RESPONSES OF UNDERSTORY RAIN FOREST BIRDS TO ROAD EDGES IN CENTRAL AMAZONIA

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Abstract. In the lowland tropical rain forest of central Amazonia, I investigated the responses of understory bird communities to forest edges bordering a narrow (<40 m width), unpaved road. From 3681 mist-net captures, bird abundance and composition were examined at three distances (10, 70, and 130 m) from forest edge. The degree to which regrowth vegetation along forest borders reduced edge effects was also assessed by contrasting bird communities near roads with varying levels of regrowth.

Forests near road margins had reduced canopy cover and height and higher numbers of fallen trees than did forest interiors. Bird communities near forest edges also differed markedly from those in forest interiors. Total bird captures and captures of insectivores increased with distance from edge, whereas captures of frugivores and nectarivores did not vary significantly. Mature regrowth on edges significantly increased the captures of insectivores. When insectivorous birds were divided into feeding guilds, birds in six of eight guilds showed significant responses to distance from edge; five of these had fewer captures near road margins whereas one guild (edge/gap specialists) had higher captures. For most guilds, significant alterations in abundance and species composition were evident within 10–70 m of road margins.

My results suggest that the majority of Amazonian understory birds respond negatively to artificial edges created by a narrow, unpaved road. Forest regrowth along road margins alleviated negative edge effects for only a limited subset of forest-dependent species.

Key words: Amazon; avian guilds; community structure; edge avoidance; edge effects; habitat fragmentation; linear barriers; lowland tropical rain forest; rain forests; roads; understory birds.

INTRODUCTION

Road construction is considered one of the most important tools for social and economic development in rural areas, but roads also can lead to significant increases in deforestation (Chomitz and Gray 1996, Laurance et al. 2002a). In Brazil, the network of paved roads doubled in the 1980s (from 87 000 to 161 500 km), with deforestation in southern and eastern Amazonia rising dramatically during this period (Fearnside 1993). To date, central Amazonia has seen relatively limited deforestation, but this is likely to change with ~7500 km of new paved roads (Cavalho et al. 2001, Laurance et al. 2001) and a dramatic expansion of logging (Verissimo et al. 2002) and industrial soybean farming (Fearnside 2001) planned for the Brazilian Amazon.

Roads can have direct and indirect effects on wildlife and their habitat. Direct effects include the initial habitat loss and animal mortality from collisions with cars (Forman et al. 2002). Indirect effects include edge-related changes in microclimate and habitat structure

of the adjoining forest, which may alter the movements and distribution of wildlife (Forman et al. 2002; Laurance et al., *in press*). In tropical rain forests, many environmental variables are altered near forest edges that border agricultural clearings, especially within the first 100 m of the edge (Laurance et al. 1997, 2002b). Solar radiation, temperature, and wind turbulence increase markedly in clearings and along forest margins (Kapos 1989, Williams-Linera 1990). In response to these changes, vegetation structure, floristic composition, and wildlife communities also may be altered in forests near the edge (Lovejoy et al. 1986, Williams-Linera 1990, Malcolm 1994, Didham 1997, Laurance et al. 1997, 1998, 2002b, Restrepo and Gomez 1998).

A newly formed forest edge is structurally open and thereby permeable to fluxes of heat, wind, and light. As edges age, however, their vegetation structure changes, with lateral expansion of tree crowns and the rapid growth of vines and pioneer trees tending to "seal" the edge, reducing the penetration of hot, desiccating winds and sunlight into the forest (Camargo and Kapos 1995, Didham and Lawton 1999, Mesquita et al. 1999). Where edges are not maintained by constant clearing or burning, forest regrowth may gradually extend into the cleared area, changing the edge habitat from an abrupt edge into a more gradual one, and creating an environmental buffer (Murcia 1995).

In response to such changes, rain forest animals may demonstrate a different response to abrupt edges than to more gradual, buffered edges.

The responses of Neotropical birds to artificial forest edges have been studied in the montane forests of Colombia (Restrepo and Gomez 1998) and lowland forests of Amazonia (Quintela 1986, Canaday 1996; Laurance et al., *in press*). Although results have varied somewhat (based partly on differences in avian communities and sampling methods), understory insectivores consistently have been found to be particularly sensitive to edge effects and other forms of forest disturbance (e.g., Lovejoy et al. 1986, Thiollay 1992, Stouffer and Bierregaard 1995, Sieving and Karr 1997, Stouffer and Borges 2001). To date, however, only three published studies have described the responses of Neotropical birds to road edges. These include a comparison of species richness at road edge and interior sites in Amazonian Ecuador (Canaday and Rivadeneyra 2001) and studies of across-road movements by understory birds (Laurance et al., *in press*) and mixed-species flocks (Develey and Stouffer 2001) in the central Brazilian Amazon.

In this study, I use extensive mist-netting data to compare capture rates of understory birds at different distances from road edges, and at sites with differing edge habitats. I focus on the following questions. Do capture rates of understory bird species and foraging guilds vary as a function of distance to forest edge? Do birds respond differently to cleared vs. buffered edges? Can edge-related changes in forest habitat explain the responses of bird communities to road edges?

METHODS

Study area

This study was undertaken as part of the Biological Dynamics of Forest Fragments Project (BDFFP), located 80 km north of Manaus, Brazil (60°00' W, 2°20' S; Lovejoy et al. 1986). The area supports nonflooded lowland tropical rain forest, which averages 28–35 m in height with emergents reaching 55 m. The understory is relatively open and dominated by palms. The soils are yellow latosols derived from ancient parent material, and are nutrient poor and highly acidic (Chauvel et al. 1987). Rainfall ranges from 1900 to 3500 mm/year and is quite seasonal, with a wet season from January to April and a dry season from June to September (Laurance 2001).

In the BDFFP study area, a 20-year-old road clearing of 30–40 m width bisects continuous rain forest for a distance of >40 km. Regrowth vegetation has regenerated along much of the road margin and varies in height and complexity in response to clearing frequency. Three different levels of forest regeneration (Fig. 1) were examined in this study:

1) *cleared-road sites*, which support a small amount of regrowth (<3 m in height) that extends ~7 m from the primary forest borders on each side of the road, resulting in a clearing width of ~25 m;

2) *intermediate-regrowth sites*, which support regrowth of 3–8 m in height that extends ~14 m into each road verge, leaving a clearing of ~12 m in width;

3) *tall-regrowth sites*, which support regrowth 15–20 m in height that extends in a discontinuous canopy across the entire road clearing, with some canopy gaps of 2–3 m width.

