and all birds seen, heard, or netted during this time were noted. Each survey lasted three days. The number of surveys conducted was not equal across zones (Table 1). However, the unit of analysis is that of the individual surveys, which are comparable because of the standardized methods used.

The biases involved in sampling this complex, highly diverse avifauna were reduced in several ways. First, in addition to extensive previous experience with neotropical birds, two months were spent in the Reserve to become familiar with the local avifauna before collecting data. Second, given that mist-net data alone do not give representative samples of neotropical bird assemblages (e.g. Terborgh *et al.*, 1990), data from birds seen and heard were included with those from capture in mist-nets. Third, two nets of a mesh larger than commonly used (60 mm) were included to increase the likelihood of capturing relatively large birds.

Factors which could confound the comparison of human impact zones were controlled in three ways. First, all observations were made by one observer (myself). Second, surveys of the different zones were highly interspersed temporally (see Table 1, Fig. 3); thus any effects of seasonality were roughly equal among the zones. Third, all sites were carefully located within one type of forest (described below), allowing the assumption that roughly the same species occupied all of the sample sites before construction of the road and associated human activity.

According to a recent classification of environmental field studies (Eberhardt & Thomas, 1991), the present study would be categorized within either 'observational studies' or 'sampling from pattern'. Both apply here, as human impacts are assumed to vary spatially.

### Survey sites

All sites were located in floristically diverse forest on hilly *terra firme* terrain with reddish clay soils (or in a coffee plantation nearby, where there had previously been such a forest). Three sets of sites were established, each including at least one site in edge forest and another in interior forest (Fig. 1). Over 1 km of trail had to be reopened to reach the interior forest sites of J4 and K4, while S4 was situated near an existing trail used by hunters. All forest sites were within the same large, contiguous forest, and the coffee plantation site was adjacent to this forest.

**Table 1. Mid-dates of 3-day surveys, grouped by zone and set. For example, Site J2 (Fig. 1) was surveyed twice, on 21–23 September and 28–30 October, 1989**

| Zone \ Set | J | K | S |
|---|---|---|---|
| 1 Coffee plantation | 1 Sep | — | — |
| 2 Edge forest | 22 Sep, 29 Oct | 13 Dec | 3 Oct |
| 3 Intermediate forest | 18 Sep, 23 Oct | 18 Dec | — |
| 4 Interior forest | 9 Sep, 2 Nov | 8 Dec | 9 Oct |

Forest sites were selected for the presence of similar vegetaion, based on overall appearance. To quantify this similarity in forest cover, the diameter at breast height of all trees (>10 cm) in ten 10 × 10 m plots was measured at each site, a total of 585 trees. The distributions of tree diameters (mean 21 cm) in the three forested zones did not differ significantly (Kolmogorov-Smirnov D = 0·0003 to 0·077, $\chi^2$=0·00004 to 1·987, *d.f.*=2, *p*>0·36), nor did basal area (mean=34 m$^2$/ha; Kruskal-Wallis *H*=1·698, *d.f.*=2, *p*=0·42) or tree density (mean=730 trees/ha; *H*=0·608, *d.f.*=2, *p*=0·74).

### Analysis

The probability of detecting a given bird species depends on the loudness and distinctiveness of its vocalizations, the conspicuousness of its colors and movements, and its propensity to fly swiftly and low to the ground (thus increasing the likelihood of capture in mist nets). In order to minimize the biases associated with this highly variable likelihood of detection, each species encountered during the study was simply considered present or absent during each survey, thus better permitting comparisons among species. This also allows auditory and visual data to be included directly with data from mist-netting, without the need of estimating the number of individuals seen or heard. Absence of a given species during a particular survey was not taken as an indication of the species' absolute absence from the site, but rather of its low population density. Birds that fly silently high in the air (e.g. vultures, swifts) were not included in any analyses.

Species accumulation curves were constructed for each zone and for the study as a whole. These curves allow for estimation of the proportion of the detectable avifauna (i.e. given methods used and observer's experience) that actually was detected, as well as the relative species richness of birds in the different zones.

Information on diets was taken from Karr *et al.* (1990), with a few cases of extrapolation within genera.

Kruskal-Wallis tests (Sokal & Rohlf, 1981) were performed to compare the number of species in each of several broadly defined guilds found in surveys in the four different human impact zones. Separate tests were carried out for each of the three most species-rich guilds: insectivores, frugivores, and omnivores.

## RESULTS

Over 1500 detections were made during the 12 surveys. Most were auditory, except in the open habitat of the coffee plantation where visual observation was more important (Fig. 2). As sampling progressed, each survey yielded fewer newly detected species (Fig. 3). In all, 178 species were detected (Appendix 1). Non-passerine birds constituted 37% of the sample, suboscine passerines 43%, and oscines 20%. The two most species-rich families were the Formicariidae and the Emberizidae (*sensu lato*), which were represented by 28 and 24 species, respectively. Only three species of North American migrants were detected during the surveys: *Contopus borealis*, *Catharus ustulatus*, and *C. minimus*. The calls of macaws (*Ara* spp.) and canopy tanagers (e.g. *Tangara* spp.) were not always distinctive and these groups were treated in the analyses as just two species.

