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## RESPONSES OF UNDERSTORY BIRDS TO ANTHROPOGENIC EDGES IN A NEOTROPICAL MONTANE FOREST

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**Abstract.** In a Neotropical montane forest in southwestern Colombia, we investigated how the distribution of understory birds changed from forest edge to forest interior (0–10 m, 30–40 m, 60–70 m, and 190–200 m from the edge) and how these changes were influenced by edge age (three old [ $>40$  yr] and three young [ $<12$  yr] edges) and month sampled. Capture rates of frugivores were highest both at the forest edge (0–10 m) and forest interior (190–200 m); for insectivores, capture rates were highest at the forest interior; for nectarivores, they were highest at the forest edge. Distance, edge age, and month interacted in various ways. Frugivores were more abundant at the forest interior than at the edge during the dry months. Insectivores were more abundant at new edges than at old edges during the wet months. Seventeen out of 25 abundant species ( $\geq 21$  captures), including the *Tangara* spp. assemblage, exhibited a non-uniform distribution, showing either an increase or decrease from forest edge to forest interior, or bimodal distributions. Extremely sparse species (one capture) were found more often than expected near the forest edge (0–10 m).

Edges resulting from large-scale, anthropogenic disturbances influenced the distribution of understory birds in complex ways. Significant interactions between distance, month, and edge age suggest that “edge effects” change over various temporal scales. Instead of emphasizing “depth” of “edge effects,” future studies should emphasize edge dynamics, i.e., how processes taking place at edges change over time, and how organisms can modify any “edge effect.” In particular, changes in the distribution of frugivores suggest that seed dispersal may be influenced by the presence of edges, leading to changes in the structure and location of edges through time. This might be particularly true in our study area, where transient corn fields, pastures, and second-growth areas of various ages are embedded in a forest matrix.

**Key words:** anthropogenic edges; disturbance; feeding guilds; forest fragmentation; frugivores; insectivores; nectarivores; Neotropical montane ecosystems; seed dispersal; understory birds.

### INTRODUCTION

Large-scale natural disturbances have contributed to the high biological diversity found in many tropical ecosystems (e.g., Gentry 1986, Johns 1986, Salo et al. 1986, Bush 1994). Conversely, large-scale anthropogenic disturbances have contributed to the biological impoverishment of these ecosystems (Laurance and Bierregaard 1997). In both cases, one consequence of disturbance is the creation of sharp boundaries or edges that may influence the movement and the distribution of organisms and, thus, the structure and location of edges through time (Wiens et al. 1985, Wiens 1992). For instance, edges may influence the behavior of pollinators and seed dispersers, and thereby affect the distribution of plants along edges.

Edges may influence the behavior of animals directly, through changes in microclimate and the distribution of suitable habitats (Wiens et al. 1985, Kui-

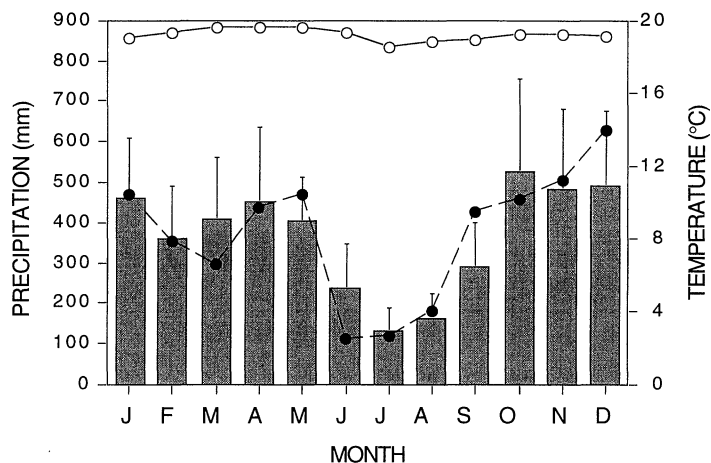
tunen and Mäkinen 1993), and indirectly, through changes in the distribution of parasites and predators (e.g., Gates and Gysel 1978, Brittingham and Temple 1983, Loye and Carroll 1995) and the resource base (Malcolm 1991, 1997). Because some of these factors are highly variable in space and time, it is unlikely that “edge effects” (the maximum distance at which changes induced by edge creation are apparent within forest stands and the disturbed area; Harris 1984, Lovejoy et al. 1986) remain constant. Rather, “edge effects” change over time and, as a result, edges become dynamic elements of landscapes.

We propose that a focus on ecological processes mediated through plant–animal interactions can contribute to our understanding of edge dynamics. Here, we report results of a study aimed at understanding how edges influence the distribution of understory birds in a neotropical montane forest. We asked, in particular, how the distribution of frugivores and nectarivores changed from forest edge to forest interior and how these changes were influenced by edge age and month. Some studies have shown that “edge effects” change with

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FIG. 1. Mean monthly rainfall (bars) and temperature (open circles) (1985–1994) at the Reserva Natural La Planada, Colombia (Reserva Natural La Planada, unpublished data). Solid circles represent mean values of rainfall for 1992–1993.



edge age (Williams-Linera 1990, Blanchard 1992, DeGraaf 1992) and season (Hansson 1983, Noss 1991), yet no study has looked at the combined effect of these two factors, or at their effect on the distribution of organisms mediating plant–animal interactions.

We concentrated on frugivores and nectarivores because high proportions of understory plants in neotropical montane ecosystems rely on them for seed dispersal and pollination (Terborgh 1977, Gentry 1983, Stiles 1985). Thus, changes in the distribution of these two groups of birds may help us to understand how edges influence the distribution of plants in Neotropical montane ecosystems affected by large-scale anthropogenic disturbances.

#### METHODS

##### Study area

We conducted this work at Reserva Natural La Planada and Finca El Bosque, municipality of Ricaurte, department of Nariño, Colombia (78°00' W, 1°10' N; Restrepo 1995). These sites (collectively, “La Planada”) are located at an altitude of 1800 m on the western slope of the Andes, in an area known for a species-rich, endemic avifauna (geographical range <50 000 km<sup>2</sup>; Terborgh and Winter 1983, Orejuela 1987). The study sites are covered by forest interspersed with pastures, second-growth and logged forests, and transient corn fields. At lower elevations, La Planada is surrounded by low-input agricultural fields interspersed with forest remnants along streams, steep slopes, and mountain ridges.

La Planada is classified as a transitional life zone between tropical premontane rain forest and wet forest (Holdridge 1967). The mean total annual rainfall and temperature (1985–1994) are 4437 mm and 19.2°C, respectively. Rainfall is distributed in two wet seasons, interrupted by a mild dry (February–March) and a strong dry (June–August) season (Fig. 1). An important climatological feature of La Planada and its surround-

ings is the presence of afternoon mist during most of the year.

The forest at La Planada has a low canopy height (average 22 m) and basal area (33.4 m<sup>2</sup>/ha for plants >4 cm dbh) compared to similar forests elsewhere in the Neotropics (De las Salas and Ballesteros 1986). In a 0.1-ha inventory of plants ≥2.5 cm dbh conducted at La Planada, Gentry (1992) recorded 121 species belonging to 40 families. The most common plant species in the canopy belonged to the Lauraceae, Hippocastanaceae, Rubiaceae, Euphorbiaceae, Bombacaceae, Myristicaceae, and Mimosaceae; in the subcanopy to the Rubiaceae, Palmae, and Melastomataceae. Epiphytes were very abundant and belonged mainly to the Araceae, Cyclanthaceae, and Ericaceae (A. Gentry, unpublished data).