Road traffic in the study area is restricted to authorized vehicles and averages just 6–10 passes per week.

To determine the positions of study sites, a 13 km long segment of the road was stratified along its length into the three regrowth classes just described (which were irregularly distributed along the road). Two replicate sites were randomly positioned in each regrowth class, with a minimum distance of 500 m between adjoining sites. Strongly curved segments of the road were avoided, because these would have confounded the grid sampling design.

Understory birds and their foraging guilds

The central Amazon rain forest supports a diverse avifauna, with 394 species detected in the vicinity of my study area (Cohn-Haft et al. 1997). Insectivorous species, particularly antbirds (Formicariidae), dominate the understory community (Bierregaard 1990). The most common insectivorous species have been placed into guilds according to their foraging behavior and habitat use (Stouffer and Bierregaard 1995, Cohn-Haft et al. 1997). Army ant followers are the most frequently captured guild, composed of three obligate species that feed almost exclusively on insects fleeing army ant swarms (Willis and Oniki 1978). Another common guild is mixed-species flocks, which are assemblages of 10–20 species pairs that forage and travel together (Powell 1989). More than a dozen species can occur within a flock at any one time, although the degree of flocking propensity varies, with species typically being separated into "core" and "regular" members (Jullien and Thiollay 1998). Many other understory species maintain a territory as a pair or family, yet occasionally join ant followers and mixed-species flocks when they pass through their territories (Harper 1987, Powell 1989). Among these nonflocking species, birds are divided on the basis of their habitat use into three guilds: terrestrial species that forage in the leaf litter and rarely fly as they forage; edge/gap species that prefer forest ecotones and treefall gaps; and solitary understory species that glean foliage or sally to capture insects in the understory.

Sampling methods for birds

At six study sites, bird abundance data were collected using mark–recapture methods in large (4.5-ha) mist-netting grids. Each grid was composed of six parallel lines that were 60 m apart and 150 m in length (Fig. 2), with the road being located in the center of the grid
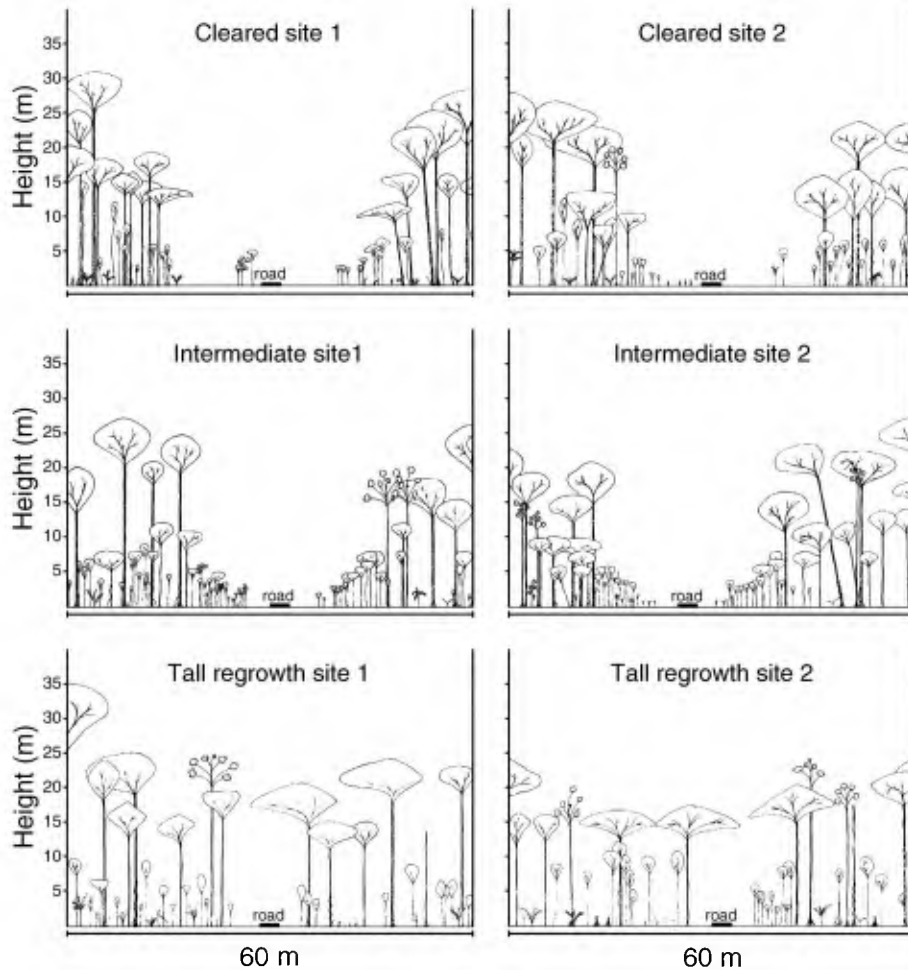
FIG. 1. Vegetation profiles for six study sites in central Amazonia. Profiles were located at the center of each mist-netting plot.

and the net lines parallel to the road. Duplicate net lines occurred at three different distances from the forest–road boundary: edge net lines (10 m from the primary forest edge), middle lines (70 m from edge), and interior net lines (130 m from edge). This sampling design was also used to assess the frequency of bird movements among net lines in the forest vs. across the road (Laurance et al., *in press*).

In this study, I sampled birds only up to 130 m from road edges, for two reasons. First, in a preliminary study of a forest edge bordering pasture, Quintela (1986) found that most changes in bird communities occurred within 50 m of the edge. Second, edge-related changes in forest microclimate and structure near narrow (≤40 m wide) road clearings were expected to be smaller in scale and intensity than those near large agricultural clearings; even near large clearings, most edge effects occur within the first 100 m of edges (Laurance et al. 1998, 2002b). In each grid, long net lines (totalling ~150 m in length) were used to sample as great a length of road and local habitat variation as
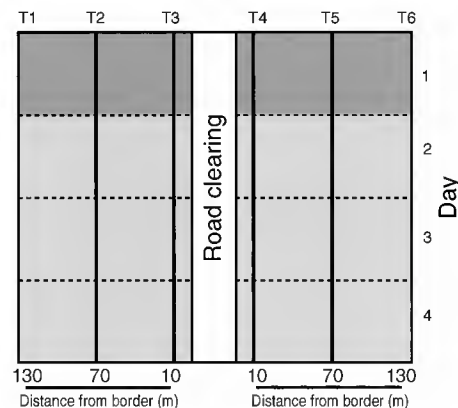

FIG. 2. Design of mist-netting plots established at each study site in central Amazonia. Net lines represented by bold vertical lines were numbered T1–T6 and were separated by 60-m distances. Mist nets were opened in sections over a four-day period as illustrated on the right-hand side of the figure.

possible, and to maximize bird captures, especially of uncommon species.