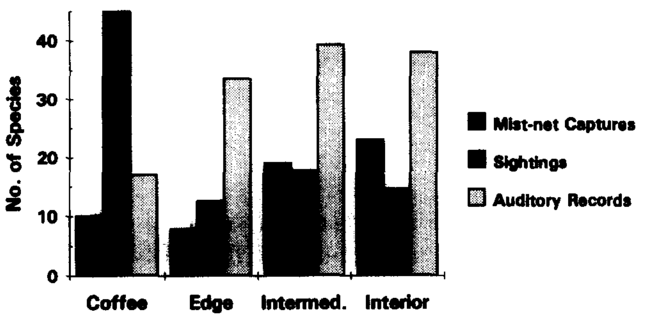

Fig. 2. Average numbers of bird species mist-netted, seen, or heard during 3-day surveys in four human impact zones in the Cuyabeno Reserve, Ecuador.

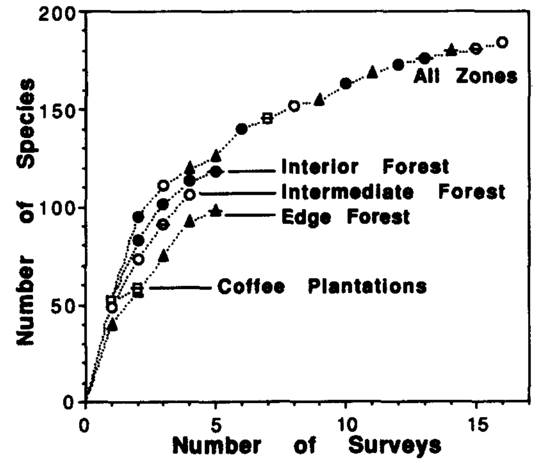

Fig. 3. Species accumulation curves for birds detected within four upland zones in the Cuyabeno Reserve, Ecuador. Surveys are arranged chronologically. Each survey lasted 3 days, except those with crossed symbols, which lasted 1 day each (2 days in the briefer coffee plantation survey). Four unidentified species with distinctive calls are included. Symbols follow Fig 1.

### Responses of broadly defined guilds

The number of insectivorous species detected varied significantly according to the zone being sampled (Kruskal-Wallis $T$=8·87, *d.f.*=3, $p$=0·03), with more being found toward the forest interior (Fig. 4). No significant differences were found among the zones in the species richness of either omnivores ($T$=3·54, *d.f.*=3, $p$=0·32) or frugivores ($T$=1·08, *d.f.*=3, $p$=0·78).

This inverse relationship between the ecological importance of insectivorous birds and the amount of human impact was also reinforced by capture rate data from the three most frequently mist-netted insectivorous species. In each case, capture rates increased dramatically with distance from roads and clearings (Table 2).

One of these frequently captured, insectivorous species, *Pithys albifrons*, apparently only bred far from human disturbance: individuals with bare, rugose brood patches (Pyle *et al.*, 1987) were only found at interior forest sites, suggesting that habitats with greater human impact were suboptimal for this species. In contrast, all of the nests that were incidentally found in coffee plantations belonged to omnivores, namely *Trogon viridis*, *Capito niger*, *Psarocolius angustifrons*, and *Cacicus cela*.

Finally, the decline in insectivores towards forest edge habitats is supported by data from this and six other studies in tropical forests which all show a significantly greater restriction of insectivorous species to interior forest habitats as compared with other foraging guilds (Table 3, Appendix 2).

## DISCUSSION

These results suggest that insectivorous birds are most sensitive to human impacts in tropical forest landscapes, affected, in the present study, for 20 years by the petroleum industry and agricultural settlement. Insectivorous birds have also been found to decline with hunting pressure in French Guiana (Thiollay,

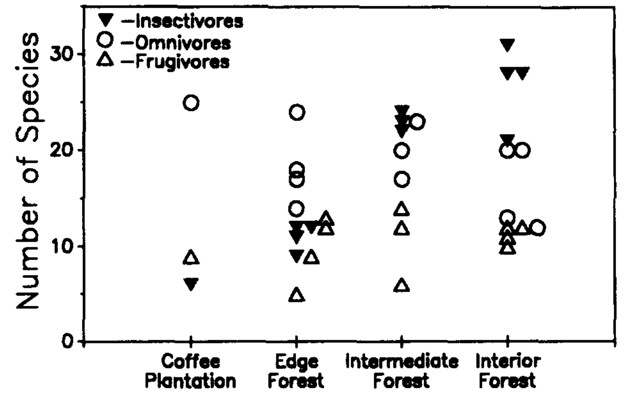

Fig. 4. Numbers of insectivorous, omnivorous, and frugivorous bird species detected during 12 3-day surveys in four human-impact zones in the Cuyabeno Reserve, Ecuador. Only the number of insectivores varies significantly among zones (Kruskal-Wallis $T$=8·87, *d.f.*=3, $p$=0·03). The interior forest survey with the lowest count of insectivores was K4 (Fig. 1).

**Table 2. Mist-net capture rates (no./1000 net-hours) in the four human-impact zones for the four species most frequently caught (representing 31% of all captures), along with the ratio of interior captures to edge captures (I/E) and the overall number of individuals netted (*N*). Data from four surveys of less than three days each are also included**

| SPECIES | Coffee plantation | Edge forest | Intermed. forest | Interior forest | I/E | *N* |
|---|---|---|---|---|---|---|
| *Pithys albifrons*[a] | 0 | 0·96 | 5·00 | 14·42 | 15·0 | 20 |
| *Gymnopithys leucaspis*[a] | 0 | 1·92 | 10·00 | 13·46 | 7·0 | 24 |
| *Glyphorynchus spirurus*[a] | 0 | 7·21 | 18·75 | 40·87 | 5·7 | 52 |
| *Pipra coronata* | 0 | 2·88 | 8·75 | 11·54 | 4·0 | 22 |
| Total no. of net-hours[b] | 400 | 1040 | 800 | 1040 | | |

[a] Insectivore.

