
Effects of Roads on Movements by Understory Birds in Mixed-Species Flocks in Central Amazonian Brazil

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Abstract: Roads through tropical forest create linear disturbances that have unknown consequences for forest birds. We studied how a narrow, rarely used road through otherwise undisturbed Amazonian forest affected the movements and area requirements of understory birds that form mixed-species flocks. Differences in road maintenance led to two distinct treatments along the same road. Trees along the "closed" road formed a partial canopy connecting the two sides of the road, although the roadway itself was kept open. The "open" road was regularly maintained, making a complete opening 10–30 m wide. We followed 15 flocks, 5 each in interior forest, along the open road, and along the closed road. These flocks were led by *Thamnomanes antsbrakes*, and each flock had a discreet, permanent territory. Flock territory size (mean = 8.5 ha) did not differ among the three locations. The open road formed the territorial boundary for all five flocks, although birds moved within a few meters of the edge of the road. The closed road was less of a barrier: 2 of 5 flocks used both sides of the closed road. Playback experiments showed that flocks readily crossed the closed road to approach agonistic vocalizations. Along the open road, even though birds responded to playback by becoming agitated and moving to the extreme edge of the roadside vegetation, they were less likely to cross the road and did so only after a longer duration of playback. Our results suggest that flocks respond to a road as they would to a long linear gap. They use the vegetation along the edges of the road, but because they are unwilling to cross the open area, it becomes a flock territory boundary. Similarly, as in forest gaps, successional change along the closed road produced suitable habitat for flocks. Although this suggests that roads are a trivial problem, we caution that this result applies only to narrow roads that are not accompanied by deforestation or other disturbance.

Efectos de los Caminos sobre los Movimientos de Aves de Sotobosque en Parvadas Mixtas en la Amazonía Central Brasil

Resumen: Los caminos en bosques tropicales crean perturbaciones lineares que tienen consecuencias desconocidas sobre las aves. Estudiamos como un camino angosto, poco usado, en bosque no perturbado afectó los movimientos y requerimientos de área de especies aves de sotobosque que forman parvadas mixtas. Las diferencias en el mantenimiento del camino condujeron a dos tratamientos distintos a lo largo del mismo. Los árboles en el camino "cerrado" formaron un dosel parcial que conectaba los dos lados del camino, aunque la vía se mantenía abierta. Al camino "abierto" se le daba mantenimiento regular, formando una abertura completa de 10–30 m de ancho. Seguimos a 15 parvadas, 5 en el interior del bosque, 5 en el camino abierto y 5 en el camino cerrado. Estas parvadas eran dirigidas por *Thamnomanes*, y cada parvada tenía un territorio permanente discreto. El tamaño del territorio (media = 8.5 ha) no difirió en las tres locaciones. El camino abierto formaba el límite territorial de las cinco parvadas, aunque las aves se movían a unos metros de la orilla del camino. El camino cerrado fue una barrera menor; 2 de 5 parvadas utilizaron ambos lados del camino cerrado. Experimentos con cantos grabados mostraron que las parvadas atravesaban el camino cerrado para acercarse a vocalizaciones agonísticas. A lo largo del camino abierto, aun cuando las aves respondieron a las grabaciones agitándose y moviéndose al borde extremo de la vegetación,

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casí no atravesaron el camino, haciéndolo solo después de una mayor duración de la grabación. Nuestros resultados sugieren que las parvadas responden a un camino como lo harían con una franja lineal larga. Utilizan la vegetación a lo largo de los bordes del camino pero, porque no están dispuestas a atravesar el espacio abierto, se convierte en un límite para el territorio de la parvada. De manera similar, como en los claros en los bosques, el cambio sucesional a lo largo del camino cerrado produjo hábitat adecuado para las parvadas. Aunque esto sugiere que los caminos son un problema trivial, aclaramos que este resultado sólo se aplica en caminos angostos no acompañados por deforestación u otra perturbación.

Introduction

The ecological effects of roads are diverse and vary among landscapes and taxonomic groups (reviews by Forman & Alexander 1998; Trombulak & Frissell 2000). Some of these effects are direct, such as the loss of habitat ("internal fragmentation"; Forman et al. 1997; Goosem 1997), edge effects (Reed et al. 1996), colonization by new species (Getz et al. 1978; Tyser & Worley 1992), mortality (Mech 1989; Goosem 1997), and altered ecosystem properties (Forman et al. 1997; Trombulak & Frissell 2000). Indirect effects of roads are probably also important in some systems. The human access provided by roads leads to hunting, timber extraction, and clearing for agriculture (e.g., Fearnside 1983).