##### Sampling design

Bird mist netting was concentrated in six sites located in the northwestern and western portions of La Planada (Restrepo 1995). These sites, hereafter referred to as edges, were active or recently abandoned pastures contiguous to forest. A sharp delineation between forest and the adjacent pasture characterized most edges. Three “old” edges, Célimo I, Célimo II, and Pialapí, were created around 1950, when colonists cleared the forest and established pastures. The other three “young” edges, Marcos, Hermógenes, and Acantayac, were created around 1982, the year La Planada was established as a private reserve (Restrepo 1995). Célimo I and Célimo II were 400 m apart on the same edge, but because of differences in the weeding regime of the adjacent pasture and in the use of the forest, we reasoned that they represented two independent sampling units. Recapture frequency between these two sites was <4%, supporting this assessment. We placed barbed wire fences along the edges at the beginning of the study to protect the mist nets from cattle entering the forest.

At each edge, we worked in an area 100 × 200 m

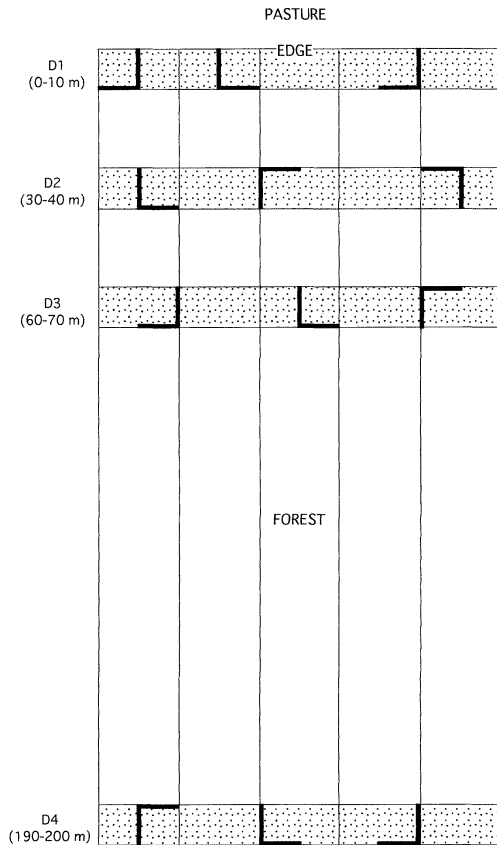


FIG. 2. Sampling design indicating the distribution of mist nets (perpendicular bold lines) at four distances (shaded areas) from forest edge (D1) to forest interior (D4).

(2 ha) and established four strips ( $100 \times 10$  m) running parallel to the edge (Fig. 2). These strips were located at four distances from the forest edge to the forest interior: 0–10 m (D1), 30–40 m (D2), 60–70 m (D3), and 190–200 m (D4). We divided each strip into five plots ( $20 \times 10$  m) and chose three of these at random to place mist nets ( $9 \times 2.5$  m with 32-mm mesh). In each strip, nets were separated by a mean distance of 40 m and were positioned 0.5 m above the ground. In each plot, we placed two mist nets, one net perpendicular to the other, to increase our sampling surface without compromising the independence of the three sampling points at each distance (Fig. 2).

We operated 12 pairs of mist nets (Fig. 2) simultaneously during the time interval 0530–1300 for two consecutive days per month per edge, trying to complete 14 h of mist netting per pair of mist nets. Mist netting started in June 1992 at the old edges. In September 1992, we included the young edges. Thus, the six edges were sampled simultaneously from September 1992 to August 1993 (excluding December 1992, when we did not sample). Because the sampling unit was a pair of mist nets instead of the traditional single net, we define mist-net hours as the hours that a pair

of nets was opened. Total mist-netting effort was 11 892 net-hours.

Mist nets were checked every 1–1.5 h, and each captured bird was characterized by species, mist net number, sex when possible, and total body mass. All birds except hummingbirds were individually marked with color bands. Hummingbirds were marked temporarily by clipping tail and wing feathers to recognize recaptures within a mist-netting session. Bird abundance is expressed throughout this paper as capture rates, defined as number of captures per pair of mist nets per 100 mist-net hours (mnh). Recaptures on the same day were excluded from analyses.

Birds were classified into four feeding guilds: frugivores, insectivores, nectarivores, and carnivores. Placement of a species in a guild was based on the analysis of fecal samples, our own observations, and published reports (Miller 1963, Stiles and Skutch 1989, Andrade 1993, Arango 1994). Frugivores were defined as species that consumed fruit and/or seeds; most of them also consumed insects to some degree. Insectivores ate primarily insects (>80% of diet items). Nectarivores relied heavily on nectar and included flower-piercing birds or nectar “thieves.” Carnivores primarily preyed on vertebrates.

The use of mist nets in the tropics vs. other sampling methods (e.g., acoustic and/or visual censuses) has been widely discussed because of the inherent sampling biases: mist nets sample only a proportion of the bird species found in an area (Terborgh and Weske 1969, Karr 1981, Remsen 1994); birds learn the position of nets if used over a prolonged period (Terborgh 1977, Bierregaard 1990); and rates of bird captures overestimate the abundance of many species (Karr 1981, Remsen and Parker 1983, Lynch 1989). In addition, capture rates can be misleading in comparing presence or abundance of many species among habitats that differ in structure (Terborgh 1971, Lynch 1989, Blake and Loiselle 1991). We stress that mist netting took place only inside the forest, and the aim of this study was to compare changes in bird abundance in forest from the edge to the forest interior. Thus, problems associated with habitat biases are minimized, and our study reflects only those bird species that are sampled effectively by understory mist nets.

One possible problem in interpreting our results, however, relates to the timing of mist netting in old and young edges. In old edges, mist netting began in June 1992; in young edges, in September 1992. Higher capture rates in young than in old edges in September and October could be attributed to birds having learned the position of nets in the old edges. If higher capture rates in young edges were a consequence of a learning process, then we would expect (1) a decrease in the proportion of recaptures over time for both old and young edges, and (2) a higher proportion of recaptures in young than in old edges during these months. The data for all species (excluding hummingbirds), frugi-

vores, and insectivores did not support these predictions, leading us to conclude that differences in capture rates were not artefactual.

#### Data analysis

To establish changes in the distribution of understory birds at La Planada as a function of distance and edge age, we analyzed capture rates for all bird species combined and for each feeding guild, except carnivores. We used ANOVAs for mixed factorial designs (Girden 1992): edge age (old vs. young) was included as a between-subject factor, and month (September 1992–August 1993) and distance (D1–D4) were included as within-subject factors or repeated measures. Month and distance were included as within-subject factors because of restrictions in the randomization procedure when “assigning” month and distance levels to each edge, which can lead to correlations between the observations (Girden 1992). Edges were treated as subjects because each edge was measured repeatedly for each of the distance and month treatment combinations.

The use of post hoc tests is precluded when ANOVAs include within-subject factors (Girden 1992). Instead, we specified contrasts of mean differences to test specific hypotheses that included single within-subject factors and interactions. For the distance effect, we specified two contrasts that compared mean capture rates at D1 and D4 against mean capture rates at D2 and D3 together. We hypothesized that changes in bird distribution, if any, would be marked at the extremes. For the distance  $\times$  edge age interaction, we specified a single contrast and compared mean capture rates at D4 between old and young edges. For the month  $\times$  edge age and the month  $\times$  distance interactions, we specified two contrasts for each and compared capture rates between dry and wet months. We hypothesized that, because of marked differences in the rainfall regime at La Planada, changes in capture rates between habitats (distance or edge age) were more likely to occur between dry and wet months than within a season. Dry months were those exhibiting the lowest rainfall records (February and July) plus the previous month when rainfall started to decrease (January and June); wet months were those that received the highest rainfall (April and October) plus the previous month when rainfall started to increase (March and September; Fig. 1). We compared the mean number of captures between old and young edges during the dry and wet months, and the mean number of captures between D1 and D4 during the dry and wet months.