[b] The number of net-hours was reduced by 20% for computation of capture rates of *Glyphorynchus*, because this species was never caught in large-mesh (60 mm) nets. Captures of the other three species were divided roughly proportionally between 60-mm and 37-mm nets.

1986) and construction of modern paved highways in the deforested landscape of Punjab, India (Dhindsa *et al.*, 1988). In addition, various studies have also shown the following two groups of insectivores to be especially sensitive to human impacts in neotropical forests: terrestrial insectivores (Willis, 1979; Johns, 1991; Thiollay, 1992; Canaday, in press) and ant-following insectivores (Willis, 1974; Bierregaard & Lovejoy, 1989; Canaday, 1991; Thiollay, 1992).

The negative association between the number of insectivorous species and the degree of human impact may be due to a number of factors, including microclimatic changes that have altered the insect prey base, greater habitat sensitivity among insectivores resulting from their high degrees of ecological specialization, changes in predation upon these birds, and interference competition from opportunistic, disturbance-adapted omnivores. All of these factors require further investigation and are discussed here solely as potential determinants of the described pattern of local avian distribution.

### Microclimate

Microclimatic changes have been shown to accompany human habitat alteration in tropical forests. In central Amazonia, drying and warming effects of large clearings have been detected 40 m into the forest, and the amount of sunlight reaching the forest floor was also higher near the edge (Kapos, 1989). Amazonian deforestation is also believed to reduce local rainfall, possibly even lengthening the dry season (Salati *et al.*, 1986). This would acutely affect insectivores, since tropical forest insects have been shown to increase in abundance

**Table 3. Numbers of species found in intact lowland tropical forest habitats during selected studies, grouped into contingency tables according to diet and whether they were also found in impacted forest or non-forest habitats. Diets: I-strictly insectivorous, O-other. Two-by-two *G* tests of independence (*d.f.*=1; Sokal & Rohlf, 1981).**

Further details in Appendix 2

| | I | O | I/O | G | *p* |
|---|---|---|---|---|---|
| A. Present study | | | | | |
| Only interior forest | 36 | 13 | 2·8 | 21·54 | 0·000004 |
| Also edge forest | 17 | 44 | 0·4 | | |
| B. Concepción, Bolivia (Davis, 1993). | | | | | |
| Only forest | 24 | 5 | 4·8 | 10·02 | 0·0015 |
| Also other habitats | 13 | 19 | 0·7 | | |
| C. Mirití, Colombia (Andrade & Rubio-Torgler, 1994). | | | | | |
| Only undisturbed forest | 20 | 2 | 10·0 | 4·06 | 0·044 |
| Also young second growth | 19 | 11 | 1·7 | | |
| D. Colombia (Hilty & Brown, 1986). | | | | | |
| Only rain forests | 91 | 45 | 2·0 | 38·98 | <0·000001 |
| Also other habitats | 138 | 245 | 0·6 | | |
| E. Peru (Parker *et al.*, 1982). | | | | | |
| Only rain forests | 192 | 170 | 1·1 | 5·65 | 0·017 |
| Also other habitats | 41 | 62 | 0·7 | | |
| F. Australia (Pizzey, 1980). | | | | | |
| Only rain forest | 10 | 1 | 10·0 | 15·88 | 0·00007 |
| Also other habitats | 23 | 69 | 0·3 | | |
| G. Madagascar (Langrand, 1990). | | | | | |
| Only rain forest | 18 | 10 | 1·8 | 3·86 | 0·049 |
| Also other habitats | 24 | 37 | 0·6 | | |

and diversity with moisture (Williams, 1941; Janzen & Schoener, 1968; Janzen, 1973; Wolda, 1978; Levings & Windsor, 1984), as well as to change in taxonomic composition (Shelly, 1988).

### Ecological specialization

Insectivorous species may, on the whole, be more specialized than other groups, and, therefore, more sensitive to changes in the particular populations they feed upon. Snow (1976) points out that it is in the very nature of insectivory for the niches of insectivores to become progressively more specialized, because the selective pressure exerted by insectivores tends to make their insect prey increasingly harder to find and consume. As an example of the extreme specialization of insectivorous Amazonian forest birds, the various species that search for insects in hanging dead leaves (Remsen & Parker, 1984) makes different use of the available habitat (Rosenberg, 1990). For example, two species of antwren had different preferences for the species of suspended dead leaves in which they searched for insects, although observed in the same bamboo-dominated habitat: *Myrmotherula ornata* strongly preferred bamboo *Guadua* sp., while *M. leucophthalmus* preferred *Cecropia* (Rosenberg, 1990: Fig. 9). The selective pressure of mutualistic frugivory, and associated seed dispersal, on species of fruiting plants, in contrast, serves to make fruits easier to find, consume, and digest (Snow, 1976).