For all six study sites, the total area sampled was 27 ha (the effective trapping area, including captures of birds whose home ranges were on the margins of the study grids, would have been larger than the area actually sampled). Notably, my samples covered 1800 m each of edge (10 m), middle (70 m), and forest-interior (130 m) habitat.

Each site was netted for four consecutive days, using standard-sized mist nets (36-mm mesh size, 2 × 12 m). On each day, three adjoining mist nets were opened on each of the six net lines (18 nets per day). At the end of each day, nets were moved to new adjoining locations along the line, to be opened the following morning. Nets were opened at 0600 hours for eight hours on the first day and six hours on the following days, except on a few occasions when heavy rain required nets to be closed early. Sites were sampled five times each from November 1997 to November 1999, with an interval of 2–8 months between samples. All sites had one wet-season sample (March–April), two early-dry-season samples (May–July), and two late-dry-season samples (September–November). Nets were checked every 1–1.5 h, and captured birds were identified, weighed, measured, and given uniquely numbered leg bands. Bird age was determined whenever possible from plumage, eye color, bill length, the presence of gape flanges, and the degree of skull ossification.

Forest structural and floristic variables

At each study site, forest structure was described by preparing vegetation profiles perpendicular to the road and by collecting forest structural and floristic data at each mist-net location. Vegetation profiles were used to illustrate typical physiognomic differences among study sites having cleared edges, intermediate regrowth, and tall regrowth (Fig. 1). Profiles were 60 m long, commencing at one edge mist-net line and running across the road to the next edge line, and situated at the center of each sampling grid. Every canopy tree and sapling that overlapped the profile transect was mapped, including its position along the transect, canopy size, and height. The height and position of all smaller plants of >1.5 m height were also recorded within a 2 m wide band along the transect.

Data on 15 habitat variables were collected at each mist-net site (72 points per grid), with 12 samples arrayed evenly along each net line. Nine structural variables were considered to be potential indicators of edge-related microclimatic changes and treefall disturbances (Laurance et al. 1998, 2002b): canopy height (mean and standard deviation); percent vegetation cover for canopy, subcanopy, understory, and ground layers; percent cover of lianas and fallen logs/wood debris; and leaf litter depth. I also recorded slope and the density of five understory plant families that were either common in forest interiors (Arecaceae [palms], Heli-

coniaceae [Heliconia spp.], Marantaceae) or abundant in treefall gaps and near forest edges (Melastomataceae, Cecropiaceae [Cecropia spp. and Pourouma spp.]).

I visually estimated canopy height, using a 4-m pole as a reference. To ensure consistency, I resampled some sites and consistently found that all measurements were within 2–3 m of one another. These data were used to estimate the mean and standard deviation of canopy height for each net line. Canopy (>18 m height), subcanopy (4–18 m height), understory (1–4 m height), and ground (<1 m) cover involved visually estimating percent cover within each stratum within an imaginary, 6 m radius cylinder that was divided into four equal sections. The same method was used to estimate the percent cover of logs/wood debris (>10 cm diameter) on the forest floor. Liana abundance was estimated as percent cover of stems and foliage within each 6 m radius circle. Four litter-depth measurements were taken near each mist-net site at random locations, using a pointed stick that was jammed into the soil; the number of leaves that the stick penetrated were counted and used as an index of litter depth. For the five indicator plant families, all individuals were counted within a 4 m radius circle at each point. For all variables, mean values were calculated for each net line (the average of 48 individual estimates per line), yielding data for 36 sites in total (6 net lines × 6 grids = 36 lines).

Data analysis

For each study site, I estimated the mean abundance of each bird species at three distances from the road (10, 70, and 130 m). These values were generated by combining data from each pair of net lines (on opposite sides of the road) that were at equal distances from the road, and averaging across all sampling intervals. Values were standardized to the number of captures per 1000 mist-net hours; same-day recaptures were excluded from analyses (Table 1). I employed nonmetric multidimensional scaling (NMS) to identify major gradients in bird community composition, using the PC-ORD package (McCune and Mefford 1999). Data were not transformed prior to analysis. Monte Carlo randomization tests (100 runs) were used to determine whether ordination axes explained significantly more variation than expected by chance. The randomization test of the NMS solution was only significant after removal of rare species (captured at <3 sites); this reduced the total number of species examined from 116 to 76. When testing for correlations between individual bird species and ordination axes, Bonferroni-corrected alpha values were used to reduce the experiment-wise error rate. For each ordination axis, the effects of distance to forest edge and edge habitat type (cleared, intermediate, and tall-regrowth edges) were tested using two-way ANOVAs. For significant ANOVAs, post hoc comparisons of sample means were made with Tukey's hsd tests.

TABLE 1. Foraging guild classification, average capture rate (number per 1000 mist-net hours), and edge responses of central Amazonian bird species, captured in six primary rain forest sites adjacent to a small (30–40 m wide) unpaved road.

