
Effects of Road Clearings on Movement Patterns of Understory Rainforest Birds in Central Amazonia

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Abstract: *The impacts of potential linear barriers such as roads, highways, and power lines on rainforest fauna are poorly understood. In the central Brazilian Amazon, we compared the frequency of local movements (≤ 300 m long) of understory birds within intact forest and across a 30- to 40-m-wide road over a 2-year period. Rainforest had regenerated along some road verges, to the extent that a nearly complete canopy was formed in some areas, so we also assessed whether this facilitated bird movement. Movement data were determined from 1212 recaptures of 3681 netted birds at six study sites. The road significantly inhibited total bird movement across roads at five of the six sites. Bird foraging guilds varied in their responses to the road and different ages of regrowth. Movements of frugivorous and edge and gap species were not inhibited at any site, whereas most forest-dependent insectivores (mixed-species flocks, terrestrial species, and army-ant followers) had markedly inhibited road-crossing movements, except at sites with extensive regrowth. Solitary understory species were especially vulnerable, rarely crossing even roads overgrown by tall regrowth. For sensitive species, road-crossing movements were inhibited because individuals tended to avoid both edge-affected habitat near the road and the road clearing itself. Our results suggest that even narrow roads with low traffic volumes can reduce local movements of many insectivorous birds in Amazonia.*

Key Words: Amazonian birds, birds and roads, roads and bird movements

Efectos de los Claros de Caminos sobre Patrones de Movimiento de Aves de Sotobosque en la Amazonía Central

Resumen: *Los impactos potenciales de barreras lineales como caminos, carreteras y líneas eléctricas sobre la fauna del bosque lluvioso son poco conocidos. Durante 2 años comparamos la frecuencia de desplazamientos locales (≤ 300 m-longitud) de aves de sotobosque en selva intacta y de un lado a otro de un camino de 30-40 m de ancho en el Amazonas Brasileño central. La selva se había regenerado en algunos bordes del camino, al grado que en algunas áreas se había formado un dosel casi completo, así que también evaluamos si esto facilitaba el desplazamiento de aves. Los datos de movimientos fueron determinados a partir de 1212 recapturas de 3681 aves en seis sitios de estudio. El camino significativamente inhibió el desplazamiento total de aves en cinco de los seis sitios. Los gremios de forrajeo variaron en su respuesta al camino y las diferentes edades de recrecimiento. Los desplazamientos de especies frugívoras y de borde y claros no fueron inhibidos en sitio alguno, mientras que los desplazamientos de la mayoría de especies insectívoras dependientes de selva (parvadas de especies mixtas, especies terrestres y seguidoras de hormigas arrieras) fueron marcadamente inhibidos, excepto en los sitios con recrecimiento extensivo. Las especies solitarias de sotobosque fueron especialmente vulnerables, raramente cruzaron caminos, aún los que tenían recrecimiento*

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alto. Los desplazamientos especies sensibles de un lado a otro de caminos fueron inhibidos debido a que los individuos tendieron a evitar tanto al hábitat afectado por borde cerca del camino como el claro del camino mismo. Nuestros resultados sugieren que aun los caminos angostos con bajos volúmenes de tráfico pueden reducir los desplazamientos locales de muchas especies insectívoras en la Amazonía.

Palabras Clave: aves amazónicas, aves y caminos, caminos y desplazamiento de aves

Introduction

The Amazon basin supports over half the world's remaining tropical rainforest (Whitmore 1997). Unfortunately, it also has the highest absolute rate of deforestation: 2–4 million ha are being cleared each year, with a comparable area degraded by logging, forest fragmentation, and invasive ground fires (Nepstad et al. 1999; Laurance et al. 2001a; Cochrane & Laurance 2002). Moreover, development activities in Brazilian Amazonia are likely to accelerate during the next decade, with over \$40 billion in planned infrastructure investments, including extensive linear clearings from new highways, roads, power lines, gas lines, and river-channelization projects (Laurance et al. 2001b).

The proliferation of human-made clearings may have important impacts on wildlife populations. To date, most fragmentation research has concentrated on large-scale clearings as barriers to wildlife movement, and it is only recently that narrow linear clearings, like those associated with roads and power lines, have been shown to have substantial effects on some species (reviews in Goosem 1997; Forman & Alexander 1998; Trombulak & Frissell 2000). In forests, linear clearings can cause important edge effects (Williams-Linera 1990), promote invasion of exotic or generalist species (Goosem 1997), and increase human disturbances and hunting (W. F. Laurance 2001; Kerley et al. 2002). For sensitive fauna, linear clearings may create partial or even complete barriers, impeding natural movements and gene flow and potentially fragmenting local populations (Bennett 1991; Forman & Alexander 1998).

Most studies of linear clearings have focused on determining their effects on the distribution and abundance of wildlife species in the adjacent habitat or on traffic-induced mortality. The influence of linear clearings on animal movements has been assessed less frequently, most often for small and medium-sized mammals (reviewed in Goosem 1997). Using baits, translocation, and playback of recorded calls, some researchers have demonstrated that wildlife species can be induced to cross a linear barrier (Burnett 1992; Desrochers & Hannon 1997; Goosem & Marsh 1997; Devey & Stouffer 2001). Although these are useful attempts to assess the movement capacity of species, they do not examine the patterns of passive (and presumably more natural) movements or home range boundaries across linear barriers.