Several studies have considered the effects of roads on birds, although most of this work has been conducted in the temperate zone. The effects of roads on the abundance of birds varies with species, road type, season, and distance from the road. For woodlands and open fields in temperate areas, several species show lower densities near roads, possibly because of noise or changes in vegetation structure (Clark & Karr 1979; van der Zande et al. 1980; Reijnen et al. 1995; Forman & Deblinger 2000). For tropical sites, some information is available on roadkills in Australia (Goosem 1997) and on roads as impediments to understory birds in a subtropical forest in Argentina (Malizia et al. 1998).

No results are available for the direct effects of roads on small birds in Amazonian forests, although research on bird use of forest fragments suggests that roads may be significant barriers to movement for some understory species. Near Manaus, Brazil, rainforest fragments isolated from continuous forest by open pastures and young secondary growth as little as 70 m wide lost many species of understory insectivorous birds (Stouffer & Bierregaard 1995). Some of these species, such as army-ant followers and mixed-species understory flocks, recolonized fragments after secondary growth provided connections to nearby forest, implying that the birds were unwilling to cross open areas (Stouffer & Bierregaard 1995). We attempted to determine whether narrow linear disturbances (roads) also impede the movements or alter the composition of mixed-species understory flocks.

Mixed-species bird flocks are a consistent and worldwide phenomenon in forests, especially in the tropics

(Powell 1985). In much of Amazonia, understory flocks are led by nuclear species of the antshrike genus *Thamnomanes* (Munn & Terborgh 1979; Powell 1985; Stotz 1993). About eight other species ("core" species) typically are considered obligate flock participants and have home ranges that overlap exactly with those of the *Thamnomanes* (Powell 1985; Jullien & Thiollay 1998). Each understory flock includes a single pair (sometimes with juveniles) of each of these species. In addition to being sensitive to fragmentation (Stouffer & Bierregaard 1995), understory flocks avoid clearings, large tree-fall gaps, and low second-growth vegetation (Jullien & Thiollay 1998; Borges & Stouffer 1999).

Our objective was to quantify the effects of roads on mixed-species understory flocks. The road we studied was narrow, was accompanied by minimal associated deforestation, and had almost no traffic, so it provided a chance to observe the consequences of the minimal level of disturbance possible for a road through rainforest. Specifically, we tried to answer the following questions: (1) Does proximity to a road affect the size of a flock's home range? (2) Do flocks avoid the edges of roads? (3) Are roads barriers to flock movements? (4) Does proximity to a road affect flock composition? (5) How do these effects vary with development of roadside vegetation?

Study Site

The study area, the Biological Dynamics of Forest Fragments Project site, is located in central Amazonian Brazil, about 80 km north of Manaus at 100–150 m elevation (lat. 2°30'S, long. 60°W). Rainfall averages about 1900–2500 mm annually, with a dry season from June to October. The area is covered mostly by primary terra firme forest, with a canopy height of about 30 m and emergents to 55 m (for a detailed description, see Lovejoy & Bierregaard 1990). We studied flocks along the ZF-3, an unpaved road that bisects the site from west to east (seen in a satellite image given by Stratford and Stouffer 1999). The road surface is about 5 m wide, but differences in road maintenance have led to two distinct disturbances along the road. From km 41 to the west, the roadside is kept open, resulting in an open area about 10 m wide with about 6 m of low secondary growth on each side.

Canopy trees do not cover the road, and insolation is high. To the east of km 41, the road is not maintained, and the edges include tall second growth. Trees, especially *Cecropia sciadophylla*, have grown to form a near complete canopy over the road surface. Vehicle traffic is minimal on both sections of road, averaging about 10 cars per week.

Methods

Field work was conducted from April to September 1999. We selected 15 mixed-species understory flocks: 5 along the open road (west of km 41), 5 along the closed road (east of km 41), and 5 in the forest interior more than 400 m from the road. For analysis of home-range size and movements, we considered the open road, the closed road, and the forest interior as three treatments, each with five replicates. The flocks were followed systematically, and their location and species composition were recorded at 30-minute intervals. The entire area where we worked is gridded with trails every 100 m. Some birds in a flock were mist-netted and color-banded, allowing us to distinguish individual flocks (although distinct flock territories made identification of individual flocks very easy; see results). We define mixed flocks as groups of two or more species in proximity moving in the same direction for at least 5 minutes without an external resource concentration (Stotz 1993). Any bird that participated in a flock for at least 10 minutes was considered part of the flock. We recorded at least 30 observations of each flock over 3–8 days. With the exception of one flock that was followed on 3 consecutive days, each flock was observed over at least 2 months, and observations were staggered to avoid seasonal differences in sampling effort among treatments.

We calculated home ranges for each flock based on minimum convex polygons (MCP) after 30 observations. The MCP analysis ignores the dispersion of points within the territory, so we also analyzed treatment differences in dispersion based on the root-mean-squared deviation (RMS deviation) calculated for each flock. The RMS deviation is the square root of the sum of the x- and y-coordinate variances, so it provides a single value for bivariate data. We also analyzed overlap of flock territories, calculated as the area shared by two adjacent MCPs.