Foraging guild and species	Capture rate		Edge response†
	Edge	Interior	
Army ant-following			
Dendrocincla merula	0.812	0.919	−
Gymnopithys rufigula	1.566	2.249	−
Pithys albifrons	3.987	8.405	−
Canopy insectivores			
Attila spadiceus	0.117	0.000	+
Bucco tamatia	0.116	0.038	+
Campephilus rubricollis	0.039	0.000	+
Celeus elegans	0.114	0.078	+
Coereba flaveola	0.000	0.000	?
Lanio fulvus	0.114	0.039	+
Pachyramphus marginatus	0.000	0.039	−
Pitylus grossus	0.114	0.039	+
Rhytipterna simplex	0.000	0.075	−
Tachyphonus cristatus	0.036	0.038	0
Tolmomyias assimilis	0.036	0.078	−
Veniliornis cassini	0.077	0.000	+
Edge and gap insectivores			
Automolus ochrolaemus	0.228	0.266	−
Cercomarca tyrannica	0.000	0.039	−
Cyanocompsa cyanoides	0.191	0.194	0
Galbula albirostris	1.400	0.683	+
Hypocnemis cantator	0.940	0.495	+
Lophotriccus galeatus	0.000	0.000	?
Monasa atra	0.000	0.075	−
Percnostola rufifrons	2.069	0.841	+
Tachyphonus surinamus	0.302	0.259	+
Thryothorus coraya	0.112	0.078	+
Troglodytes aedon	0.039	0.000	+
Frugivores			
Catharus fuscescens	0.000	0.036	−
Corapipo gutturalis	0.194	0.116	+
Crypturellus variegatus	0.039	0.000	+
Geotrygon montana	0.947	1.060	−
Odontophorus gujanensis	0.000	0.000	?
Phoenicircus carniflex	0.000	0.039	−
Pipra erythrocephala	0.457	0.270	+
Pipra pipra	3.303	2.661	+
Pipra serena	0.536	0.495	+
Ramphastos vitellinus	0.000	0.038	−
Schiffornis turdinus	0.494	0.599	−
Trogon rufus	0.000	0.037	−
Trogon violaceous	0.000	0.038	−
Turdus albicollis	0.613	1.303	−
Mixed-species flocks, core members			
Hylophilus ochraceceips	0.000	0.945	−
Myrmotherula gutturalis	0.694	0.903	−
Myrmotherula longipennis	0.380	0.958	−
Myrmotherula menetriesii	0.348	0.417	−
Philydor erythrocercus	0.039	0.306	−
Piculus flavigula	0.000	0.000	?
Thamnomanes ardesiacus	0.614	2.387	−
Thamnomanes caesius	0.723	1.636	−
Xiphorhynchus pardalotus	1.413	0.870	+
Mixed-species flocks, regular members			
Automolus infuscatus	0.345	1.206	−
Deconychura longicauda	0.149	0.190	−
Deconychura stictolaema	0.310	0.799	−
Glyphorynchus spirurus	2.590	3.059	−
Myiobus barbatus	0.570	0.987	−
Myrmotherula axillaris	0.571	0.188	+
Rhynchocyclus olivaceus	0.077	0.192	−
Xenops minutus	0.224	0.152	+

TABLE 1.   Continued.

Foraging guild and species	Capture rate		Edge response†
	Edge	Interior	
Midstory insectivores			
Bucco capensis	0.116	0.038	+
Campylorhamphus procurvoides	0.039	0.039	0
Cymbilaimus lineatus	0.039	0.000	+
Dendrocolaptes certhia	0.155	0.000	+
Dendrocolaptes picumnus	0.000	0.000	?
Hemitriccus zosterops	0.039	0.000	+
Hylexetastes perrotii	0.230	0.073	+
Jacamerops aurea	0.038	0.000	+
Laniocera hypopyrrah	0.039	0.000	+
Momotus momota	0.039	0.452	−
Nonnula rubecula	0.000	0.077	−
Platyrinchus platyrinchus	0.068	0.500	−
Sittasomus griseicapillus	0.039	0.000	+
Terenotriccus erythrurus	0.282	0.153	+
Thamnophilus murinus	0.337	0.187	+
Nectarivores			
Campylopterus largipennis	0.382	0.039	+
Florisuga mellivora	0.000	0.037	−
Heliothryx aurita	0.000	0.077	−
Phaethornis bourcieri	0.879	0.310	+
Phaethornis ruber	0.000	0.000	?
Phaethornis superciliosus	0.493	0.346	+
Thalurania furcata	0.269	0.419	−
Terrestrial insectivores			
Arremon taciturnis	0.039	0.074	−
Conopophaga aurita	0.000	0.116	−
Corythopis torquata	0.153	0.268	−
Cyphorhinus arada	0.000	0.147	−
Formicarius analis	0.000	0.075	−
Formicarius colma	0.495	1.067	−
Grallaria varia	0.000	0.037	−
Hylopezus macularis	0.000	0.154	−
Myrmeciza ferruginea	0.264	0.421	−
Myrmornis torquata	0.000	0.268	−
Myrmothera campanisona	0.000	0.038	−
Sclerurus caudacutus	0.039	0.075	−
Sclerurus mexicanus	0.000	0.039	−
Sclerurus rufigularis	0.039	0.340	−
Solitary understory insectivores			
Automolus rubiginosus	0.073	0.304	−
Choroceryle aenea	0.000	0.039	−
Dendrocincla fuliginosa	0.796	0.424	+
Frederickena viridis	0.000	0.039	−
Hylophylax naevia	0.229	0.075	+
Hylophylax poecilinota	0.948	2.997	−
Malacoptila fusca	0.077	0.566	−
Microbates collaris	0.307	0.975	−
Microcerculus bambla	0.377	0.114	+
Myrmotherula guttata	0.039	0.903	−
Onychorhynchus coronatus	0.039	0.152	−
Philydor pyrrhodes	0.000	0.000	?
Platyrinchus coronatus	0.000	0.447	−
Platyrinchus saturatus	0.268	0.500	−
Shistocichla leucostigma	0.000	0.000	?
Synallaxis rutilans	0.039	0.000	+

† Key to edge response: +, species increase on edges; −, decrease on edges; 0, no change; ?, insufficient data.

I also assessed whether edge-related changes in habitat variables could explain bird community responses to road edges, using canonical correspondence analysis (CCA), a multivariate technique that identifies principle axes that simultaneously explain the maximum amount of variation in two different data matrices. In ecological applications, CCA is used most commonly to explore species–environment relationships for communities of plants and animals (McCune and Mefford 1999). Because CCA is based on parametric data assumptions, bird species abundances were $\log(x + 1)$-transformed before analysis. CCA solutions were com-

○ Edge, cleared   ● Middle, cleared   ● Interior, cleared
⊔ Edge, intermediate   ■ Middle, intermediate   ■ Interior, intermediate
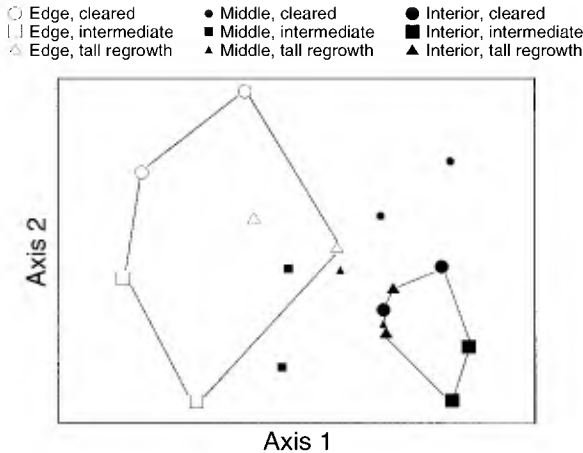△ Edge, tall regrowth   ▲ Middle, tall regrowth   ▲ Interior, tall regrowth

FIG. 3. An ordination of bird communities at three different distances from a small, unpaved road with varying levels of roadside regrowth. Three sets of sites are delineated: edge sites (open symbols linked by solid lines), middle-distance sites (small filled symbols), and forest-interior sites (large filled symbols linked by solid lines). Axis 1 distinguishes an edge-to-interior gradient, with edge sites clustered to the left-hand side of the figure and interior sites clustered to the right. Middle-distance sites overlap these two distinct groups. Axis 2 illustrates differences among bird communities near roads bordered by cleared edges (circles), intermediate regrowth (squares), and tall regrowth (triangles).

pared to results from Monte Carlo tests (100 runs) to determine if the analysis captured more variation than expected by chance. The habitat data in the CCA analysis consisted of a site-by-attribute matrix based on the 15 habitat parameters collected at each net line.