### Predation

Changes in the activity of predators following human habitat alteration could also affect insectivorous bird populations; the forest edge may support species of predators that hunt in different ways than those present in the interior of the forest. This may particularly affect mixed-species understory flocks of birds, which are composed almost exclusively of insectivores, and are hypothesized to have evolved in response to predation, primarily by raptors (Powell, 1985). In tropical forests of the Ivory Coast, Mexico, and the Guianas, significant differences in the relative abundance of different raptor species have been detected along gradients of human habitat alteration, with some species only being present in disturbed habitats (Thiollay, 1985).

### Furnarioidea

The majority of sensitive insectivorous lowland tropical forest species discussed here belong to the superfamily Furnarioidea (Wetmore, 1960), which consists of the families Dendrocolaptidae (woodcreepers), Furnariidae (ovenbirds), Formicariidae (antbirds), Conopophagidae (gnateaters), and Rhinocryptidae (tapaculos). Of the insectivorous species restricted to intact rain forest enumerated in Table 3, 75% (present study), 70% (Hilty & Brown, 1986), and 50% (Davis, 1993) were furnarioids. This group has been divided into two closely related parvorders (Furnarii and Thamnophili; Sibley & Ahlquist, 1985), but its monophyly was reaffirmed in the process.

Over half of the species of New World suboscine passerines belong to the Furnarioidea. All are insectivorous inhabitants of forests and woodlands, except for a considerable number of ovenbirds and a few woodcreepers that occupy open habitats (Ridgely & Tudor, 1994). The species of Furnarioidea use a wide variety of foraging substrates (e.g. ground for antpittas, hanging dead leaves for certain antwrens and foliage-gleaners, twigs for xenops, live leaves for many others, and tree bark for woodcreepers) and together occupy all strata of the forest. Many participate in mixed-species flocks of up to 16 regular member species, each represented by a single pair (Powell, 1985). Some species specialize in feeding on the insects that flee from advancing swarms of army ants, thus the name 'antbird', although most antbirds do not exhibit this behavior.

Kattan (1992) assigned 'rarity' scores to the cloud forest avifauna of the Cordillera Central of Colombia, based on the number of the following criteria that each species met: (a) distribution limited to the Andes from Peru north, (b) use of only forested habitats, and (c) relatively infrequent observation at sites where known to exist. The only group shown to be particularly 'rare', or in other words vulnerable to deforestation, was one composed of woodcreepers, ovenbirds, and antbirds ($\chi^2$=10·01, *d.f.*=3, *p*=0·018).

Willis (1976) noticed that during a period of unusually cold weather furnarioids became less apparent, while other birds behaved fairly normally. This temporary climate change was in a way analogous to the more permanent change that comes with deforestation and the furnarioids' inactivity in response to it suggests that they may be less well adapted than other birds to conditions foreign to these warm, moist forests.

Perhaps the Furnarioidea has had a particularly long evolutionary history in tropical American forests. In any case, it may represent a case in which characteristics inherent to a particular lineage are as important as contemporary ecological traits in determining species' responses to habitat alteration.

### The issue of scale

An alternative explanation of the results of this study is that all species may have been equally affected by human habitat disturbance (i.e. the populations of all local species decline to the same degree) but that these effects were most evident among the insectivores, which tend to maintain small, fixed territories (Munn, 1985; Powell, 1985; Greenberg & Gradwohl, 1986) and therefore disappear from impacted areas. On the other hand, omnivores and frugivores, although hypothetically equally reduced in number, tend to be more wide-ranging and continue to visit these areas. Even if all species were equally affected by human activity, for which there is no evidence in the present study, insectivores nonetheless would remain the most sensitive indicators of the degree of human impact present in particular places.

### Width of edge

An indication of the distance that effects of human habitat alteration reach into the forest can be derived from the results of this study. Although there were not significantly more insectivore species in interior forest surveys than in intermediate forest surveys (Fig. 4; Mann-Whitney $T=9$, $n=3,4$, $p=0.29$), a principal components analysis of the numbers of species detected within 20 narrowly defined foraging guilds produced a complete separation of intermediate and interior forest surveys along its first artificial axis (Canaday, 1991, in press). The interior forest survey with the lowest number of insectivores was located adjacent to the natural edge between upland forest and floodable forest (Fig. 1: K4), so the low number of insectivorous species may have been due to the proximity of this natural edge.

Effects of human activities on birds were, therefore, detectable in the 'intermediate' forest surveys, and edge effects appear to extend over 200 m from small clearings, about 1·5 km from the large contiguous clearing, and 2 km from the road. This assumes that the 'interior' forest sites sampled in this study were free of human impacts, so the width of the edge could well be greater. In any case, the edge defined here in terms of Amazonian birds is orders of magnitude wider than that described for North American trees (10–15 m; Ranney *et al.*, 1981). Despite the growing recognition of this negative edge effect (Lovejoy *et al.*, 1986; Hunter, 1990), even among Amazonian birds at natural edges (Terborgh *et al.*, 1990), the width of this biological edge associated with human alteration of tropical forests is as yet not well known.

### Conservation implications

The results of this study have several direct applications in the determination of priorities and methods for conservation and related research. First, given that species vary greatly in their sensitivity to human impacts, it would be more effective to use the number of sensitive species rather than total species richness in the evaluation of the intactness of faunas, since loss of sensitive species may be masked in the total species richness by invasion of species adapted to disturbed conditions. Second, the indication of pervasive edge effects in the present study reinforce the idea that relatively large areas of tropical forest must be protected to conserve the biota found there (Vuilleumier, 1988). Third, the mechanisms that drive sensitive species (e.g. many insectivorous birds) from impacted areas require further explanation in order to be minimized in the design and management of protected areas.