Because capture rates were zero for many pairs of mist nets, depending on month/distance/edge combination, we averaged capture rates for each three pairs of mist nets/month/distance/edge. This procedure reduced the dimensionality of the data and made them more normally distributed. Most data sets did not meet the assumptions for ANOVAs; therefore, we square-root transformed the data to obtain a plot of the resid-

uals vs.  $y$ -fitted values with a constant band width (Manly 1992). In addition, we verified the assumption of compound symmetry (i.e., the covariation between each pair of treatments is equal for all subjects) for ANOVAs that included within-subject factors (Girden 1992). When compound symmetry is violated, the probability of committing a Type I error increases. To account for this, the degrees of freedom are corrected by  $\epsilon$ , yielding a corrected  $F$  value (Girden 1992). In this paper, we report the corrected  $F$  values and associated probabilities based on the liberal Huynh-Feldt method ( $F_{H-F}$ ). All analyses were performed using SuperANOVA (Abacus 1989).

We used a replicated goodness-of-fit test ( $G$  statistic) (Sokal and Rohlf 1981) to determine how edge age influenced the distribution of individual species from forest edge to forest interior. For some species, however, the data precluded the comparison between old and young edges and we simply used a goodness-of-fit test ( $G$ -statistic) to determine if the number of captures at the four distances departed significantly from a uniform distribution. We used data collected between June 1992 and August 1993 and we pooled monthly captures for each species. The  $G$  statistic departs from the  $\chi^2$  distribution when  $<80\%$  of the expected cell frequencies  $>5$  (Siegel and Castellan 1988). Thus, species that did not meet this criterion were excluded from this analysis. Five species were an exception: two (*Lipaugus cryptolophus* and *Ocreatus underwoodii*) because of the clear trends they exhibited, and the other three (*Tangara arthus*, *T. labradorides*, and *T. nigroviridis*); because many similarities in their life history made their grouping under the *Tangara* spp. assemblage reliable (Isler and Isler 1987).

To evaluate the influence of edges on those species that did not meet the criteria, we classified birds into five abundance categories and assigned capture numbers for each species to the four distances. The categories were defined based on capture frequency: extremely sparse (one capture), very sparse (2–5 captures), sparse (6–20 captures), abundant (21–50 captures), and very abundant ( $\geq 51$  captures). We used a chi-square test to evaluate the association between species abundance and distance, and used the residuals to determine the contribution of each cell to the overall result (Siegel and Castellan 1988).

For all of our analyses, we used  $\alpha < 0.10$  because our design could lead to increases in Type II errors (reduced power of our tests; Zolman 1993). This departure from ecological tradition was justified for two reasons. First, the scale at which we worked precluded inclusion of more replicates, which is often the case when dealing with large-scale ecological phenomena (Scheiner 1993). The area encompassed by the six edges was equivalent to 12 ha and access was difficult due to steep terrain. Second, in a mixed-factorial design, the number of degrees of freedom is reduced, in comparison to a factorial design, because of multiple nest-

TABLE 1. Results of four ANOVAs for mixed-factorial designs (1 between-, 2 within-factors) on mean capture rates  $\times$  100 mist-net hours (mnh) of all birds, frugivores, insectivores, and nectarivores. The month (M) and month  $\times$  distance  $\times$  age effects were excluded from this table.  $F_{H-F}$  is the  $F$  value based on the liberal Huynh-Feldt method.

ANOVA	ANOVA Results									
	Age, A (df = 1, 4) $F$	Error: Edge, E(Age) SS	Distance, D (df = 3, 12) $F_{H-F}$	D $\times$ A (df = 3, 12) $F_{H-F}$	Error: D $\times$ E(A) SS	M $\times$ A (df = 10, 40) $F_{H-F}$	Error: M $\times$ E(A) SS	M $\times$ D (df = 30, 120) $F_{H-F}$	Error: D $\times$ M $\times$ E(A) SS	
All birds‡	2.89	11.39	7.63**	3.54*	22.39	1.78†	30.07	1.10	85.84	
Frugivores‡	1.77	14.27	4.85*	2.75†	25.03	0.79	33.99	1.93**	106.78	
Insectivores‡	0.24	18.42	2.7†	1.32	27.86	3.23**	39.91	0.78	114.94	
Nectarivores	0.05	17.78	1.78	1.83	24.67	0.52	41.85	0.82	147.25	

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

†  $P < 0.10$ .

‡ Based on square-root transformed data.

ing (Zolman 1993). In the field, we were limited by the number of edges we could reach within walking distance from the field station.

## RESULTS

### All birds

From September 1992 through August 1993, we accumulated 1789 captures representing 80 species. Results of our ANOVAs on bird captures yielded no significant three-way interactions. However, several two-way interactions were significant for the four variables describing bird captures, although these relationships were not consistent. We describe first the single effect of distance on bird captures, and then the interactions involving this term.

Bird captures differed significantly among the four distances (ANOVA,  $P = 0.004$ ; Table 1, Fig. 3), suggesting that the overall distribution of understory birds at La Planada is influenced by the presence of edges. Mean capture rates were significantly higher at D1 (16.9 captures per pair of nets per 100 mist-net hours) and D4 (mean 19.3) than at D2 and D3 together (mean 12.1) (contrast of mean differences,  $F_{1,12} = 10.7$ ,  $P = 0.007$  and  $F_{1,12} = 18.4$ ,  $P = 0.001$ , respectively). The significant distance  $\times$  edge age interaction, however, indicates that differences in capture rates among the four distances depend on edge age (ANOVA,  $P = 0.05$ ; Table 1, Fig. 4). Capture rates were similar at D1, D2, and D3 in old and young edges, but differed at D4, where they were higher in young edges (mean 24.2) than in old edges (mean 14.1) (contrast of mean differences,  $F_{1,12} = 12.0$ ,  $P = 0.005$ ).

The significant edge age  $\times$  month interaction (ANOVA,  $P = 0.09$ ; Table 1) indicates that edge age influenced capture rates, depending on month. During the wet months, bird captures differed between old and young edges (contrast of mean differences,  $F_{1,40} = 13.1$ ,  $P = 0.0008$ ), but there was no difference during the dry months (contrast of mean differences,  $F_{1,40} = 1.5$ ,  $P = 0.2$ ).

### Feeding guilds

Distance significantly influenced capture rates of both frugivores and insectivores (ANOVA,  $P = 0.02$  and  $P = 0.08$ , respectively; Table 1, Fig. 3). Capture rates for frugivores were significantly higher at D1 (mean 5.6) and D4 (mean 7.0) compared to D2 and D3 together (mean 3.5) (contrast of mean differences,  $F_{1,12} = 7.0$ ,  $P = 0.02$ , and  $F_{1,12} = 12.0$ ,  $P = 0.005$ , respectively). Capture rates for insectivores were significantly higher at D4 (mean 8.0) compared to D2 and D3 together (mean 5.0) (contrast of mean differences,  $F_{1,12} = 8.3$ ,  $P = 0.01$ ). The overall ANOVA showed that distance from the forest edge did not affect capture rates of nectarivores (Table 1, Fig. 3). Nevertheless, the specific hypotheses tested by contrast of mean differences showed that capture rates of nectarivores were higher at D1 (mean 5.4) than at D2 and D3 together (mean 3.5) ( $F_{1,12} = 4.9$ ,  $P = 0.05$ ).