Finally, I examined the effects of edge distance and edge habitat type on total species richness and total bird abundance, and on the species richness and abundance of eight foraging guilds (Table 1), using two-way ANOVAs followed by Tukey's tests when significant. Standardized abundance data (captures per 1000 mist-net hours, excluding same-day recaptures) were $\log(x + 1)$-transformed prior to analysis. To reduce pseudoreplication (Hurlbert 1984), data at each site were averaged for pairs of net lines at the three different edge distances: edge (10 m), middle (70 m), and interior (130 m) lines. Guild identifications of birds (Table 1) were based on previous work in my study area (Stouffer and Bierregaard 1995, Cohn-Haft et al. 1997, Develey and Stouffer 2001; M. Cohn-Haft, P. Stouffer and P. Develey, *personal communications*).

RESULTS

Ordination of bird communities

In total, 3681 bird captures (116 species) were recorded in 13 212 mist-net hours of sampling effort. Bird community composition varied strongly in response to distance from edge and type of regrowth bordering the edge. Community composition was summarized by the NMS ordination, which identified two major axes that

collectively explained 91% of the total variation in the data set (Fig. 3). Axis 1, which captured 57% of the variation, clearly described an interior-to-edge gradient in species composition. Bird species that were significantly correlated with Axis 1 (Table 2) included mixed-species flock members such as *Automolus infuscatus*, *Deconychura stictolaema*, *Hylophilus ochraceceips*, *Thamnomanes ardesiacus*, and *Thamnomanes caesius*, and the solitary understory species *Hylophylax poecilinota* and *Platyrinchus coronatus*, all of which occurred mainly at interior and middle net lines. Also associated with Axis 1 was the edge/gap specialist *Percnostola rufifrons*, which was more abundant near edges. As expected, a two-way ANOVA revealed highly significant differences among Axis 1 ordination scores for edge, intermediate, and interior net lines ($F_{2,17} = 22.93$, $P < 0.0003$), with mean values for edge lines differing significantly from those of the middle ($P = 0.004$) and interior ($P < 0.001$) lines (Tukey's tests). Axis I scores were not significantly influenced by regrowth type or its interaction with edge distance.

Axis 2 captured 34% of the total variation in the data set, and appeared to describe a gradient among sites with differing types of regrowth, particularly at edge lines (Fig. 3). Edge lines encompassed the full range of variation along Axis 2, whereas interior lines and sites bordered by intermediate regrowth had low values on Axis 2. Fewer species were significantly correlated with Axis 2 (Table 2). The terrestrial frugivore *Geotrygon montana* and gap-favoring insectivore *Galbula albirostris* were more abundant at sites with cleared borders, whereas sites bordered by intermediate or tall regrowth had more captures of the frugivore *Pipra serena*, the ant follower *Pithys albifrons*, and the mixed-species flock member *Rhynchoclycus olivaceus*. A two-way ANOVA revealed no significant effect on Axis 2 of edge distance, regrowth type, or their interaction.

Canonical correspondence analysis

The CCA of bird species and environmental parameters identified two major axes that explained about

TABLE 2. Significant Pearson correlations of 13 bird species with two ordination axes produced by nonmetric multidimensional scaling.

Species	Axis 1	Axis 2
Automolus infuscatus	**0.758**	−0.284
Deconychura stictolaema	**0.661**	−0.183
Galbula albirostris	−0.304	**0.651**
Geotrygon montana	0.165	**0.596**
Hylophilus ochraceceips	**0.657**	−0.485
Hylophylax poecilinota	**0.756**	−0.254
Percnostola rufifrons	**−0.811**	−0.005
Pipra serena	−0.231	**−0.655**
Pithys albifrons	0.576	**−0.729**
Platyrinchus coronatus	**0.620**	−0.184
Rhynchocyclus olivaceus	0.205	**−0.663**
Thamnomanes ardesiacus	**0.732**	−0.179
Thamnomanes caesius	**0.726**	−0.283

Note: Correlation values in boldface were significant using a Bonferroni-corrected alpha value ($P = 0.00099$).

○ Edge, cleared   ● Middle, cleared   ● Interior, cleared
□ Edge, intermediate   ■ Middle, intermediate   ■ Interior, intermediate
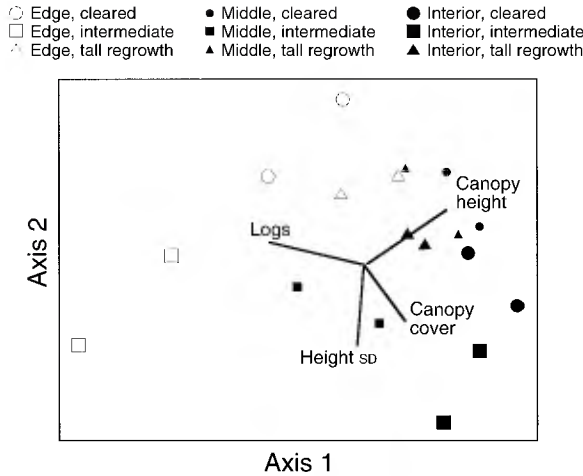△ Edge, tall regrowth   ▲ Middle, tall regrowth   ▲ Interior, tall regrowth

FIG. 4. Responses of central Amazonian bird communities to measured habitat variables, generated by canonical correspondence analysis.

one-third of the total variation (Fig. 4). Fifteen of the 76 bird species included in the analysis, and four of the 15 environmental parameters, were significantly correlated with the CCA axes (Table 3). Axis 1, which explained 17% of the variation in the two matrices, described a gradient in edge distance and habitat disturbance. Interior lines, which tended toward high values on Axis 1, had significantly taller canopies and higher abundances of the mixed-species flock members *Automolus infuscatus*, *Thamnomanes ardesiacus*, and *Thamnomanes caesius*, and of the solitary understory species *Hylophylax poecilinota* and *Microbates collaris*. Edge lines (particularly those bordered by intermediate regrowth) and some middle lines tended toward low values on Axis 1, had significantly more fallen logs, and higher abundances of the nectarivore *Campylopternis largipennis* and the edge specialist *Percnostola rufifrons*.