To reinforce the first point, in the present study, there was a set of omnivorous species (e.g. *Cacicus cela*, *Psarocolius angustifrons*, *Pitangus sulfuratus*) which were abundant and bred in coffee plantations. These are examples of species that require the least attention of conservation efforts, for they adapt well to habitats modified by people. In a study of birds in forests at different stages of regeneration in Gabon, Brosset (1986) found a guild including canopy omnivores and frugivores to be among the first to recolonize young, second-growth forests. Also, the tendency for opportunistic species to benefit from forest disturbance in Amazonia appears to extend beyond birds to include other taxa (e.g. *Drosophila*; Martíns, 1989).

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## APPENDIX 1

**Bird species detected in terra firme moist tropical forest and nearby coffee plantations in the Cuyabeno Reserve, Ecuador, May to December, 1989.**

Determinations of *Diet* follow Karr *et al.* (1990): i, insectivore; o, omnivore; f, frugivore; n, nectarivore; p, predator of vertebrates; c, carrion eater. Local distribution (*Distr*): 1, coffee plantations; 2, edge forest; 3, intermediate forest; and 4, interior forest. (Species in parentheses if not detected during actual surveys, or flies silently over the forest. These species are not included in any analyses.) *Mass* (in grams) of each species is as given by Karr *et al.* (1990), unless local data were obtained.

| | *Diet* | *Distr* | | | | *Mass* |
|---|---|---|---|---|---|---|
| *Tinamidae* | | | | | | |
| Tinamus major | f | 1 | 2 | 3 | | 1170 |
| Crypturellus soui | f | | 2 | 3 | 4 | 205 |
| Crypturellus undulatus | f | | 2 | | | 540 |
| Crypturellus variegatus | f | | 2 | | 4 | 352 |
| *Ardeidae* | | | | | | |
| Tigrisoma lineatum | p | | 2 | | | 840 |
| *Cathartidae* | | | | | | |
| (Cathartes melambrotus | c | 1 | | | | 1130 ) |
| (Sarcoramphus papa | c | 1 | | 3 | | 200 ) |
| *Accipitridae* | | | | | | |
| Buteo magnirostris | i | 1 | 2 | | | 311 |
| Spizaetus tyrannus | p | | | | 4 | 1025 |
| *Falconidae* | | | | | | |
| Micrastur gilvicollis | p | | | | 4 | 215 |
| Daptrius americanus | o | 1 | 2 | 3 | 4 | 583 |
| Herpetotheres cachinnans | p | | 2 | 3 | 4 | 650 |
| Falco rufigularis | p | | | | 4 | 155 |
| *Cracidae* | | | | | | |
| Ortalis motmot | f | 1 | 2 | | | 402 |
| Crax salvini | f | | | 3 | 4 | 2200 [a] |
| (Notocrax urumutum | f | | | | 4 | 1250 [a]) |
| Penelope jacquacu | f | | 2 | | 4 | 1325 |
| *Phasianidae* | | | | | | |
| Odontophorus gujanensis | o | | | 3 | | 310 |
| *Psophiidae* | | | | | | |
| Psophia crepitans | o | | | | 4 | 1240 |
| *Rallidae* | | | | | | |
| (Aramides cajanea | i | | | | 4 | 500 ) |
| Anurolimnas fasciatus | i | | 2 | | | 60 |
| Anurolimnas castaneiceps | i | | 2 | | | 60 |
| *Eurypygidae* | | | | | | |
| Eurypyga helias | i | | | 3 | | 220 |
| *Columbidae* | | | | | | |
| Columba subvinacea | f | 1 | 2 | 3 | 4 | 126 |
| Columba plumbea | f | | | 3 | 4 | 207 |
| Leptotila rufaxilla | f | 1 | 2 | 3 | 4 | 160 |
| Geotrygon montana | f | | 2 | 3 | 4 | 120 |
| *Psittacidae* | | | | | | |
| Ara manilata | f | 1 | | | | 370 |
| Ara severa | f | 1 | | 3 | | 430 |
| Ara ararauna | f | 1 | 2 | 3 | 4 | 1125 |
| Ara macao | f | | | | 4 | 1015 |
| Pyrrhura melanura | f | | 2 | 3 | 4 | 70 |
| Forpus sp. | f | | | 3 | 4 | 27 |
| Brotogeris cyanoptera | f | 1 | 2 | 3 | 4 | 67 |
| (Touit purpurata | f | | | 3 | | 71 [b]) |