Among frugivores, the significant interaction between distance and edge age indicates that distance from forest edge affected capture rates, but depended on edge age as well (ANOVA,  $P = 0.09$ ; Table 1, Fig. 4). Capture rates at D1, D2, and D3 were similar between old and young edges. However, capture rates at D4 were significantly higher at young (mean 9.4) than at old (mean 4.5) edges (contrasts of mean differences,  $F_{1,12} = 7.2$ ,  $P = 0.02$ ). Although the distance  $\times$  edge age interaction was not significant for nectarivores (Table 1, Fig. 4), the specific hypothesis involving these two factors, tested by contrast of mean differences, showed that capture rates were significantly higher at D4 in young (mean 5.5) than in old (mean 3.3) edges ( $F_{1,12} = 4.0$ ,  $P = 0.07$ ).

Among frugivores, capture rates varied significantly with distance but depended on month (ANOVA,  $P = 0.007$ ; Table 1, Fig. 5). We found that capture rates of frugivores were significantly higher at D4 (mean 8.4) than at D1 (mean 4.7) during the dry months (contrast of mean differences,  $F_{1,120} = 7.3$ ,  $P < 0.008$ ), but the difference disappeared during the wet months. The distance  $\times$  month interaction was not significant for in-

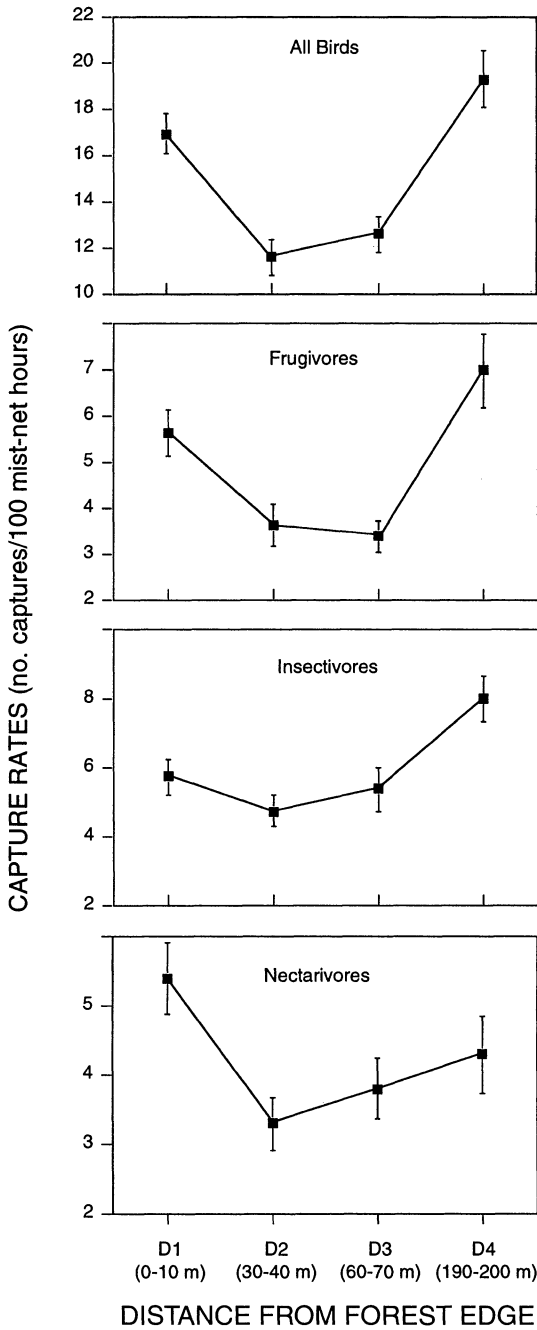


FIG. 3. Capture rates of understory birds in relation to distance from the forest edge. Points represent means  $\pm$  1 SE.

sectivores and nectarivores (Table 1, Fig. 5). The specific hypotheses that we tested by contrast of mean differences showed that capture rates of insectivores were higher at D4 than at D1 during both the wet (mean 8.4 vs. 6.6, respectively;  $F_{1,120} = 2.8$ ,  $P = 0.09$ ) and dry (mean 8.0 vs. 4.2, respectively;  $F_{1,120} = 6.7$ ,  $P = 0.01$ ) season. Capture rates of nectarivores were higher

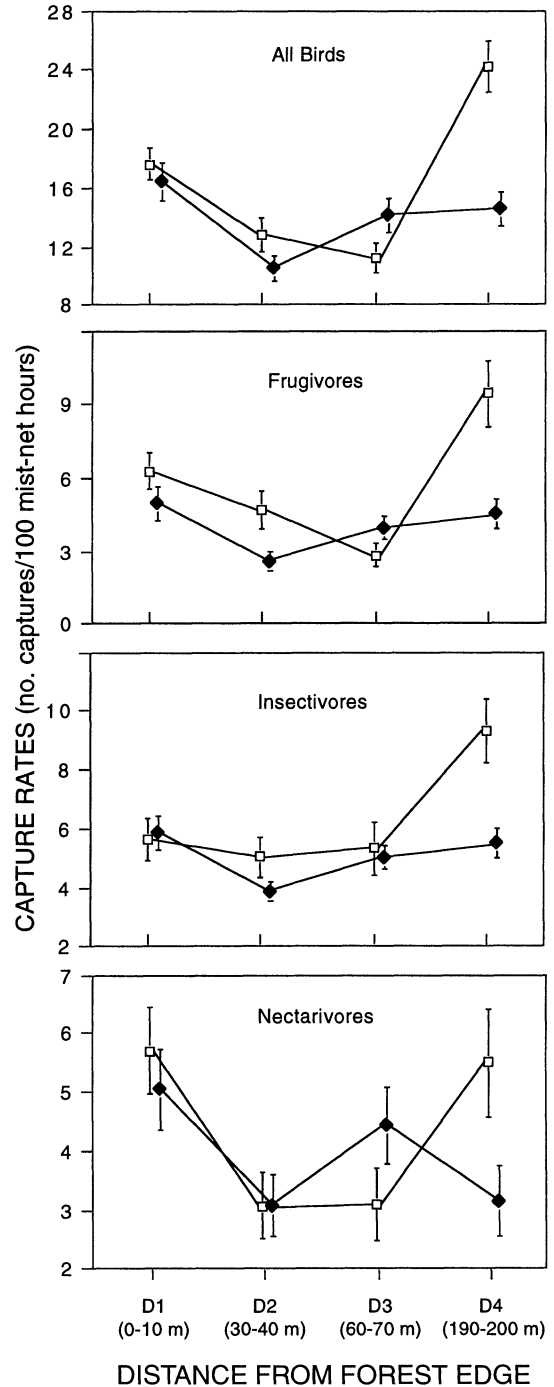


FIG. 4. Capture rates of understory birds in relation to distance from the forest edge and edge age. □, new edges; ◆, old edges. Points are means  $\pm$  1 SE.

at D1 (mean 5.6) than at D4 (mean 3.2) only during the dry season ( $F_{1,120} = 5.7$ ,  $P = 0.02$ ).

A significant edge age  $\times$  month interaction for insectivores (ANOVA,  $P = 0.01$ ; Table 1) indicated that capture rates between old and young edges changed with month. We found that capture rates of insectivores

were higher at young (mean 7.9) than at old (mean 5.4) edges during the wet season (contrast of mean differences,  $F_{1,40} = 7.0$ ,  $P = 0.01$ ), but not during the dry season.