It was not always possible to determine flock composition each time location was recorded, so the sample size for analysis of composition varied among flocks. We analyzed flock composition based on the number of species per observation. To analyze treatment effects on the number of species present in flock observations, we used a mixed-model analysis of variance (ANOVA), with individual flock observations nested within flocks and flocks nested within the fixed treatment effects.

We used playback of taped song to determine whether flocks were willing to cross the road (e.g., Sieving et al. 1996). This technique was modified from methods used to map territory boundaries or examine interspecific aggression (Falls 1981; Stouffer 1997). Many species at our site would travel a short distance outside their normal territory in response to playback (P.F.D. and P.C.S., personal observation). We utilized the same sequence of calls from *Thamnomanes caesius* and *T. ardesiacus*, the two nuclear species, for all playback experiments. The calls were recorded at our site from birds responding to simulated territorial conflict (i.e., playback of other vocalizations). The sequence we used included vocalizations that appear to be used only during agonistic encounters with other flocks. In addition to the *Thamnomanes*, the core species also responded to this vocalization, and on some occasions were attracted even before the *Thamnomanes*. All trials were done with a Sony TCM-5000 tape recorder.

We conducted playback trials on flocks detected from the road, which included only four flocks that were also followed for home-range observations. No flock was tested more than once, and we did not include locations during playback trials in the home-range or flock-composition calculations. Once a flock was detected, we crossed to the opposite side of the road, entered the cover at the road edge, and played the tape sequence for a maximum of 10 minutes or until at least one individual of *Thamnomanes* crossed the road. In addition to trials along the open road and along the closed road, we conducted control playback trials in forest. For the interior forest controls, we began the playback about 30 m away from the flock to simulate the width of the road, although most roadside flocks actually occurred <30 m from the road. For controls, we considered an approach by the flock to within 5 m to be a positive response. For all positive responses we also recorded the time at which the flock crossed the road or approached to within 5 m, and we tried to record the species that crossed the road and the order in which they crossed. We compared the three treatments based on the time of response and the number of positive responses.

Results

Flock Territory Characteristics

Based on 30 observations of each flock, each had discreet, minimally-overlapping territories of 6–11 ha (Table 1; Fig. 1). Unambiguous identification of flocks was facilitated by the fact that each flock assembled at dawn every day at the same place (see also Jullien & Thiollay 1998). The open road formed the territorial limits of the five flocks living along it, although each flock foraged in the vegetation to within a few meters of the road clearing. Along the closed road, three of five flocks were restricted to

Table 1. Home-range characteristics of mixed-species flocks based on 30 observations of each flock.^a

Location	n	MCP ^b size (ha)	Overlap (ha)	Dispersion
		mean ± SE	mean ± SE	mean ± SE
Interior	5	8.24 ± 0.83	0.31 ± 0.27	1.39 ± 0.11
Closed road	5	8.81 ± 0.71	0.38 ± 0.17	1.46 ± 0.10
Open road	5	8.50 ± 1.00	0.41 ± 0.21	1.33 ± 0.08

^aNeither size of multiple convex polygon, overlap, nor dispersion differed among locations.

^bMinimum convex polygon.

just one side, but two other flocks had territories that spanned the road (Fig. 1). Despite the road's effects on territorial boundaries, territory size did not differ among the three treatments (ANOVA: $F_{2,12} = 0.112$, $p = 0.895$). Mean overlap of adjacent study flocks was 0.362 ha but did not differ among treatments (Kruskal-Wallis test, $\chi^2 = 1.069$, $df = 2$, $p = 0.586$). Dispersion of points within territories, as measured by RMS deviation, did not differ among treatments (Table 1; ANOVA: $F_{2,12} = 0.518$, $p = 0.608$). This indicates that the use of space within the territory was similar for all treatments even if a road formed a territorial boundary.

Playback Experiments

Flocks responded aggressively to playback of *Thamnomanes* calls in the interior of the forest, approaching to within 5 m of the tape in 11 of 12 trials (Table 2). Birds that approached but did not come within 5 m of the tape were not scored as positive responses. Along the closed road, birds crossed in all trials (11 of 11 trials; Table 2). One or both of the *Thamnomanes* spp. usually