Understory rainforest birds are an ideal group for assessing the potential environmental effects of roads. They are highly diverse, readily sampled, and strongly associated with forest habitat. They have also been observed to decline or disappear in habitats that are disturbed by fragmentation (Stouffer & Bierregaard 1995), logging (Thiollay 1992), and artificial forest edges (Canaday 1996; Restrepo & Gomez 1998). Furthermore, they are generally considered poor colonists with limited dispersal abilities (Lovejoy et al. 1986; Sieving & Karr 1997). For example, immigration by understory birds to central Amazonian forest fragments was sharply reduced by clearings as narrow as 70–100 m (Harper 1989; Stouffer & Bierregaard 1995). Some understory birds appear so specialized for dark forest conditions that they have been observed avoiding even tree-fall gaps and forest regrowth (Thiollay 1992; Borges & Stouffer 1999).

We assessed the local movement patterns of Amazonian understory birds across roads and within adjoining forest over a 2-year period. By studying six road sites with varying levels of forest regeneration we were able to address several questions: Do roads affect the movement patterns of understory birds? Which foraging guilds are most affected? Does the presence of forest regrowth along road verges facilitate road crossing by these birds?

Methods

Study Area

This study was undertaken as part of the Biological Dynamics of Forest Fragments Project (BDFFP), which encompasses a 1000-km² study area located 80 km north of Manaus, Brazil (60°00'W, 2°20'S; for detailed descriptions, see Lovejoy et al. 1986; Laurance et al. 2002). The area supports nonflooded, lowland tropical rainforest, which averages 28–35 m in height and has emergent trees reaching 55 m. The understory is relatively open and dominated by stemless palms. Soils are yellow latosols and are nutrient-poor and highly acidic. Rainfall averages about 2600 mm/year and is seasonal, with a wet season from January to April and a dry season from June to September.

The BDFFP study area is spanned along its east-west axis by a 40-km-long dirt road, which was bulldozed through

the forest in the late 1970s to provide access to local farms and cattle ranches. Originally, a clearing 30–40 m wide was created, which included a 4- to 6-m-wide road surface and verges along either side. Regrowth vegetation has regenerated along the road verge and varies in height and complexity. We examined three different levels of forest regeneration: (1) cleared-road sites supported a small amount of regrowth (<3 m in height) that extended about 7 m from the primary forest borders on each side, resulting in a road-clearing width of about 25 m; (2) intermediate-regrowth sites had regrowth 3–8 m in height that extended about 14 m into each road verge, leaving a clearing of about 12 m wide; (3) tall-regrowth sites supported regrowth 15–20 m in height that extended in a noncontinuous canopy across the entire road clearing, with some canopy gaps 2–3 m wide. All sites were separated by >500 m. Road traffic was restricted to authorized vehicles and averaged 6–10 passes per week. In all six study sites, intact forest (unlogged and unfragmented) extended for >20 km on each side of the road.

Sampling Methods

At each of the six study sites, we assessed local bird movements (≤ 300 m long) within a large study plot (4.5 ha). Plots were centered on the road and consisted of six 150-m transects oriented parallel to the road and 60 m apart (Fig. 1). By comparing movement frequencies of birds between adjacent net lines within the forest versus those across the road, we could quantitatively assess the effects of the road on bird movement (Fig. 1).

We sampled each site five times, each time for 4 consecutive days. Each day, we opened three neighboring mist nets on each line and afterward moved the nets to new adjoining locations along the line. Standard-size mist nets (36-mm mesh, 2 × 12 m) were opened at 0600 hours for 8 hours on the first day and 6 hours on following days, except when heavy rain required nets to be closed early. Although the total transect length netted was 150 m, only 36 m was netted per day on each transect. We sampled from November 1997 to November 1999, with an interval of 1.5–8 months between samples (although sampling intervals varied somewhat among sites, all sites were sampled with similar frequency in the dry and wet seasons). Nets were checked every 1–1.5 hrs, and captured birds were identified, weighed, measured, and given unique numbered bands. We determined bird age where possible based on plumage, eye color, bill length, and presence of gape flanges.

Vegetation Structure along Roadsides

Profiles of roadside vegetation were prepared for each study site to illustrate structural differences in vegetation among sites. Profiles were 60 m long and were perpendicular to the road, with the midpoint of the profile located at the road center. They were situated at the center of

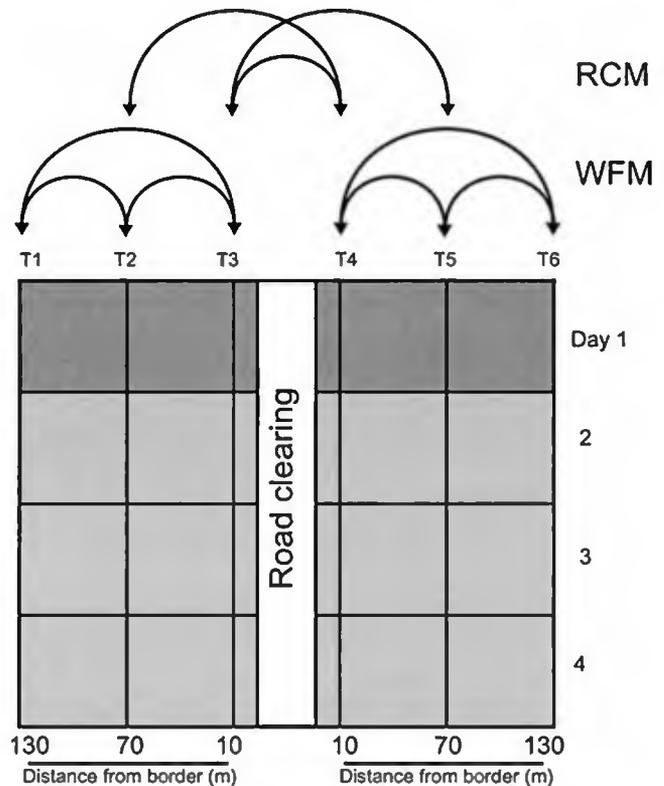


Figure 1. Design of mist-netting plots established at each study site. All net lines were separated by 60 m. Arrows at the top of the figure illustrate the types of movement considered in the analysis: road-crossing movements (RCM) and within-forest movements (WFM).

each netting plot. Every canopy tree and sapling that intercepted the linear transect was mapped, including its position along the transect, canopy size, and height. We also recorded the height and position of all smaller plants (>1.5 m) within a 2-m-wide band along the transect. In addition to the vegetation profiles, quantitative studies revealed significant changes in several forest structural variables within 10–15 m of road edges (reduced canopy height and cover, increased subcanopy cover and logs) relative to forest interiors (130 m from edge; S. G. W. Laurance 2001).