### Species

Of the 2101 captures between June 1992 and August 1993, 92% represented 25 species that were classified as abundant (21–50 captures) and very abundant ( $\geq 51$  captures) (Appendix). Fourteen species were evaluated to determine the combined effect of distance from the edge and edge age on the number of captures (Fig. 6). Five species (*Euphonia xanthogaster*, *Mionectes striaticollis*, *Myadestes ralloides*, *Premnoplex brunnescens*, and *Agelaiocercus coelestis*) showed a significant distance  $\times$  edge age interaction ( $G$ -heterogeneity,  $P < 0.1$ ); that is, the distribution of bird captures from edge to forest interior differed between old and young edges. In the remaining species, the distribution of bird captures from edge to forest interior was similar between old and young edges ( $G$ -heterogeneity,  $P > 0.1$ ; Fig. 6). Within these two groups, bird captures at old and young edges showed either a uniform ( $P > 0.1$ ) or non-uniform distribution ( $P < 0.1$ ; Fig. 6). Thus, our results suggest that edge features, such as edge age, in combination with distance from forest edge, can influence the distribution of bird species in complex ways.

We established the overall influence of distance on the distribution of the 14 bird species previously mentioned, plus 11 additional abundant species, including the *Tangara* spp. assemblage. The distribution of bird captures for 17 out of the 25 common species departed significantly from a uniform distribution across the four distances (Table 2). Given a 10% probability of obtaining a species that shows a non-uniform distribution, it is very unlikely that 17 or more species out of 25 would have shown such a distribution by chance alone (binomial test,  $P = 1.6 \times 10^{-12}$ ). Based on the observed and expected cell frequencies, we further divided the species exhibiting a non-uniform distribution into three groups: (1) species increasing from edge to interior ( $n = 8$ ), (2) species decreasing from edge to interior ( $n = 4$ ), and (3) species increasing both at the edge and interior ( $n = 5$ ; Table 2). These results suggest that some species avoid edges, others are attracted to edges, and still others may be influenced by factors other than distance from forest edge (as suggested by those species increasing both at forest edge and forest interior).

The distribution of sparse species ( $< 21$  captures) was not independent of distance from forest edge ( $\chi^2 = 22.6$ ,  $df = 12$ ,  $P = 0.03$ ; Table 3). An examination of the residuals showed that extremely sparse and very sparse species were found more often than expected at D1 than at any other distance. A survey of the types of habitat frequented by the extremely sparse species showed that the vast majority were characteristic of edge, canopy, second growth, large gaps, and semiopen areas (Table 4).

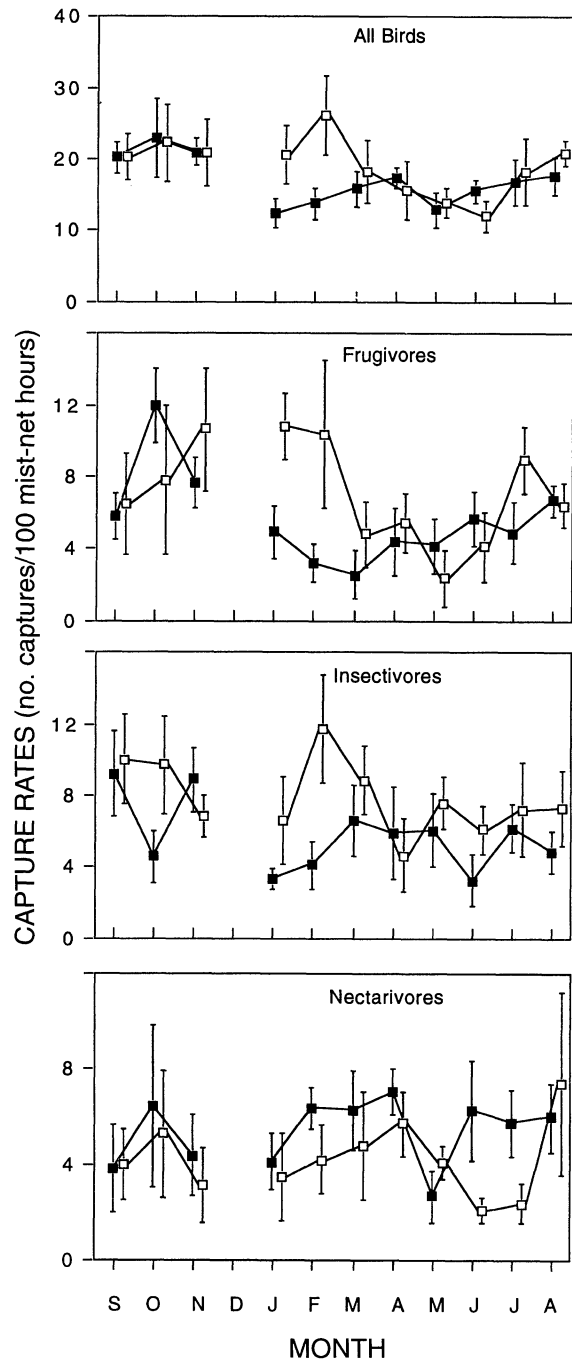


FIG. 5. Capture rates of understory birds in relation to distance from forest edge and month. ■, D1; □, D4. Points are means  $\pm 1$  SE.

### DISCUSSION

The distribution of understory birds at La Planada varied from forest edge to forest interior in complex ways, as shown by (1) differences among feeding guilds and (2) significant interactions between distance from edge, month, and edge age. Differences among