Appendix 1 – continued

| | *Diet* | *Distr* | | | | *Mass* |
|---|---|---|---|---|---|---|
| Pionites melanocephala | f | 1 | 2 | 3 | 4 | 122 |
| Pionus menstruus | f | 1 | 2 | 3 | 4 | 293 |
| Amazona ochrocephala | f | 1 | 2 | 3 | 4 | 510 |
| *Cuculidae* | | | | | | |
| Piaya cayana | i | 1 | 2 | 3 | 4 | 104 |
| Piaya melanogaster | i | | | | 4 | 107 |
| Crotophaga ani | i | 1 | 2 | | | 105 |
| *Strigidae* | | | | | | |
| (Otus choliba | i | 1 | 2 | | | 143 ) |
| Pulsatrix perspicillata | p | | | 3 | | 795 |
| Glaucidium brasilianum | i | 1 | 2 | | | 67 |
| *Apodidae* | | | | | | |
| (Streptoprocne zonaris | i | 1 | | | | 111 ) |
| (Reinarda squamata | i | 1 | | | | 14 [b]) |
| *Trochilidae* | | | | | | |
| Threnetes leucurus | n | | 2 | 3 | | 6 |
| Phaethornis malaris [c] | n | 1 | 2 | 3 | 4 | 7 |
| Phaethornis bourcieri | n | | 2 | 3 | 4 | 4 |
| Phaethornis ruber | n | 1 | 2 | | | 2 |
| Campylopterus largipennis | n | 1 | | | | 8 |
| Thalurania furcata | n | | 2 | 3 | 4 | 5 |
| (Polyplancta aurescens | n | | 2 | | | 6 ) |
| *Trogonidae* | | | | | | |
| Pharomachrus pavoninus | o | | 2 | 3 | 4 | 200 |
| Trogon melanurus | o | | | | 4 | 122 |
| Trogon viridis | o | 1 | 2 | 3 | 4 | 60 |
| Trogon rufus | o | | | | 4 | 66 |
| *Momotidae* | | | | | | |
| (Baryphthengus ruficapillus | o | | | 3 | | 162 ) |
| Momotus momota | o | | | | 4 | 120 |
| *Galbulidae* | | | | | | |
| Jacamerops aurea | i | | | | 4 | 79 |
| Galbula albirostris | i | | | | 4 | 18 |
| *Bucconidae* | | | | | | |
| Malacoptila fuscus | i | | | 3 | 4 | 42 |
| (Nonnula rubecula + | i | | | | 4 | 20 [b]) |
| Monasa morpheus | i | | 2 | 3 | 4 | 70 |
| *Capitonidae* | | | | | | |
| Capito niger | o | 1 | 2 | 3 | 4 | 64 |
| *Ramphastidae* | | | | | | |
| Pteroglossus pluricinctus | o | 1 | 2 | 3 | | 140 |
| Pteroglossus inscriptus | o | 1 | 2 | | | 126 |
| Pteroglossus flavirostris | o | | 2 | 3 | | 148 |
| Selenidera reinwardtii | o | | | 3 | 4 | 141 |
| Ramphastos culminatus | o | | 2 | 3 | 4 | 369 |
| Ramphastos tucanus | o | 1 | 2 | 3 | 4 | 734 |
| *Picidae* | | | | | | |
| Picumnus rufiventris | i | | 2 | 3 | 4 | 14 |
| Chrysoptilus punctigula | o | 1 | | | | 76 |
| Piculus chrysochloros | i | | 2 | | | 88 |
| Celeus elegans | o | | | 3 | 4 | 136 |
| Dryocopus lineatus | o | 1 | 2 | | | 209 |
| Melanerpes cruentatus | o | 1 | 2 | 3 | 4 | 59 |
| Campephilus melanoleucos | o | | 2 | 3 | | 225 |
| Campephilus rubricollis | o | | | | 4 | 220 |

Appendix 1 – continued

| | Diet | Distr | | | | Mass |
|---|---|---|---|---|---|---|
| *Dendrocolaptidae* | | | | | | |
| Dendrocincla fuliginosa | i | | | | 4 | 31 |
| Glyphorynchus spirurus | i | | 2 | 3 | 4 | 14 |
| Dendrocolaptes certhia | i | | 2 | 3 | | 75 |
| Xiphorhynchus ocellatus | i | | 2 | 3 | 4 | 40 |
| Xiphorhynchus guttatus | i | 1 | 2 | 3 | 4 | 63 |
| Campylorhamphus trochilirostris | i | | | | 4 | 38 |
| *Furnariidae* | | | | | | |
| Synallaxis rutilans | i | | | 3 | 4 | 18 |
| Hyloctistes subulatus | i | | | 3 | 4 | 29 |
| Ancistrops strigilatus | i | | | | 4 | 37 |
| Philydor pyrrhodes | i | | | | 4 | 30 |
| Philydor erythropterus | i | | | 3 | | 30 |
| Automolus infuscatus | i | | | 3 | 4 | 38 |
| (Automolus ochrolaemus | i | | | 3 | | 34 ) |
| Automolus melanopezus | i | | | | 4 | 31 |
| Xenops minutus | i | | | | 4 | 12 |
| Sclerurus mexicanus | i | | | | 4 | 20 |
| Sclerurus caudacutus | i | | | 3 | | 35 |
| *Formicariidae* | | | | | | |
| Cymbilaimus lineatus | i | | | | 4 | 40 |
| Thamnophilus schistaceus | i | | | 3 | 4 | 20 |
| Megastictus margaritatus | i | | | | 4 | 28 |
| Thamnomanes ardesiacus | i | | | | 4 | 19 |
| Thamnomanes caesius | i | | 2 | 3 | 4 | 17 |
| Myrmotherula brachyura | i | | | 3 | | 8 |
| Myrmotherula hauxwelli | i | | | 3 | 4 | 11 |
| Myrmotherula erythrura | i | | | 3 | | 10 |
| Myrmotherula ornata | i | | | 3 | | 10 |
| Myrmotherula axillaris | i | | 2 | 3 | 4 | 9 |
| (Myrmotherula longipennis | i | | | | 4 | 9 ) |
| Myrmotherula sunensis | i | | | 3 | 4 | 8 |
| (Myrmotherula menetriesii | i | | | 3 | 4 | 9 ) |
| Dichrozona cincta | i | | | | 4 | 15 |
| Cercomacra cinerascens | i | | | 3 | 4 | 18 |
| Myrmoborus myotherinus | i | | | 3 | 4 | 20 |
| Hypocnemis hypoxantha | i | | | | 4 | 13 |
| Percnostola schistacea + | i | | 2 | 3 | | 26 |
| Myrmeciza fortis | i | | 2 | 3 | 4 | 53 |
| Gymnopithys leucaspis | i | | 2 | 3 | 4 | 26 |
| Gymnopithys lunulata | i | | | | 4 | 23 |
| Rhegmatorhina melanosticta | i | | | 3 | 4 | 28 |
| Hylophylax poecilonota | i | | 2 | | 4 | 18 |
| Phlegopsis erythroptera | i | | 2 | 3 | 4 | 57 |
| Pithys albifrons | i | | 2 | 3 | 4 | 19 |
| Formicarius colma | i | | | | 4 | 45 |
| Chamaeza nobilis | i | | | 3 | | 130 |
| Myrmothera campanisona | i | | | 3 | 4 | 47 |
| *Conopophagidae* | | | | | | |
| (Conopophaga aurita | i | | | | 4 | 24 ) |
| *Rhinocryptidae* | | | | | | |
| Liosceles thoracicus | i | | | 3 | 4 | 81 |
| *Cotingidae* | | | | | | |
| Phoenicircus nigricollis | f | | | 3 | 4 | 80 |
| Iodopleura isabellae | o | 1 | 2 | | | 30 |
| Lipaugus vociferans | o | | 2 | 3 | 4 | 81 |