Understory Birds and Their Foraging Guilds

The central Amazon rainforest supports a highly diverse avifauna community with approximately 400 species in the vicinity of the BDFFP study area (Stotz & Bierregaard 1989; Cohn-Haft et al. 1997). Insectivorous species, particularly antbirds (Formicariidae), dominate the understory community (Bierregaard 1990). We placed the most common insectivorous species into guilds, according to their foraging behavior and habitat use (Stouffer & Bierregaard 1995; Cohn-Haft et al. 1997). Army-ant followers are the most frequently captured guild, comprised of

three obligate species that feed almost exclusively on insects fleeing army-ant swarms (Willis & 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 among species (Jullien & 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 1989; Powell 1989). Among these nonflocking species, we divided birds 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 and gap species that prefer forest ecotones and treefall gaps, and solitary understory species that glean foliage or sally to capture insects in the understory. Understory frugivores are also commonly captured in mist nets and were examined in this study.

Data Analysis

Two potentially distinctive behavioral mechanisms may collectively determine the frequency with which wildlife will traverse roads or clearings. The first mechanism is edge avoidance. Some species decline in abundance near forest edges (Quintela 1985; Restrepo & Gomez 1998; S. G. W. Laurance 2004) and may rarely cross road clearings simply because they are uncommon near roads. The second mechanism is gap avoidance, whereby species avoid forest clearings (Greenberg 1989). To our knowledge, the relative importance of these two mechanisms, and the degree to which they are correlated within guilds, has not been assessed previously.

The net effect of road clearing on bird movements results from the combined effects of edge and gap avoidance. We evaluated the net effect of the road on bird movements with mark-recapture data by comparing locations between consecutive captures. Our null hypothesis was that if the road had no net effect on bird movement, then the frequency of recorded movements between net lines on opposite sides of the road should not differ significantly from that of similar lines in nearby intact forest. We considered that the frequency of bird movements between adjacent net lines, which were 60 m apart, represented 60-m movements irrespective of diagonal distances. The same applied to movements between lines that were 120 m apart. Recorded bird movements included those that occurred within a single 4-day netting session and those occurring between different trapping sessions. Few movements were recorded between different study sites (4.1% of total captures), and these were excluded from the analysis.

In our study design (Fig. 1), if the road had no net effect on bird movement, there should have been four times as many 60-m movements within the forest (between adja-

cent net lines T1 and T2; T2 and T3; T4 and T5; and T5 and T6) as across the road (between adjacent lines T3 and T4). In addition, there should have been equal numbers of 120-m movements within the forest (between lines T1 and T3; and T4 and T6) as across the road (between lines T2 and T4; and T3 and T5). Thus, the total number of expected road-crossing movements for any group of birds was 20% of their recorded 60-m movements, plus 50% of their recorded 120-m movements. For example, if a species had 20 movements of 60 m and 4 movements of 120 m, then their expected road-crossing movements would be 6. The 60- and 120-m movements were pooled because the latter were relatively infrequent (<29% of all movements) and hence could not be assessed separately, and because pooling the data increased sample sizes for rare species and guilds.

The net effect of the road on bird movement was assessed at each site with *G* tests for goodness of fit, with Williams's correction for sample size (Sokal & Rohlf 1995). Data at replicate sites were pooled according to regrowth type when bird communities at those sites responded similarly to the road (Bailey 1995), meaning that if both sites showed either significant or nonsignificant results they were pooled. We assessed net road effects for both the entire bird community and several distinct feeding guilds (Appendix 1). A simple index of road avoidance was generated to illustrate bird responses to road clearings: net road avoidance = $[1 - (\text{observed road crossings}/\text{expected road crossings})] \times 100$.

In addition, we quantified edge and gap avoidance for each feeding guild (limited sample sizes precluded these analyses for individual species). An index of edge avoidance was calculated for each guild by dividing its mean abundance (no. individuals/1000 net hours) on net lines farthest from the road (130 m from the road verge) by its abundance on net lines nearest the road (10–15 m from the verge). We tested gap avoidance for each guild by considering only bird movements that originated on net lines nearest the road (thereby eliminating any effect of edge avoidance) and then comparing the frequency of within-forest versus road-crossing movements, with *G* tests for goodness of fit with Williams's correction for sample size. For this analysis, if the birds exhibited no gap avoidance, then 50% of all 60- and 120-m movements should be road-crossing movements, and 50% should be within-forest movements. We summarized these data for each guild with the following index: gap avoidance = $(\text{observed road crossings} - \text{expected road crossings})/\text{expected road crossings}$. For these analyses, data for tall-regrowth sites were excluded to reduce the potentially confounding effects of dense regrowth on edge and gap avoidance.

Movements of longer distances (180–300 m) within the same study plot, which inevitably involved road crossings, occurred relatively infrequently and could not be compared statistically to the frequency of within-forest movements because the maximum possible length of

within-forest movements was 120 m (Fig. 1). We did assess these data qualitatively, however, and contrasted their relative frequency among different bird guilds and among study sites with differing levels of regrowth with a two-way analysis of variance (ANOVA).