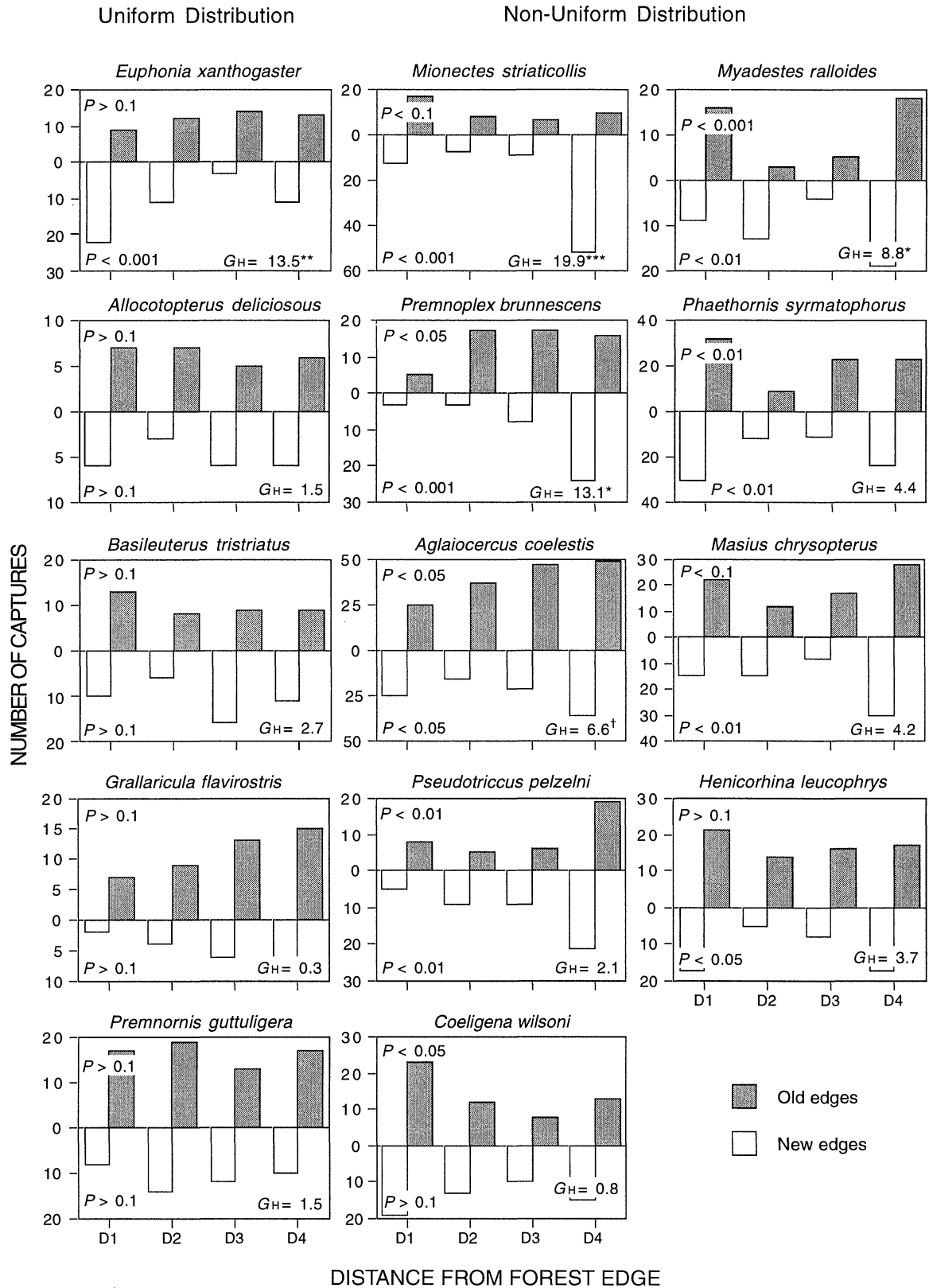


FIG. 6. Distribution of abundant bird species ( $\geq 21$  captures) from forest edge (D1) to forest interior (D4), depending on edge age. The statistic  $G_H$  refers to G-heterogeneity. Species grouped in the first column showed an overall uniform distribution, and species in the second and third columns showed an overall non-uniform distribution from forest edge to forest interior. Significance is noted as in Table 2. Values represent the total number of captures between June 1992 and August 1993.

TABLE 2. Distribution of abundant ( $\geq 21$  captures) understory birds from forest edge (D1) to forest interior (D4). Data are numbers of observed captures.

Species	Distance (m)				G
	D1 0–10	D2 30–40	D3 60–70	D4 190–200	
Uniform distribution					
<i>Alcotopterus deliciosus</i>	13	10	11	12	0.42
<i>Euphonia xanthogaster</i>	32	22	17	24	4.16
<i>Pipreola riefferii</i>	7	5	4	5	0.89
<i>Tangara</i> spp.	8	4	4	11	5.08
<i>Basileuterus tristriatus</i>	23	14	25	20	3.54
<i>Grallaricula flavirostris</i>	9	13	19	21	6.14
<i>Myiophobus flavicans</i>	9	6	3	5	3.27
<i>Premnornis guttuligera</i>	25	33	25	27	1.52
Non-uniform distribution					
A) Increase from edge to interior					
<i>Atlapetes brunneinucha</i>	3	4	11	10	7.5†
<i>Lipaugus cryptolophus</i>	1	2	5	8	7.8†
<i>Glyphorhynchus spirurus</i>	10	9	10	30	18.2***
<i>Myiotriccus ornatus</i>	11	6	9	23	12.5**
<i>Premnoplex brunnescens</i>	8	20	25	40	23.9***
<i>Pseudotriccus pelzelni</i>	13	14	15	40	21.6***
<i>Agelaiocercus coelestis</i>	50	53	68	85	11.8**
B) Decrease from edge to interior					
<i>Chlorospingus semifuscus</i>	13	2	3	5	13.6**
<i>Coeligena wilsoni</i>	42	25	18	28	10.5*
<i>Haplophaedia lugens</i>	20	11	13	7	6.8†
<i>Ocreatus underwoodii</i>	10	3	4	1	9.6*
C) Other patterns					
<i>Masius chrysopterus</i>	37	27	25	58	17.5***
<i>Mionectes striaticollis</i>	30	16	15	61	41.6***
<i>Myadestes ralloides</i>	25	16	9	37	20.6***
<i>Henicorhina leucophrys</i>	38	19	24	34	8.12*
<i>Syndactyla subalaris</i>	14	6	6	14	6.6†
<i>Phaethornis syrmatorphorus</i>	62	21	34	47	23.3***

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .†  $P < 0.10$ .

feeding guilds suggest that ecological processes mediated through plant–animal interactions may not be equally affected by the presence of edges. Moreover, changes in the distribution of birds from forest edge to forest interior with month and edge age suggest that “edge effects” (Harris 1984, Lovejoy et al. 1986)

TABLE 3. Distribution of sparse ( $< 21$  captures) to abundant ( $\geq 21$  captures) understory birds from forest edge to forest interior. Numbers are observed captures. In parentheses are the post hoc cell contributions.

Species abundance	Distance (m)			
	D1 0–10	D2 30–40	D3 60–70	D4 190–200
Extremely sparse (one capture)	11 (2.3)*	4 (-0.9)	6 (0.4)	3 (-1.8)
Very sparse (2–5 captures)	31 (3.4)*	11 (-0.6)	12 (-0.6)	14 (-2.2)*
Sparse (6–20 captures)	41 (0.5)	32 (1.2)	24 (-1.0)	43 (-0.6)
Abundant (21–50 captures)	70 (1.0)	39 (-0.8)	46 (-0.1)	75 (-0.1)
Very abundant ( $\geq 51$ captures)	423 (-3.1)*	314 (0.4)	342 (0.9)	557 (1.8)

\*  $P < 0.05$ .

change over various temporal scales. When we examined individual bird species, we found that a high proportion showed a non-uniform distribution from forest edge to forest interior; however, the shape of the distributions was highly variable among the different species. Although part of this variability could be attributed to the presence of edges, factors other than edges, e.g., social behavior of animals (Wiens 1992), could also have contributed to it. This may partially explain bimodal patterns of “edge effects” (Murcia 1995).

#### Patterns of bird distributions from edge to forest interior

We found that capture rates of all understory birds taken together increased from forest edge to forest interior. Our results resemble those of a study conducted in central Amazonia (Quintela 1986); however, results from both studies differ from those reported by Sisk (1991) for a site in the mountains of Costa Rica. At this site, the distribution of bird captures from forest edge to forest interior was uniform (Sisk 1991). Two other studies based on point count surveys (Kroodsm

TABLE 4. Extremely sparse species (one capture) and their habitats. I, forest, including near ground, middle canopy, and upper-under canopy; O, other, including canopy, edge, second growth, large gaps, semiopen habitats, ravines, and pastures with scattered trees.

Species	I	O
D1 (0–10 m)		
<i>Adelomyia melanogenys</i>	x	x
<i>Colibri thalassinus</i>		x
<i>Urosticte benjamini</i>	x	
<i>Campephilus pollens</i>	x	x
<i>Anabacerthia variegaticeps</i>	x	x
<i>Pachyramphus versicolor</i>		x
<i>Catharus ustulatus</i>		x
<i>Vireo leucophrys</i>		x
<i>Iridosornis porphyrocephala</i>		x
<i>Tachyphonus luctuosus?</i>		x
<i>Catamblyrhynchus diadema</i>		x
D2 (30–40 m)		
<i>Glaucidium jardinii</i>		x
<i>Schizoeaca fuliginosa</i>		x
<i>Pachyramphus albobruius</i>		x
<i>Turdus serranus</i>		x
D3 (60–70 m)		
<i>Amazilia franciae</i>		x
<i>Chlorostilbon mellisugus</i>		x
<i>Doryfera ludovicica</i>		x
<i>Xiphocolaptes promeropyrhynchus</i>	x	
<i>Myiobius barbatus</i>		x
<i>Pseudotriccus ruficeps</i>	x	x
D4 (190–200 m)		
<i>Eutoxeres aquila</i>	x	x
<i>Cranioleuca erythrops?</i>		x
<i>Diglossa indigotica</i>	x	x

Note: Habitat data are from Hilty and Brown (1986) and Stiles and Skutch (1989).