Axis 2, which captured 14.1% of the total variation, described a gradient in edge regrowth type, which also coincided with variation in forest canopy height and canopy cover (Fig. 4). Sites with cleared borders or with tall regrowth had relatively high values on Axis 2 and high abundances of the edge species *Galbula albirostris*. Intermediate-regrowth sites had low values on Axis 2, a variable canopy height, and high abundances of the understory insectivores *Autmolus rubiginosus* and *Myrmotherula guttata*, the leaf-litter insectivore *Corythopis torquata*, the mixed-species flock member *Hylophilus ochraceceips*, and the frugivore *Pipra serena*.

Effects of edge distance and regrowth on species richness and abundance

Although species richness of birds appeared to increase somewhat with increasing distance from road edge (Fig. 5), there was no significant effect of edge

distance ($F_{2,17} = 1.60$, $P = 0.254$), regrowth type ($F_{2,17} = 0.95$, $P = 0.423$), or their interaction ($F_{2,17} = 0.56$, $P = 0.697$) on species richness. When birds were divided into three trophic categories based on their predominant food type, there was no significant effect of edge distance on the richness of frugivores ($F_{2,17} = 0.12$, $P = 0.888$) or nectarivores ($F_{2,17} = 0.01$, $P = 0.989$), although insectivores did tend to increase in forest interiors ($F_{2,17} = 4.20$, $P = 0.052$). Regrowth type had a significant effect on nectarivores ($F_{2,17} = 7.09$, $P = 0.017$), with sites bordered by intermediate regrowth having greater species richness than those with cleared borders ($P = 0.018$), but it had no significant effect on frugivore ($F_{2,17} = 0.22$, $P = 0.80$) or insectivore ($F_{2,17} = 1.62$, $P > 0.251$) richness. There was no significant interaction between edge distance and regrowth in any comparison.

When the diverse assemblage of insectivorous birds was divided into eight feeding guilds (Table 4), only two guilds (solitary understory species and core members of mixed-species flocks) had species richness that was significantly affected by edge distance and regrowth type. Both guilds had more species on interior than on edge lines, with core flock members also having more species on middle than on edge lines. With respect to edge habitat, more solitary understory species were recorded at sites with intermediate regrowth than at sites with cleared edges. Core flock members, however, had higher species richness at tall-regrowth and cleared-edge sites than at those with intermediate regrowth.

TABLE 3. Pearson correlations for bird species and for habitat parameters with each of two axes, using canonical correspondence analysis.

Species or habitat parameter	Axis 1	Axis 2
Species		
Automolus infuscatus	**0.713**	−0.429
Automolus rubiginosus	0.133	**−0.698**
Campylopternis largipennis	**−0.793**	−0.394
Corythopis torquata	−0.272	**−0.702**
Galbula albirostris	0.001	**0.721**
Hylophilus ochraceceips	0.538	**−0.714**
Hylophylax naevia	−0.701	−0.351
Hylophylax poecilinota	**0.809**	−0.160
Microbates collaris	**0.724**	0.228
Microcerculus bambla	**−0.617**	−0.048
Myrmotherula guttata	0.393	**−0.667**
Percnostola rufifrons	**−0.725**	0.105
Pipra serena	−0.468	**−0.769**
Thamnomanes ardesiacus	**0.784**	−0.156
Thamnomanes caesius	**0.791**	−0.102
Habitat parameter		
Canopy height	**0.523**	0.469
Variation in canopy height	−0.107	**−0.532**
Canopy cover	0.215	**−0.530**
Logs	**−0.602**	0.122

Note: Correlation values in boldface were significant for bird species (using a Bonferroni-corrected alpha level, $P < 0.001$) and for habitat variables ($P < 0.05$).
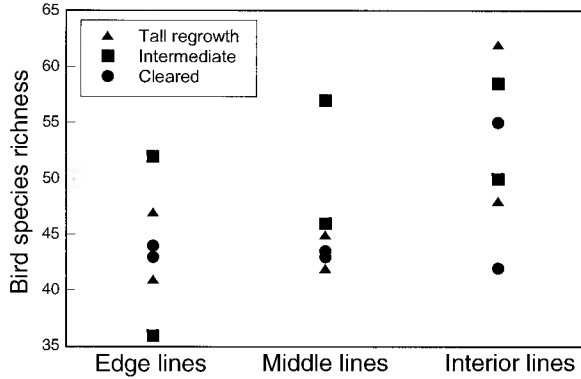
FIG. 5. Species richness of understory birds in relation to edge distance and regrowth type at six sites in central Amazonia.

Total bird abundance (measured as total captures; Fig. 6) varied significantly as a function of distance from forest edge ($F_{2,17} = 10.27$, $P = 0.005$). More birds were captured on interior than on edge ($P = 0.009$) or middle ($P = 0.026$) lines. Regrowth type did not have a pronounced effect on overall bird captures ($F_{2,17} = 3.96$, $P = 0.058$), although there were significantly ($P < 0.05$) more captures at sites bordered by tall regrowth than at cleared-edge sites (Fig. 5). There was no significant interaction between edge distance and regrowth type.

When birds were divided into three trophic groups (Fig. 5), edge distance significantly influenced the abundance of insectivores ($F_{2,17} = 16.30$, $P < 0.0001$), but not frugivores ($F_{2,17} = 0.12$, $P = 0.888$) or nectarivores ($F_{2,17} = 1.35$, $P = 0.307$). Insectivore abundance was significantly higher at interior than at edge ($P < 0.001$) and middle ($P = 0.016$) net lines. Insectivore abundance was also significantly influenced by regrowth type ($F_{2,17} = 5.68$, $P = 0.025$), with sites bordered by tall regrowth having greater abundance than cleared-edge sites ($P = 0.027$), but frugivore ($F_{2,17}$

$= 0.11$, $P = 0.90$) and nectarivore ($F_{2,17} = 1.27$, $P > 0.328$) abundances were unaffected. There was no significant interaction between edge distance and regrowth in any comparison.

When abundances of the eight feeding guilds of insectivores were examined (Table 5), six guilds (all but midstory and canopy species) were significantly affected by distance to road edge. Five of the guilds had significantly higher abundances on interior than edge lines, whereas edge/gap species had an opposite response (Fig. 6). In addition, solitary understory species declined in abundance between the interior and middle lines, and between the middle and edge lines, whereas core members of mixed-species flocks were less abundant on edge than middle lines (Table 4). Thus, five of eight insectivore guilds exhibited significant declines in abundance on edge lines, and solitary insectivores also declined on middle lines relative to interior lines.