Results

A total of 3681 captures was recorded from 13,176 mist-net hours. Bird recaptures were about one-third (1212) of all captures, of which 810 were recorded bird movements (i.e., birds captured in one net line then recaptured in a different line). Of 116 species we caught, we recaptured 66 at least once and recorded movements of 56 (Appendix 1). The 10 most commonly recaptured species were *Hylophylax poecilinota*, *Glyphorhynchus spirurus*, *Gymnophthys rufigula*, *Thamnomanes ardesiacus*, *Pithys albifrons*, *Myrmotherula gutturalis*, *Xiphorhynchus pardalotus*, *Percnostola rufifrons*, and *Turdus albicollis*.

Total Bird Movements

Roads sharply reduced the net rate of bird movement. For five of the six study sites, significantly fewer road crossings occurred than were expected by chance (Fig. 2a). Road crossings for all birds were reduced at cleared sites ($G_{\text{adj}} = 12.45$, $p = 0.0004$), intermediate-regrowth sites ($G_{\text{adj}} = 4.77$, $p = 0.029$), and tall-regrowth site 2 ($G_{\text{adj}} = 7.75$, $p = 0.006$), but not at tall-regrowth site 1 ($G_{\text{adj}} = 0.15$, $p = 0.70$; $df = 1$ in all cases), which had the tallest and most continuous canopy cover of any site.

At each site, on average more than twice as many bird species were recorded moving within the forest ($x \pm \text{SD} = 26.50 \pm 3.02$ species) as across roads (11.83 ± 2.12 species). For all sites combined, 50 species were recorded moving within the forest, whereas only 31 species crossed roads (Appendix 1). Road-crossing species were a limited subset of those moving within the forest, except for *Corythopsis torquata* and *Hylexetastes perrotii*, both of which are forest birds whose lack of recorded within-forest movements most likely resulted from low abundances rather than a preference for edge habitats.

Juvenile Birds

We analyzed net movements of juvenile birds separately (Fig. 2b) because they are more likely to be transient and might cross roads in search of vacant territories. Juveniles exhibited a significant reduction in movements at cleared sites ($G_{\text{adj}} = 4.31$, $p = 0.038$), but not at either intermediate-regrowth ($G_{\text{adj}} = 0.93$, $p = 0.33$) or tall-regrowth ($G_{\text{adj}} = 0.71$, $p = 0.40$) sites.

Foraging Guilds

Three species of army-ant followers in our study area are considered obligate (or “professional”) ant-following

birds: *Pithys albifrons*, *Gymnophthys rufigula*, and *Dendrocincla merula*. All were recorded moving within the forest at all six sites, but at five of the six sites only one or two species were recorded crossing the road (Fig. 2c). The net rate of movement across the road was significantly reduced at cleared sites ($G_{\text{adj}} = 7.19$, $p = 0.007$), intermediate-regrowth sites ($G_{\text{adj}} = 4.06$, $p = 0.044$), and tall-regrowth site 2 ($G_{\text{adj}} = 7.01$, $p = 0.008$) but not at tall-regrowth site 1 ($G_{\text{adj}} = 0.39$, $p = 0.53$). The White-plumed Antbird (*Pithys albifrons*) was the most frequently captured bird in this guild for both within-forest and across-road movements.

Nine solitary understory species had recorded movements between net lines (Fig. 2d). Overall, this guild exhibited the highest degree of sensitivity: net road-crossing movements were sharply reduced at all six study sites (cleared: $G_{\text{adj}} = 5.08$, $p = 0.024$; intermediate regrowth: $G_{\text{adj}} = 11.04$, $p = 0.0008$; tall regrowth: $G_{\text{adj}} = 9.43$, $p = 0.002$).

Fifteen species that regularly forage in mixed-species flocks had recorded movements (Fig. 2e). Net road-crossing movements were significantly less frequent than expected at cleared sites ($G_{\text{adj}} = 8.84$, $p = 0.003$) and at tall-regrowth site 2 ($G_{\text{adj}} = 7.69$, $p = 0.006$). However, road-crossing movements were as frequent as expected at intermediate-regrowth sites ($G_{\text{adj}} = 1.45$, $p = 0.23$) and nearly more frequent than expected at tall-regrowth site 1 ($G_{\text{adj}} = 3.80$, $p = 0.051$), where flocks often foraged in the mature regrowth spanning the road (S. G. W. Laurance, personal observation). Almost two-thirds of the road crossings in this guild were made by just two species, *Xiphorhynchus pardalotus* and *Glyphorhynchus spirurus* (Appendix 1).

Movements were recorded for seven terrestrial species, but these birds were uncommon in mist-net captures because they usually walk rather than fly through the forest. Despite the small number of recorded movements ($n = 20$), significantly fewer movements than expected occurred at cleared sites ($G_{\text{adj}} = 4.08$, $p = 0.043$) but not at sites of intermediate regrowth ($G_{\text{adj}} = 0.05$, $p = 0.82$) and tall regrowth ($G_{\text{adj}} = 0.30$, $p = 0.59$) (Fig. 2f).

Six insectivore species that commonly forage on forest edges or gaps had recorded movements (Fig. 2g). For this guild, there was no net inhibitory effect of the road at cleared sites ($G_{\text{adj}} = 1.25$, $p = 0.26$) and tall-regrowth sites ($G_{\text{adj}} = 1.11$, $p = 0.29$), and road crossings were actually more frequent than expected at intermediate-regrowth sites ($G_{\text{adj}} = 4.94$, $p = 0.026$).