1984) and mist netting (Lopez de Casenave et al., *unpublished manuscript*) that were conducted in temperate regions reported opposite results from those of our study.

We reanalyzed Quintela's (1986) data after classifying bird species into feeding guilds, and found that captures of both understory insectivores and frugivores were not uniform (goodness-of-fit test,  $G = 49.6$ ,  $P < 0.001$  and  $G = 5.8$ ,  $P < 0.1$ , respectively), and that they increased from the edge to the forest interior (500 m from forest edge). Conversely, captures of understory nectarivores (goodness-of-fit test,  $G = 7.1$ ,  $P < 0.05$ ) decreased from the edge to the forest interior. Although Quintela's study and ours showed that the abundance of all understory birds, frugivores, and insectivores was highest at the forest interior, whereas the abundance of nectarivores was highest at the forest edge, we do not know if these patterns are general. In both sites, pastures and second-growth areas are embedded in a forest matrix (Lovejoy et al. 1986), yet their understory avifauna differs markedly (Bierregard and Lovejoy 1989).

The distribution of understory birds at La Planada, based on capture rates, revealed significant interactions between distance and edge age/month for frugivores,

and between edge age and month for insectivores. Two other studies have also shown that "edge effects" vary with season. In central Sweden, bird density was greater at "edge" ( $\leq 50$  m from the edge) than at "interior" ( $> 50$  m from the edge) sites, especially during summer (Hansson 1983). Conversely, in central Florida, bird density was greater at "edge" ( $\leq 50$  m from the edge) than at "interior" ( $> 700$  m from the edge) sites during winter (Noss 1991). The within-year variability in bird abundance from forest edge to forest interior suggests that edges are temporally dynamic. In addition, differences among feeding guilds suggest that the mechanisms underlying the observed patterns differ.

#### *Factors influencing bird distributions from edge to forest interior*

Edges may influence the behavior of birds in a variety of ways. Changes in microclimate and the distribution of suitable habitats, for example, can affect the dispersal abilities, physiological condition, and home range size of birds, and thus have a direct effect on the distribution of birds from forest edge to forest interior (Wiens et al. 1985, Kuitunen and Mäkinen 1993). On the other hand, changes in the distribution of parasites and predators can affect rates of parasitism and predation, and thus influence the distribution of host and prey (e.g., Brittingham and Temple 1983, Wilcove et al. 1986, Andrén and Algestam 1988, Gibbs 1991, Laurance 1993, Loye and Carroll 1995, Arango-Velez and Kattan 1997). Another example of the indirect effects of edges on the distribution of organisms was documented by Malcolm (1991, 1994), who found that the abundance of small mammals differed between "edge" and "interior," mirroring changes in the abundance of insects. He postulated that changes in the resource base resulting from edge creation triggered changes in the distribution of small mammals.

At La Planada, differences in capture rates of frugivores from forest edge to forest interior might be partially explained by changes in the distribution of their resource base. Fruit abundance (total number of fruits) decreased significantly from edge to forest interior (Restrepo 1995), as did capture rates of understory frugivorous birds up to 70 m from the edge. The sharp decrease of nectarivores from edge to forest interior, although not significant, was similar to the trend shown by nectarivores in central Brazil (Quintela 1986). At our study site, the distribution of hummingbird-pollinated plants showed a significant decrease from edge to forest interior (goodness-of-fit test,  $\chi^2 = 23.01$ ,  $df = 3$ ,  $P < 0.05$ ; C. Restrepo, *unpublished data*). Our results strengthen Malcolm's (1997) proposition only partially. The patterns we observed at La Planada, particularly for frugivores, cannot be explained entirely by changes in the food resource base.

At D4 (190–200 m from forest edge), fruit abundance was the lowest (Restrepo 1995), yet capture rates of frugivores were the highest. Two species, *Mionectes*

*striaticollis* and *Masius chrysopterus*, contributed 42% of all frugivore captures. This, together with some aspects of their behavior, may explain the paradox. Moreover, these two species can provide some insights into how conditions existing prior to edge creation may have the potential to influence the distribution of organisms from forest edge to interior.

Capture rates of *M. striaticollis* and *M. chrysopterus* by two pairs of mist nets located at D4 in one of our young edges (Hermógenes) were unusually high. The recapture of the same individuals (*M. striaticollis*) and the capture of a high proportion of males (*M. chrysopterus*) (C. Restrepo and N. Gómez, unpublished data) suggested to us that these two pairs of mist nets were located near their leks (Prum and Johnson 1987, Westcott and Smith 1994). Further observations in the field confirmed our suspicion. The long-term use of the same display area by lekking species (Höglund and Alatalo 1995) may indicate that the leks of *M. striaticollis* and *M. chrysopterus* existed prior to edge creation in 1982. These leks can certainly behave as points of attraction that influence not only the distribution of birds from forest edge to interior, but also edge structure, through the process of seed dispersal. Thus, the distribution of organisms from edge to forest interior is influenced not only by physical or structural attributes of edges, but also by species characteristics, such as social behavior (Wiens 1992).

Increased capture rates of insectivores at D4, however, suggest that some structural feature (e.g., vertical distribution of foliage, tree diameter) of the forest changed at D4, and that both frugivores and insectivores might have responded in the same way. However, the only structural feature that we quantified for each distance/edge was percentage of gap area, which did not differ significantly among the four distances (repeated-measures ANOVA,  $F_{3,12} = 0.2$ ,  $P = 0.8$ ). It still remains unknown if, indeed, changes in some structural feature of the forest or in the distribution of predators and parasites can explain the observed patterns.

#### *Where do the sparse species come from?*

We found that extremely sparse and very sparse species of birds were found more often than expected at the forest edge. A “veil line” effect (Preston 1948) cannot explain these results. First, capture rates were highest at D4, yet capture rates of extremely sparse and very sparse species were lowest. Second, understory fruiting plants showed a similar pattern (Restrepo 1995). Third, extremely sparse species were characteristic of disturbed areas (Table 4). This suggests that (1) the nearby disturbed area is influencing the contiguous forest, and (2) edges might also influence the nearby disturbed habitat. In Neotropical montane ecosystems, landslides represent one type of large-scale natural disturbance (e.g., Garwood et al. 1979, Mora and Mora 1994) that could represent the natural habitat for many of the sparse species. If this is true, then in areas

like La Planada, where transient corn fields, pastures, and second-growth areas of various ages are embedded in a forest matrix, the avifauna may respond to anthropogenic edges in a fashion similar to the way they respond to natural edges.

#### *Edge effects or edge dynamics?*

Studies designed to establish “edge effects” (sensu Harris 1984) have emphasized the maximum distance at which changes induced by edge creation are apparent within forest stands (e.g., Williams-Linera 1990, Blanchard 1992, Chen et al. 1992). Our study has shown that the distribution of birds from forest edge to forest interior changes with month and edge age, and that feeding guilds respond in different ways. Unexpectedly, our study has shown that certain bird features, such as social behavior, generate patterns in the distribution of birds from edge to forest interior that may be independent of the creation of edges. However, such features may have the potential to influence the structure and even the location of edges over time. In addition, our data indicate that edges may influence both the disturbed area and adjacent forest.