Two of the eight insectivore guilds also exhibited significant responses to edge habitat (Table 4). Army ant followers were more abundant on edges bordered by tall regrowth than on cleared edges, whereas core members of mixed-species flocks were more abundant on tall-regrowth edges than those with intermediate regrowth. Core members of mixed-species flocks and solitary understory birds also showed a marginally significant interaction between edge distance and regrowth type (Table 4), possibly because edge avoidance was reduced at sites bordered by tall regrowth.

DISCUSSION

Bird responses to road edges

In the lowland rain forests of central Amazonia, I found that a small (< 40 m wide), unpaved road caused a major alteration in the distribution and abundance of many understory birds. Total bird captures declined significantly near road edges, irrespective of the height and density of regrowth forest adjoining the edge. Many understory insectivores exhibited strong edge

TABLE 4. Results of two-way ANOVAs testing for effects of edge distance and edge habitat type on species richness of eight foraging guilds of insectivorous understory birds in central Amazonia.

Guild	Edge distance			Edge habitat			Distance × habitat	
	$F_{2,17}$	P	Tukey's test P	$F_{2,17}$	P	Tukey's test P	$F_{2,17}$	P
Solitary understory spp.	8.86	0.008	interior > edge, 0.007 middle > edge, 0.046	4.44	0.045	intermediate > clear, 0.046	0.39	0.814
Army ant followers	1.63	0.250		1.55	0.260		0.84	0.530
Mixed-species flock, core	14.50	0.002	interior > edge, 0.002 middle > edge, 0.011	6.82	0.016	tall > intermediate, 0.024 clear > intermediate, 0.031	4.02	0.039
Mixed-species flock, reg.	2.43	0.143		1.03	0.396		0.38	0.815
Edge/gap spp.	1.42	0.290		1.08	0.380		1.77	0.21
Terrestrial spp.	3.29	0.085		0.33	0.735		0.81	0.55
Midstory spp.	3.29	0.085		0.75	0.49		0.64	0.650
Canopy spp.†								

† Data are insufficient for two-way ANOVAs.

avoidance, with captures of army ant followers, solitary species, members of mixed-species flocks, and terrestrial species declining sharply near road margins, whereas edge/gap specialists increased near the road. Species richness was also found to decline near edges for two insectivorous guilds, solitary understory species and mixed-species flocks. Frugivores, nectarivores, and canopy and midstory insectivores did not vary significantly in richness or abundance as a function of distance to forest edge.

Over what distance did edge avoidance occur? Birds in four guilds (army ant followers, terrestrial species, and regular and core members of mixed-species flocks) exhibited a significant decline in abundance within 10 m of the road, relative to forest interiors. A fifth guild, solitary understory species, declined in abundance within 70 m of the road. These results suggest that edge avoidance was strongest within the first 10–70 m of the road margin (Fig. 6), where the margin is defined as the edge of primary forest (not including adjoining regrowth forest along road verges). This guild-based interpretation accords with the ordination analysis of avian community structure, based on 76 commonly captured species (Fig. 3). In this analysis, the high similarity among bird communities at interior net lines (130 m from the road) is evidenced by their close clustering, irrespective of adjoining edge habitat. Edge lines (10 m from the road) showed greater variation in community composition (Fig. 3), and were grouped in accordance with their type of bordering regrowth. At 70 m from the edge, the bird community at middle lines was generally more similar to that at interior than edge lines. Bird communities on edge lines bordered by tall regrowth overlapped somewhat with those on middle lines, suggesting that edges adjoined by mature regrowth supported a bird assemblage that was more similar to sites 70 m from the edge than those 10 m from the edge (Fig. 3).

In general, my results accord with those of several other studies in the Amazonian lowlands, which have found that understory insectivores are highly vulnerable to habitat modification. For example, Quintela (1986) studied a single edge bordered by a large clearing in my study area in central Amazonia, and found higher captures of all insectivores, ant followers, and mixed-species flocks at 50 m than at 10 m from forest edge. In Amazonian Ecuador, species richness of insectivorous birds (Canaday 1996) and terrestrial insectivores (Canaday and Rivadeneyra 2001) was significantly higher at forest interiors than near road and clearing edges, whereas the richness of frugivores and omnivores did not vary significantly. Working along the same unpaved road that I studied, Develey and Stouffer (2001) found that the home range boundaries of mixed-species flocks were often aligned with the road border. My results extend Develey and Stouffer's findings and suggest that, although mixed-species flocks can use edge habitat near the road, they are much more frequently captured in the forest interior (130 m from the road) than near forest edge.

However, the results of a study in montane forest fragments in Colombia were rather different from mine and the other Amazonian studies. Restrepo and Gomez (1998) found that total bird captures and captures of frugivores did not differ significantly between forest edges (0–10 m) and interiors (190–200 m), but declined at intermediate distances (30–40 and 60–70 m) from edge. Insectivores also had high capture rates at edges and interiors, and declined significantly at intermediate sites relative to interior sites. The reasons for these differences between the Colombian and Amazonian studies are unknown, but might relate in part to a smaller proportion and diversity of insectivores in montane regions relative to the Amazonian lowlands.

Effects of regrowth along road edges

For some guilds, regrowth bordering the road clearly reduced edge avoidance. First, on edges bordered by tall regrowth, core members of mixed-species flocks did not decline as sharply in abundance as they did on edges with little or intermediate regrowth; in fact, I often observed members of this guild foraging in tall regrowth along road verges. Second, army ant followers were captured more frequently on edges bordered by intermediate and tall regrowth than along cleared edges. Third, although solitary understory insectivores exhibited the most extreme edge avoidance of all guilds (occurring in very low numbers near edges, irrespective of the adjoining habitat) their numbers at middle net lines (70 m from the edge) were nearly as high as those in forest interiors when the edge was bordered by tall regrowth. At sites lacking tall regrowth, however, their capture rates at middle lines were significantly depressed (as reflected by a significant interaction between edge distance and regrowth type; Table 5). Finally, captures of nectarivores were relatively high along edges with intermediate regrowth, which appeared to reflect a greater abundance of flowering plants in those areas. Thus, for some guilds, tall regrowth along roads evidently functions as an environmental buffer, and may even augment their food resources. In my study area, regrowth adjoining forest edges also has been shown to reduce the intensity of edge-related changes in forest microclimate (Didham and Lawton 1999) and tree mortality (Mesquita et al. 1999).