For seven frugivore species (Fig. 2h), no significant net effects of the road were detected at any study site (cleared sites: $G_{\text{adj}} = 0.44$, $p = 0.51$; intermediate-regrowth sites: $G_{\text{adj}} = 0.08$, $p = 0.78$; tall-regrowth sites: $G_{\text{adj}} = 0.60$, $p = 0.40$). The most abundant member of this guild, the White-crowned Manakin (*Pipra pipra*), accounted for about 70% of road crossings (Appendix 1). Two other frugivores, *Schiffornis turdinus* and *Turdus albicollis*, may

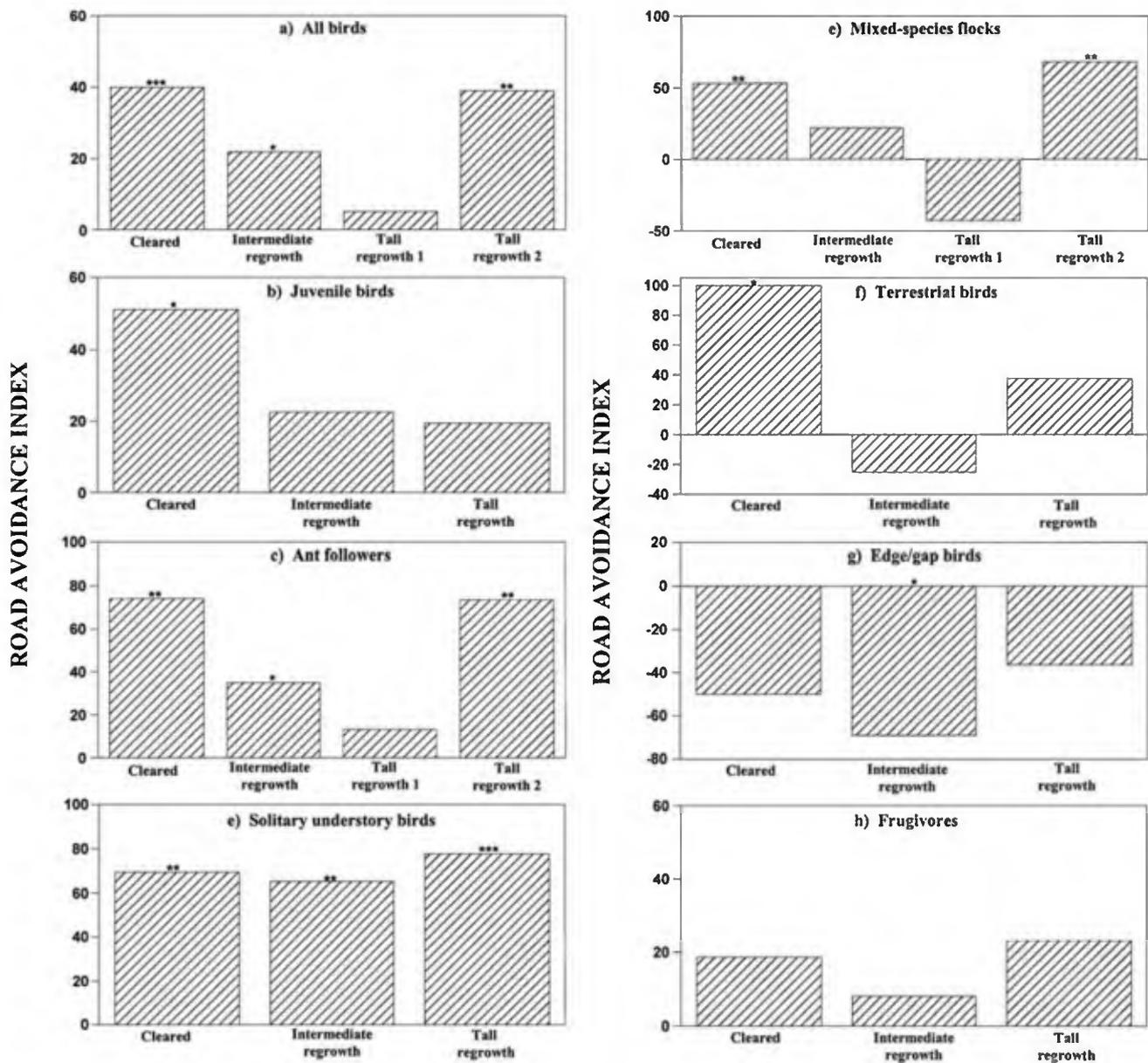


Figure 2. Road avoidance by insectivorous birds in central Amazonia in response to differing levels of roadside vegetation. Positive road-avoidance values indicate the road reduced bird movements relative to rates inside the forest, whereas negative values indicate an opposite trend (significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

be more sensitive to roads than this guild-level analysis suggests. For these two species, there were 26 within-forest movements and only a single road-crossing movement.

Edge and Gap Avoidance

Edge avoidance varied greatly among the six guilds. As indicated by edge-avoidance values of < 1 , edge and gap species (0.45) and frugivores (0.91) increased in abundance near the road, whereas army-ant followers (2.00), solitary species (2.41), mixed-species flocks (1.79), and

terrestrial species (2.52) all declined near the road (Table 1). Gap avoidance also varied among guilds, with positive values indicating gap avoidance and negative values indicating the opposite trend. Despite limited sample sizes in this particular analysis (Table 1), army-ant followers ($G_{adj} = 8.0$, $p = 0.005$) and solitary species ($G_{adj} = 3.85$, $p = 0.05$) exhibited significant gap avoidance, and results were nearly significant for mixed-species flocks ($G_{adj} = 3.60$, $p = 0.058$). Terrestrial species could not be tested because of inadequate sample sizes, whereas edge and gap species ($G_{adj} = 0.35$, $p = 0.55$) and frugivores ($G_{adj} = 0.31$, $p = 0.58$) showed no significant gap avoidance.