Appendix 1 – continued

| | *Diet* | *Distr* | | | | *Mass* | |
|---|---|---|---|---|---|---|---|
| Querula purpurata | o | 1 | 2 | 3 | 4 | 125 | |
| *Pipridae* | | | | | | | |
| Piprites chloris | i | | 2 | 3 | 4 | 20 | |
| Tyranneutes stolzmanni | o | | 2 | 3 | 4 | 9 | |
| Machaeropterus regulus | f | | 2 | | 4 | 10 | |
| Pipra coronata | f | | 2 | 3 | 4 | 9 | |
| Pipra erythrocephala | f | | 2 | | 4 | 12 | |
| Pipra filicauda | f | 1 | | | | 14 | b |
| Chiroxiphia pareola | f | | | 3 | 4 | 17 | |
| Manacus manacus | f | | | 3 | 4 | 17 | |
| *Tyrannidae* | | | | | | | |
| Tyrannulus elatus | o | 1 | 2 | 3 | | 8 | |
| Elaenia sp. | o | 1 | 2 | | | | |
| Mionectes oleaginea | o | 1 | 2 | 3 | 4 | 11 | |
| Corythopis torquata | i | | | 3 | 4 | 16 | |
| Cnipodectes subbrunneus | i | | | 3 | | 26 | |
| Terenotriccus erythrurus | i | | | | 4 | 8 | |
| Contopus borealis | i | 1 | | | | 31 | |
| Attila spadiceus | i | | | | 4 | 35 | |
| Rhytipterna simplex | i | | 2 | | | 36 | |
| Myiarchus sp. | i | 1 | | | | | |
| Pitangus sulfuratus | o | 1 | 2 | | | 55 | |
| Megarhynchus pitangua | o | 1 | 2 | | | 66 | |
| Myiozetetes similis | o | 1 | | | | 33 | |
| Myiozetetes granadensis | o | 1 | | | | 32 | |
| Legatus leucophaius | f | 1 | 2 | 3 | 4 | 23 | |
| Tyrannus melancholicus | o | 1 | | | | 47 | |
| (Tyrannus tyrannus | o | 1 | | | | 40 | ) |
| Platypsaris minor | o | | | 3 | | 70 | |
| Tityra cayana | o | 1 | 2 | 3 | | 66 | |
| Tityra inquisitor | o | 1 | | | | 45 | |
| *Hirundinidae* | | | | | | | |
| (Progne chalybea | i | 1 | | | | 39 | ) |
| *Corvidae* | | | | | | | |
| Cyanocorax violaceus | o | 1 | 2 | 3 | 4 | 262 | |
| *Troglodytidae* | | | | | | | |
| Campylorhynchus turdinus | i | 1 | 2 | 3 | | 33 | |
| (Thryothorus coraya | i | | 2 | | | 17 | ) |
| Henicorhina leucosticta | i | | 2 | 3 | 4 | 16 | |
| Microcerculus marginatus | i | 1 | 2 | 3 | 4 | 18 | |
| Cyphorhinus arada | i | | 2 | | | 30 | |
| *Muscicapidae* | | | | | | | |
| Catharus ustulatus | o | | 2 | 3 | 4 | 27 | |
| Catharus minimus | o | | 2 | | 4 | 31 | |
| Turdus lawrencii | o | | 2 | 3 | 4 | 68 | |
| Turdus albicollis | o | | 2 | | 4 | 45 | |
| Ramphocaenus melanurus | i | | | 3 | | 10 | |
| Microbates collaris + | i | | | | 4 | 11 | |
| *Emberizidae: Thraupinae* | | | | | | | |
| Cissopis leveriana | o | 1 | 2 | | | 73 | |
| (Hemithraupis flavicollis | o | | 2 | | | 17 | ) |
| Tachyphonus surinamus | o | | | 3 | 4 | 18 | |
| (Thraupis episcopus | o | 1 | | | | 40 | ) |
| Thraupis palmarum | o | 1 | | | 4 | 38 | |
| Ramphocelus carbo | o | 1 | | | | 27 | |
| Ramphocelus nigrogularis | o | 1 | | | | 26 | |