Even though edges are recognizable as more or less fixed entities of landscapes, the responses of organisms, and of the processes they mediate, seem to vary at various temporal (e.g., this work) and spatial scales (e.g., Crist et al. 1992, Restrepo et al. 1997). Rather than focusing on maximum distances at which “edge effects” are felt, studies should focus on edge dynamics. Why would this matter? Recent efforts to design reserves in fragmented landscapes (e.g., Harris 1984) and to measure the impact of deforestation at large scales (e.g., Skole and Tucker 1993) have assumed that edges have a detrimental effect. In fact, depth of “edge effects” is used to establish the amount of edge vs. intact forest habitat left. Although this approach may have an operational value, it clearly disregards the fact that “edge effects” may vary over time and space, and that the structure and location of edges may change. Focusing on edge dynamics rather than on “edge effects” might be particularly useful for the study of fruit–frugivore interactions, because one outcome of such interactions is seed dispersal. Landscape pattern is changed not only as a consequence of disturbance; it is also changed in fundamental ways by the process of seed dispersal.

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## APPENDIX

Bird captures in the understory of La Planada and El Bosque, Colombia (June 1992–August 1993). Abundance categories (AB), feeding guild (FG), and body mass are provided for each species.

Species	AB†	FG‡	Body mass (g)
<b>Accipitridae</b>			
<i>Accipiter collaris</i>	VS	C	166.3
<b>Columbidae</b>			
<i>Columba cayennensis</i>	VS	F	
<b>Strigidae</b>			
<i>Glaucidium jardinii</i>	ES	C	75.0
<i>Otus columbianus</i>	VS	C	165.0
<b>Trochilidae</b>			
<i>Adelomyia melanogenys</i>	ES	N	5.2§
<i>Aglaiocercus coelestis</i>	VA	N	
<i>Amazilia franciae</i>	ES	N	5.0§
<i>Boissonneaua jardini</i>	VS	N	9.8
<i>Chlorostilbon mellisugus</i>	ES	N	4.0
<i>Coeligena torquata</i>	VS	N	8.2
<i>Coeligena wilsoni</i>	VA	N	7.1
<i>Colibri thalassinus</i>	ES	N	
<i>Doryfera ludoviciae</i>	ES	N	6.0
<i>Eutoxeres aquila</i>	ES	N	9.5
<i>Haplophadja lugens</i>	VA	N	6.0
<i>Heliodoxa imperatrix</i>	VS	N	8.2
<i>Lafresnaya lafresnayi</i>	VS	N	5.0
<i>Ocreatus underwoodii</i>	S	N	2.9
<i>Phaethornis syrmatorophorus</i>	VA	N	6.0
<i>Schistes geoffroyi</i>	VS	N	4.0
<i>Urosticte benjamini</i>	ES	N	4.4
<b>Trogonidae</b>			
<i>Trogon personatus</i>	S	F	58.6
<b>Capitonidae</b>			
<i>Semnormis ramphastinus</i>	VS	F	92.1
<b>Ramphastidae</b>			
<i>Andigena laminirostris</i>	VS	F	349.5
<b>Picidae</b>			
<i>Campephilus pollens</i>	ES	I	206.0
<b>Dendrocolaptidae</b>			
<i>Dendrocincla tyrannina</i>	VS	I	53.4
<i>Glyphornychus spirurus</i>	VA	I	14.3
<i>Lepidocolaptes affinis</i>	VS	I	29.0
<i>Xiphocolaptes promeropirhynchus</i>	ES	I	161.0
<b>Furnariidae</b>			
<i>Anabacerthia variegaticeps</i>	ES	I	25.0
<i>Cranioleuca erythrops?</i>	ES	I	14.0
<i>Margarornis stellatus</i>	S	I	20.7
<i>Premnoplex brunnescens</i>	VA	I	15.9
<i>Premnornis guttuligera</i>	VA	I	14.8
<i>Schizoeaca fuliginosa</i>	ES	I	15.5
<i>Sclerurus mexicanus</i>	S	I	22.3
<i>Syndactyla subalaris</i>	A	I	32.9
<i>Thripadectes ignobilis</i>	S	I	45.5
<i>Thripadectes virgaticeps</i>	S	I	58.9
<b>Formicariidae</b>			
<i>Drymophila caudata</i>	VS	I	10.5
<i>Formicarius rufipectus</i>	VS	I	68.5
<i>Grallaricula flavirostris</i>	VA	I	20.4
<i>Thamnophilus unicolor</i>	S	I	23.3
<b>Cotingidae</b>			
<i>Pachyrhamphus albogriseus</i>	ES	F	16.1

## APPENDIX. Continued.

Species	AB†	FG‡	Body mass (g)
<i>Pachyrhamphus versicolor</i>	ES	F	15.0
<i>Pipreola riefferii</i>	A	F	51.5
<i>Lipaugus cryptolophus</i>	S	F	80.4
<b>Pipridae</b>			
<i>Allocoptes deliciosus</i>	A	F	12.4
<i>Masius chrysopterus</i>	VA	F	11.5
<b>Tyrannidae</b>			
<i>Mionectes striaticollis</i>	VA	F	13.8
<i>Myiobius barbatus</i>	ES	I	12.0
<i>Myiophobus flavicans</i>	A	I	12.9
<i>Myiorticus ornatus</i>	A	I	10.4
<i>Myiodynastes chrysocephalus</i>	VS	I	38.8
<i>Ochoeca cinnamomeiventris</i>	VS	I	12.2
<i>Pogonotriccus ophthalmicus</i>	VS	I	9.5
<i>Pseudotriccus pelzelni</i>	VA	I	11.8
<i>Pseudotriccus ruficeps</i>	ES	I	9.5
<i>Zimmerius viridiflavus</i>	VS	F	10.2
<b>Troglodytidae</b>			
<i>Henicorhina leucophrys</i>	VA	I	15.6
<b>Turdidae</b>			
<i>Catharus ustulatus</i>	ES	F	29.5
<i>Entomodestes coracinus</i>	VS	F	14.5
<i>Myadestes ralloides</i>	VA	F	28.5
<i>Turdus serranus</i>	ES	F	28.4
<b>Vireonidae</b>			
<i>Vireo leucophrys</i>	ES	I	22.0
<b>Parulidae</b>			
<i>Basileuterus coronatus</i>	S	I	17.1
<i>Basileuterus tristriatus</i>	VA	I	13.1
<i>Myioborus miniatus</i>	VS	I	8.2
<b>Thraupidae</b>			
<i>Anisognathus flavinucha</i>	VS	F	44.4
<i>Chlorochrysa phoenicotis</i>	S	F	20.6
<i>Chlorospingus semifuscus</i>	A	F	28.1
<i>Diglossa albilatera</i>	S	N	9.9
<i>Diglossa indigotica</i>	ES	N	12.0
<i>Euphonia xanthogaster</i>	VA	F	13.6
<i>Iridosornis porphyrocephala</i>	ES	F	26.0
<i>Tachyphonus luctuosus?</i>	ES	F	35.0
<i>Tangara arthus</i>	S	F	20.8
<i>Tangara labradorides</i>	VS	F	14.2
<i>Tangara nigroviridis</i>	S	F	16.9
<b>Catamblyrhynchidae</b>			
<i>Catamblyrhynchus diadema</i>	ES	I	18.0
<b>Fringillidae</b>			
<i>Amaurospiza concolor</i>	VS	F	16.0
<i>Atlapetes brunneinucha</i>	A	F	45.6

† Abundance categories: ES, extremely sparse (one capture); VS, very sparse (2–5 captures); S, sparse (6–20 captures); A, abundant (21–50 captures); VA, very abundant (≥51 captures).

‡ Feeding guild: C, carnivore; F, frugivore; I, insectivore; N, nectarivore.

§ Miller (1963).

|| Arango (1994).