Table 1. Data used to derive indices of edge and gap avoidance for each guild in this study.^a

Guild	Mean abundance ^b		Edge avoidance	Observed movements ^c		Gap avoidance
	edges	interiors		within forest	across road	
Ant followers	10.84	21.72	2.00	22	7	0.52
Solitary species	5.86	14.11	2.41	8	2	0.60
Mixed-species flocks	14.94	26.77	1.79	30	17	0.28
Terrestrial species	1.93	4.88	2.52	1	1	—
Edge/gap species	11.32	5.08	0.45	11	14	-0.12
Frugivores	13.61	12.44	0.91	16	13	0.10

^aTo avoid biasing results, we excluded tall-regrowth sites from these analyses.

^bNumber of individuals per 1000 net hours.

^cIncludes only movements that originated on net lines adjoining the road.

For most guilds, the indices of edge and gap avoidance were strongly and positively associated (Fig. 3). Except for terrestrial species, which were captured too infrequently near edges to allow reliable estimates of gap avoidance (Table 1), the remaining five guilds exhibited a highly significant correlation between edge and gap avoidance ($r = 0.976$, $df = 3$, $p = 0.004$; Pearson correlation). This pattern suggests that, at least among the avian guilds examined in our study, edge and gap avoidance are correlated traits and both likely contribute to the net reduction of road-crossing movements in sensitive species.

Long-Distance Movements

In addition to localized movements of 60–120 m, some birds were recorded moving longer distances (180–300 m) between net lines at the same study plot, which inevitably involved crossing the road (Table 2). Although

no experimental controls are available to quantify the frequency of such movements in intact forest, the relative frequency of long-distance movements (as a proportion of all recorded movements) can be compared among each guild and study area (Table 2). This analysis, using a two-way ANOVA with arcsine-transformed data, revealed that the guilds varied significantly in their frequency of long-distance movements ($F_{5,18} = 3.17$, $p = 0.032$). On average, army-ant followers exhibited a significantly higher frequency ($p < 0.05$) of long-distance movements (28% of all movements) than did either edge and gap species (3%) or solitary understory species (5%) (Tukey's post hoc tests). The remaining guilds and juvenile birds had intermediate frequencies of long-distance movements (13–15%). There was no significant effect of regrowth type on the frequency of long-distance movements ($F_{2,18} = 0.95$, $p = 0.41$) or any interaction between guild and regrowth type ($F_{10,18} = 0.45$, $p = 0.90$). Thus, for highly mobile species like army-ant followers, the potential barrier effects of roads may be less severe than for more sedentary, forest-dependent species like solitary understory insectivores.

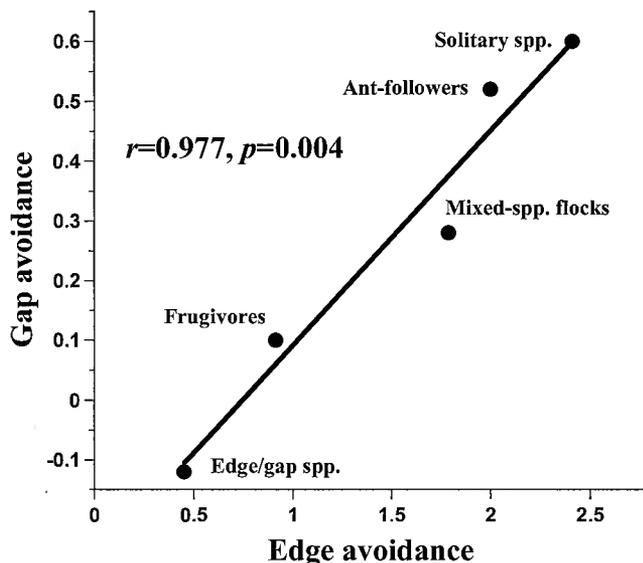


Figure 3. Positive association between indices of edge avoidance and gap avoidance in five guilds of Amazonian understory birds.

Discussion

Our results suggest that even a relatively narrow, unpaved road with little traffic significantly reduces the road-crossing movements of many Amazonian understory birds. This reduction in movements apparently has two distinct but interrelated causes: edge avoidance and gap avoidance. Sensitive species exhibited edge avoidance, tending to avoid the general vicinity of forest edges near roads, and they exhibited gap avoidance, rarely traversing the road clearing itself. At least at a guild level, these two behaviors were strongly and positively correlated (Fig. 3), and both contributed to the observed impact of the road on bird movements. To our knowledge, ours is the first study to distinguish the effects of these two distinctive mechanisms that can lead to reduced wildlife movements across roads.

Table 2. Percentage (and number) of long-distance movements (180–300 m) recorded for each avian guild and study site.

Guild	Cleared sites		Medium regrowth		Tall regrowth		Mean (sum)
	site 1	site 2	site 1	site 2	site 1	site 2	
Ant followers	32 (7)	41 (11)	22 (8)	25 (14)	29 (20)	23 (8)	28 (68)
Solitary species	7 (1)	0 (0)	0 (0)	5 (1)	19 (3)	0 (0)	5 (5)
Mixed-species flocks	3 (1)	16 (6)	10 (4)	17 (7)	18 (11)	27 (10)	15 (39)
Terrestrial species	0 (0)	14 (1)	50 (1)	0 (0)	50 (1)	0 (0)	13 (3)
Edge/gap species	0 (0)	0 (0)	5 (1)	10 (1)	0 (0)	0 (0)	3 (2)
Frugivores	6 (1)	0 (0)	11 (2)	26 (6)	15 (2)	11 (2)	13 (13)
Juveniles	5 (1)	22 (4)	12 (4)	27 (7)	5 (1)	9 (2)	14 (19)
Total birds	10 (10)	17 (18)	12 (16)	19 (29)	22 (37)	15 (20)	16 (130)

Mechanisms Promoting Road Avoidance

Why do many Amazonian understory birds avoid forest edges and clearings? First, many species may have had little reason to traverse clearings in their evolutionary history, so avoidance of such areas is probably an innate response (e.g., Greenberg 1989). Interestingly, species that readily traverse road clearings, such as the mixed-species flock members *Glyphorhynchus spirurus* and *Xiphorhynchus pardalotus*, have persisted in small (1–10 ha) forest fragments in our study area, whereas other members of this guild, which rarely use road clearings, have declined significantly or disappeared (Stouffer & Bierregaard 1995; S. G. W. Laurance 2001).