Appendix 1 – continued

| | *Diet* | *Distr* | | | | *Mass* |
|---|---|---|---|---|---|---|
| Euphonia xanthogaster | f | | | 3 | | 14 |
| Euphonia rufiventris | o | | 2 | 3 | 4 | 17 |
| Euphonia chysopasta | f | 1 | | | | 15 |
| Tangara chilensis | f | | 2 | 3 | 4 | 22 |
| Tangara schrankii | o | | 2 | 3 | 4 | 18 |
| Tangara gyrola | o | | | 3 | | 22 |
| Tangara velia | o | | 2 | | | 21 |
| Chlorophanes spiza | o | | | | 4 | 18 |
| *Emberizidae: Cardinalinae* | | | | | | |
| Pitylus grossus | o | | 2 | 3 | 4 | 45 |
| Cyanocompsa cyanoides | o | | | 3 | 4 | 27 |
| Saltator maximus | o | | | | 4 | 46 |
| *Emberizidae: Icterinae* | | | | | | |
| Psarocolius decumanus | o | | 2 | 3 | 4 | 202 |
| Psarocolius angustifrons | o | 1 | 2 | 3 | | 310 |
| (Psarocolius bifasciatus | o | | | 3 | | ) |
| Cacicus cela | o | 1 | 2 | 3 | 4 | 90 |
| Cacicus solitarius | o | 1 | | | | |
| Icterus jamacaii | o | 1 | 2 | | | 59 |

+New species for the country of Ecuador.

[a] Mass taken from Delacour and Amadon (1973). However, no mass was given for *Crax salvini*, so the mass of *C. tomentosa* is indicated in its place.

[b] Mass taken from tags on specimens at the Museo Ecuatoriano de Ciencas Naturales, Quito.

[c] This very large (≤7·5 g), red-lower-mandibled, and often tawny-colored hermit was attributed to *Phaethornis malaris* through correspondence (including measurements and photographs) with R. Bleiweiss and C. Hinklemann. It is either synonymous with *Phaethornis superciliosus moorei* or more properly identified as such (pers. com., R. Ridgely).

## APPENDIX 2

**Additional information concerning Table 3.**
The contingency tables presented in Table 3 require the following information in order to be fully understood or replicated. Data from other areas were chosen on the basis of having ample coverage of a variety of habitats (including intact forest), clear delineation of the habitats used by each species, and availability of diet information.

Two-by-two *G* tests of independence (*d.f.* = 1; Sokal & Rohlf, 1981) were carried out to test the hypothesis that insectivorous species are more likely to be restricted to interior, undisturbed forest than are other species. These tests demonstrate that in all seven cases a significantly higher proportion of insectivorous species was limited to primary forest.

In each case, the species recorded in intact forest were divided in two ways: according to diet; and according to whether or not they were also found in disturbed, or non-forest, habitats. The details of how species were tallied in each of the seven cases are as follows:

A. Cuyabeno Reserve, Ecuador (present study). Species found during Interior Forest surveys divided according to their presence or absence in Edge Forest (with equal sampling effort). Data from an additional 1-day survey in each zone are also included.

B. Concepción, Bolivia, southern Amazonia (Davis, 1993). Species found in intact forest habitats ('dry semideciduous', 'semihumid semideciduous', or 'gallery' forest) divided according to their presence or absence in other local habitats (including 'forest edge' and 'forest islands').

C. Mirití-Paraná Watershed, Colombian Amazon (Andrade & Rubio-Torgler, 1994). Species mist-netted in 'undisturbed understory' of terra firme forest divided according to whether or not they were also captured in 'young secondary growth' of abandoned slash-and-burn agricultural fields.

D. Colombia (Hilty & Brown, 1986). Species found within lowland (<500 m) rain forests ("wet", "humid", "terra firme", "várzea", "swamp", and "sandy belt" forests) divided according to presence or absence in other habitats (including edges and borders of the above forests). Diet classification follows Karr *et al.* (1990), with extrapolation within genus for 13% of species, extrapolation within family in 0·6% of species. In 12% of species, diet was classified according to information given by Hilty & Brown (1986), which was given priority over the former source in cases of conflicting information. Species with insufficient information on diet or habitat use were omitted.

E. Peru (parker *et al.*, 1982). Species found in 'humid terra firme forest' or 'humid low-lying forest' divided according to presence or absence outside of interior humid forest habitats. Species indicated with simply a '+' (i.e. >3 habitats) were included only if registered from forest in Manu National Park (Karr *et al.*, 1990). Diet classification according to Terborgh et al. (1990) and secondarily Karr *et al.* (1990). In addition, the diets of 12% of the species were extrapolated within genus, 3% within family, and 0·4% were classified according to Hilty and Brown (1986). One species was omitted due to lack of diet information.

F. Australia (Pizzey, 1980). Species found in 'tropical rainforest' divided according to their presence or absence in other habitats.

G. Madagascar (Langrand, 1990). Species found in 'rainforest' divided according to their presence or absence in other habitats. Diet was extrapolated within genus for six species, and within family for one species.