Edge-related environmental changes

The specific mechanisms responsible for edge avoidance in understory birds remain poorly understood. For some species, food abundance may decline near edges, so that birds either avoid edges or have larger territories to compensate for fewer resources. In Amazonian forest fragments, changes in microclimate (Kapos 1989) and forest structure (Laurance et al. 1998) are most pronounced within 60 m and 100 m of forest edges,

Legend (All birds panel):
- ● Cleared
- ■ Intermediate
- ▲ Tall regrowth

Y-axis (overall): Capture rate (no. captures/1000 mist-net hours)

X-axis: Distance from edge (m)

Panel titles:
- All birds
- Terrestrial spp.
- Insectivores
- Edge/gap species
- Frugivores
- Midstory spp.
- Nectarivores
- Canopy spp.
- Solitary understory spp.
- Mixed-species flock, core spp.
- Ant followers
- Mixed-species flock, regular spp.

TABLE 5. Results of two-way ANOVAs testing for effects of edge distance and edge habitat type on abundances (capture rates) of eight foraging guilds of insectivorous understory birds in central Amazonia.

Guild	Edge distance			Edge habitat			Distance × habitat	
	$F_{2,17}$	P	Tukey's test P	$F_{2,17}$	P	Tukey's test P	$F_{2,17}$	P
Solitary under-story spp.	75.00	0.000	interior > edge, <0.001 interior > middle, <0.001 middle > edge, <0.001	3.40	0.079		3.57	0.052
Army ant follow-ers	6.39	0.019	interior > edge, 0.017	4.45	0.045	tall > clear, 0.047	1.24	0.359
Mixed-species flock, core	17.19	0.001	interior > edge, <0.001 middle > edge, 0.025	5.28	0.030	tall > intermediate, 0.038	3.63	0.050
Mixed-species flock, reg.	4.85	0.037	interior > edge, 0.041	2.91	0.106		0.79	0.562
Edge/gap spp.	4.67	0.041	edge > interior, 0.048	1.20	0.347		1.26	0.354
Terrestrial spp.	6.38	0.019	interior > edge, 0.016	0.32	0.735		0.44	0.778
Midstory spp.	0.37	0.701		0.06	0.944		0.33	0.845
Canopy spp.	1.03	0.395		0.27	0.768		0.37	0.823

respectively. Despite the fact that my study sites bordered only a narrow road clearing, the interior lines had significantly taller forest with more canopy cover, whereas edge lines were more disturbed, with higher abundances of fallen logs. Some insect groups decline in abundance in drier microhabitats (Janzen and Schoener 1968, Shelly 1988) like forest edges (Kapos 1989), but the increased leaf flush and wood debris near forest edges (Lovejoy et al. 1986; Nascimento and Laurance, *in press*) may attract more herbivorous insects and wood-boring larvae. In fact, in forest fragments in my study area, insect biomass and the abundance of overstory, understory, and leaf litter species generally increase near forest edges (Fowler et al. 1993, Didham 1997). Edge-related declines in habitat quality may have caused breeding Ovenbirds (*Seiurus aurocapillus*) in temperate forests to have territories that were 25% larger near road edges than in forest interiors (Ortega and Capen 1999). However, at least for mixed-species flocks in my study area, home range size did not differ significantly between interior sites and road edges (Develey and Stouffer 2001).

Understory birds might also avoid forest edges because of increased competition from edge or invasive species, or from canopy and midstory species that forage at lower vertical levels along forest margins (Cohn-Haft 1995). However, I found no detectable increase in captures of canopy and midstory species between edge lines and interior lines, suggesting that they were unlikely to displace understory birds near edges. Invasive species also appeared unimportant, as only a single capture of a species not associated with rain forest (House Wren, *Troglodytes aedon*) was recorded. Edge- and gap-favoring species, however, clearly did increase near edges, and might have reduced edge use

by some forest-interior species. Comparable results were observed along an 80 m wide power line clearing in Tennessee, where bird species of edge and open habitats increased substantially in abundance near forest borders (Kroodsma 1982).

Finally, understory birds may exhibit a psychological avoidance of open or edge habitats (Greenberg 1989), possibly because of elevated predation pressure in those environments (e.g., Gates and Gysel 1978, Paton 1994). For example, in a related study, I found that road clearings strongly inhibited local bird movements at five of my six study sites (Laurance et al., *in press*). At a guild level, there was a strong, positive correlation between edge avoidance and the degree to which local movements across the road were reduced; movements of edge/gap and frugivorous species were not inhibited, whereas those of most forest-dependent insectivores (mixed-species flocks, terrestrial species, solitary understory species, army ant followers) were sharply reduced. Thus, two distinct but interrelated behavioral mechanisms, edge avoidance and clearing avoidance, collectively impeded road-crossing movements of sensitive species (Laurance et al., *in press*).

CONCLUSIONS

My results demonstrate that forest edges bordering a small, unpaved road with very little traffic had an important structuring effect on the understory bird community in central Amazonia, with the abundance of several insectivore guilds declining significantly within 10–70 m of road margins. Species and guilds that avoided forest edges usually exhibited significantly reduced movements across the road (Laurance et al., *in press*). Road avoidance on similar roads with higher traffic volumes, and hence more noise, dust, and dis-

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FIG. 6. Abundances of Amazonian understory birds and their foraging guilds in response to edge distance and edge habitat type, based on mist-netting capture rates (mean ± 1 SE). Note the different *y*-axis scales for each guild.

lurbance, could be even greater than that observed in this study.

Although a single, narrow road is unlikely to have major demographic impacts on local bird communities, ~43 000 km of unpaved roads and 5000 km of paved highways currently ramify throughout the Brazilian Amazon (S. Bergen, *personal communication*). If edge disturbances are conservatively assumed to penetrate 50 m into forests along each road margin, then ~4.8 × 10⁵ ha of potential habitat would be affected for understory birds. Although individual roads are unlikely to cause the local extinction of understory birds, prevailing land uses in Amazonia, such as mechanized logging (Thiollay 1992) and forest colonization projects (Laurance 1998), create high-density labyrinths of roads and clearings that could have far greater effects. Moreover, clearings for paved highways, power lines, and gas lines are typically much wider (> 80 m) than the narrow clearing that I examined, and are likely to have more deleterious effects on forest-interior birds. My findings suggest that roads and other linear clearings should be greatly minimized in tropical conservation areas. In addition, these results highlight the potentially serious environmental impacts of dramatically increased road and highway development currently being undertaken in Brazil (Laurance et al. 2001, 2002a) and other Amazonian countries.

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