Second, abrupt forest ecotones near roads and clearings are subject to diverse edge effects that alter forest structure, light levels, thermal regimes, floristic composition, and invertebrate abundance (e.g., Lovejoy et al. 1986; Kapos 1989; Didham 1997; Laurance et al. 1998, 2002; S. G. W. Laurance 2001). Such environments probably seem harsh or unfamiliar to bird species adapted to the dark, humid conditions of forest interiors. Edge avoidance might also occur because diurnal predators such as White Hawks (*Leucopternis albicollis*) and Bat Falcons (*Falco ruficularis*) tend to hunt along forest edges (R. O. Bierregaard, personal communication). Territorial behavior by invasive edge or generalist species could potentially cause edge avoidance, but incursions of non rainforest birds (e.g., *Troglodytes aedon*, *Ramphocelus carbo*) are rare in our study area except in large clearings (Stouffer & Bierregaard 1995; Stouffer & Borges 2001).

Third, territorial animals such as birds are known to align their territories or home ranges along sharp habitat discontinuities such as road margins (reviewed in Bennett 1991; Goosem 1997; Forman & Alexander 1998). Normal territorial defense by resident birds would therefore tend to reduce road-crossing movements. For guilds such as mixed-species flocks, however, regeneration of tall regrowth along road verges “softened” the forest edge to the degree that the entire road was incorporated into the birds’ home range (Develey & Stouffer 2001). Other species, such as certain edge and gap insectivores, appeared to establish home ranges that spanned the road

and adjoining forest on either side, especially where there was limited regrowth along road verges (S. G. W. Laurance 2001).

Finally, some wildlife species avoid the vicinity of roads because of human or traffic-related disturbances (e.g., Rost & Bailey 1979; van der Zande et al. 1980; Goosem 1997). Songbirds, for example, appear sensitive to even low levels of noise (Forman & Alexander 1998). Such effects are unlikely in this study, however, because traffic volume was low (6–10 vehicle passes/week) and because our study area is protected from hunters, loggers, and other human disturbances. There was no observed road mortality of birds during this study.

Effects of the Road and Adjoining Regrowth

The narrow road we studied sharply reduced overall bird movements across the road, but the net effect of the road varied greatly among birds in different foraging guilds. Two guilds, frugivores and edge- and gap-favoring insectivores, were little affected by the road, regardless of the clearing width and amount of adjoining forest regrowth. Two other guilds, mixed-species flocks and terrestrial species, exhibited significantly reduced movement across cleared roads with little regrowth along their verges. Finally, the two remaining guilds, solitary understory species and army-ant followers, appeared to be strongly affected by road clearings, with sharply diminished movements across both cleared roads and those with substantial regrowth along their verges.

These conclusions, however, must be tempered by the fact that our study focused on short-distance movements (≤ 120 m) across roads and in forest. Some longer-distance movements (180–300 m) across roads also occurred, especially by army-ant followers (Table 2), probably because they often forage widely with few fixed territorial boundaries as they track marauding swarms of army ants (Willis & Oniki 1978; Harper 1989). This suggests that army-ant followers in particular, and highly mobile species in general, may be less vulnerable to road clearings than are sedentary, territorial species, especially when the latter are strongly dependent on forests. Notably, experimental studies of the ant-following species

have shown that birds translocated into forest fragments will cross clearings 100 to 320 m wide to return to primary forest (Harper 1989), although clearings of only 100 m preclude their movements under normal circumstances (Bierregaard & Lovejoy 1989; Stouffer & Bierregaard 1995).

Our results are in accord with those of other studies suggesting that many understory insectivorous birds are highly sensitive to habitat alteration (Thiollay 1992; Stouffer & Bierregaard 1995; Canaday 1996; Sieving & Karr 1997; Restrepo & Gomez 1998; Stratford & Stouffer 1999). Our findings may be conservative for guilds such as terrestrial species that are relatively rare and difficult to capture in mist nets. Most terrestrial species are highly vulnerable to forest fragmentation (Stratford & Stouffer 1999) and may have exhibited more significant, negative responses to roads had our sample sizes been larger.

For certain guilds, the height and density of forest regrowth along road verges had a strong effect on bird movement. This was especially evident for mixed-species flocks, which had few short-distance movements across cleared roads but appeared little affected at sites with well-developed regrowth spanning the road. At tall-regrowth site 1, which had the most mature regrowth of any site, at least one mixed-species flock incorporated the road into its home range, as the birds were often observed foraging in trees adjoining and above the road. Similarly, edge- and gap-favoring species appeared to favor road sites with intermediate regrowth, actually traversing them more frequently than they did in intact forest. Solitary insectivores rarely crossed roads, however, even those with considerable regrowth along their verges.

Although clear differences were evident among the different bird guilds, species within the same guild occasionally responded very differently to roads. As a group, for example, understory frugivores appeared little affected by roads, and some species fed on fruits of weedy shrubs (Family Melastomataceae) that proliferated along road verges. However, two frugivore species, *Schiffornis turdinus* and *Turdus albicollis*, appeared to be strongly inhibited by the road (Table 1), and both are also far more vulnerable than other frugivores to forest fragmentation (Bierregaard & Stouffer 1997).

Implications for Conservation

Our results have important implications for forest conservation. First, the narrow dirt road we studied had surprisingly large effects on some species and guilds of understory insectivorous birds. Indeed, our results are probably a best-case scenario because our study area is protected from hunters, loggers, and heavy vehicle use, which would increase disturbances to wildlife. If the movements of mobile organisms such as birds are being inhibited by this narrow road, then less mobile species, such as arboreal vertebrates and sedentary invertebrates, might be

even more vulnerable. For such species, it is not inconceivable that major roads could subdivide populations, increasing their vulnerability to random demographic and genetic effects and increasing the probability of local extinction (Wilcox & Murphy 1985; Gilpin & Soulé 1986).

Among the avian guilds we studied, the movement-inhibiting effects of the road appeared greatest for more sedentary, forest-specialist species. Solitary understory insectivores were most vulnerable, followed by mixed-species flocks, ant-following birds, and terrestrial species. These species often decline in abundance near forest edges, avoid clearings (S. G. W. Laurance 2001), and are highly vulnerable to forest fragmentation (Bierregaard & Lovejoy 1989; Stouffer & Bierregaard 1995; Stratford & Stouffer 1999). Notably, these same guilds are most strongly affected by selective logging operations, which create networks of roads and small clearings in forests (Thiollay 1992).

Regrowth along road verges markedly affected road-crossing movements by forest birds. Our road site with the tallest regrowth, which formed a nearly continuous canopy over the road, was readily used by mixed-species flocks and ant followers, guilds that rarely crossed road sites with little regrowth. In nature reserves, resource managers can help minimize the impacts of roads on sensitive wildlife by encouraging forest regeneration along road verges and establishing continuous canopy cover over the road surface. Roads, power lines, and other linear clearings in reserves should be minimized and the widths of clearings limited (i.e., to no more than 15–20 m) so that nearly continuous canopy cover is maintained above the clearing.

The dramatic growth of logging operations, forest-colonization projects, and new infrastructure developments in the Amazon (Laurance et al. 2001b) suggests that the extent and number of linear clearings will increase sharply in the future. By greatly increasing physical access to frontier areas, such projects could sharply accelerate rates of forest loss and fragmentation (Laurance et al. 2001a, 2001b). Efforts are needed to plan and actively manage the design of roads and other linear clearings in the Amazon to reduce their deleterious effects on forest-dependent wildlife.

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Appendix 1. Number of within-forest and road-crossing movements recorded for each species and guild of Amazonian understory bird.

Species/guild	Within-forest movements	Road-crossing movements
Army-ant followers		
<i>Pithys albifrons</i>	103	20
<i>Gymnopithys rufigula</i>	36	6
<i>Dendrocincla merula</i>	8	3
subtotal	147	29
Solitary understory species		
<i>Hylophylax poeclimota</i>	57	5
<i>Hylophylax naevia</i>	1	0
<i>Microbates collaris</i>	7	0
<i>Microcerculus bambla</i>	1	1
<i>Automolus rubiginosus</i>	4	0
<i>Dendrocincla fuliginosa</i>	2	1
<i>Platyrrinchus saturatus</i>	9	0
<i>Myrmotherula gattata</i>	2	0
<i>Frederickena viridis</i>	1	0
<i>Onychorhynchus coronatus</i>	0	0
<i>Malacoptila fusca</i>	4	0
subtotal	88	7
Mixed-species flocks		
<i>Tbannomanes ardesciacus</i>	23	4
<i>Tbannomanes caesiis</i>	15	3
<i>Myrmotherula axillaris</i>	6	2
<i>Myrmotherula gatturalis</i>	15	1
<i>Myrmotherula longipennis</i>	5	2
<i>Myrmotherula menetriesii</i>	1	0
<i>Hylophilus ochraceiceps</i>	4	0
<i>Myiobius barbatus</i>	6	2
<i>Automolus infuscatus</i>	10	2
<i>Philydor erythrocerus</i>	1	0
<i>Xenops minutus</i>	4	0
<i>Deconychura stictolaema</i>	12	1
<i>Deconychura longicauda</i>	1	1
<i>Glyphorhynchus spirurus</i>	46	21
<i>Xiphorhynchus pardalotus</i>	16	12
subtotal	165	51

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Appendix 1. (continued)

Species/guild	Within-forest movements	Road-crossing movements
Terrestrial species		
<i>Arremon taciturnis</i>	1	0
<i>Corythopsis torquata</i>	0	1
<i>Formicarius colma</i>	9	1
<i>Formicarius analis</i>	0	0
<i>Myrmeciza ferruginea</i>	5	0
<i>Sclerurus caudacutus</i>	2	0
<i>Sclerurus rufigularis</i>	1	0
subtotal	18	2
Edge/gap species		
<i>Galbula albirostris</i>	11	5
<i>Trogon rufus</i>	1	0
<i>Hypocnemis cantator</i>	5	2
<i>Percnostola rufifrons</i>	15	15
<i>Automolus ocbrolaenus</i>	1	3
<i>Cyanocompsa cyanoides</i>	3	0
<i>Tachyphonus surinamus</i>	2	1
<i>Tbryotborus coraya</i>	2	0
subtotal	41	26
Frugivore species		
<i>Geotrygon montana</i>	3	2
<i>Pipra pipra</i>	36	16
<i>Pipra serena</i>	2	3
<i>Schiffornis turdinus</i>	7	0
<i>Turdus albicollis</i>	19	1
subtotal	67	22
Rare guilds not included in guild-level analyses		
solitary mid-story species		
<i>Momotus monota</i>	3	0
<i>Bucco capensis</i>	1	0
<i>Helexetastes perrotii</i>	0	1
<i>Omnivore species</i>		
<i>Mionectes macconnelli</i>	8	3
Canopy species		
<i>Tachyphonus cristatus</i>	0	1
Nocturnal carnivore species		
<i>Otus watsoni</i>	1	0
All birds	538	142