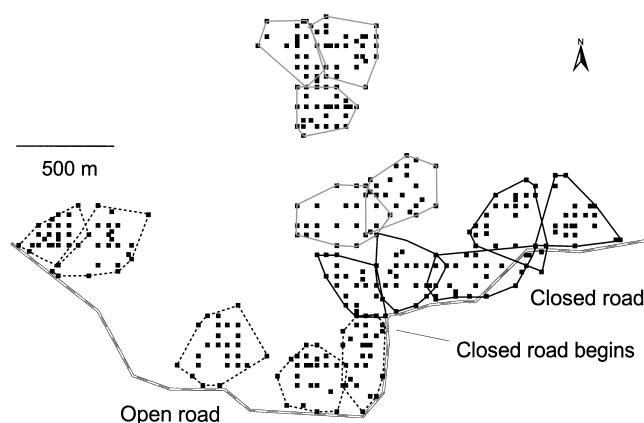


Figure 1. Location points (30/flock) and minimum convex polygon home-range estimates of flocks along the open road (dashed black lines), closed road (solid black lines), and forest interior (solid gray lines). Points <50 m apart appear to overlap on this figure, so not all locations are distinctly visible.

Table 2. Number and mean time (seconds) of bird responses during playback experiments.

Treatment	n	No. of responses*	Response time
			(seconds) mean ± SE*
Interior	12	11 a	99.5 ± 24.2 a
Closed road	11	11 a	229.3 ± 35.0 b
Open road	15	4 b	449.4 ± 49.4 b

*Different letters indicate significant differences among treatments.

crossed first, followed by the other core species, but in some trials the antwrens *Myrmotherula longipennis* and *M. menetriesii* were the first birds to cross and approach the tape. In contrast, flocks crossed the open road in significantly fewer trials, just 4 of 15 ($\chi^2 = 20.18$, $df = 2$, $p < 0.001$; Table 2). Along the open road, only one or two *Thamnomanes* individuals crossed the road. The *Thamnomanes* approached the tape, then returned quickly to the original side while the other flock birds remained right on the edge, obviously agitated. Similar behavior was recorded during all trials when no birds crossed the open road. Birds always reacted strongly to the playback, vocalizing and approaching the edge of the road, but they did not leave the cover of the roadside vegetation. Two of the closed-road trials were conducted on flocks that we knew did not cross the road as part of their normal movements, yet they crossed in response to playback. Thus, birds did move a short distance outside of their territory in response to aggression.

The mean time that the flocks took to respond to playback differed among the three treatments (Table 2; ANOVA: $F_{2,23} = 8.59$, $p = 0.002$). The two types of road caused a similar hesitation in response time, in contrast to the interior of the forest, where approach was more rapid (Table 2).

Flock Composition

A total of 20–36 observations of composition was made for each of 15 flocks. Overall, the mean number of species per flock observation was 10.94 ± 0.17 (SE). As expected, the understory flocks formed around the nuclear species *Thamnomanes caesius*, which was present in 99% of flock observations. Eight other species were present in >50% of flock observations (“core species”; Table 3). With the exception of 1 flock along the open road, from which *Philydor erythrocerus* and *Myrmotherula longipennis* were absent, core species were present in all 15 flocks. The number of core species per observation did not differ among treatments (Table 4; $F_{2,12} = 0.763$, $p = 0.488$). Another 11 “regular” species were present in 11 to 15 flocks and in 15–36% of flock observations. Similarly, the number of regular species per observation did not differ among treatments (Table 4; $F_{2,12} = 2.469$, $p = 0.126$).

Table 3. Frequency of occurrence of core bird species ($n = 444$ observations).

Core species	Overall frequency	Mean \pm SD frequency		
		interior	open road	closed road
<i>Thamnomanes caesius</i>	0.99	0.98 \pm 0.02	1.00 \pm 0.02	0.99 \pm 0.03
<i>Thamnomanes ardestiacus</i>	0.97	0.97 \pm 0.03	0.96 \pm 0.04	0.99 \pm 0.02
<i>Xipborhynchus pardalotus</i>	0.96	0.97 \pm 0.04	0.97 \pm 0.03	0.97 \pm 0.03
<i>Myrmotherula longipennis</i>	0.92	0.98 \pm 0.03	1.00 \pm 0.04	0.80 \pm 0.45
<i>Myrmotherula gutturalis</i>	0.74	0.59 \pm 0.13	0.81 \pm 0.07	0.86 \pm 0.12
<i>Myrmotherula menetriesii</i>	0.59	0.54 \pm 0.16	0.55 \pm 0.16	0.69 \pm 0.16
<i>Tolmomyias assimilis</i>	0.57	0.61 \pm 0.10	0.60 \pm 0.14	0.50 \pm 0.20
<i>Hylophylus ochraceiceps</i>	0.50	0.62 \pm 0.33	0.47 \pm 0.39	0.44 \pm 0.28
<i>Philydor erythrocerus</i>	0.50	0.56 \pm 0.08	0.56 \pm 0.26	0.38 \pm 0.32

Finally, a long tail of 55 “uncommon” species was present in 0.23–14% of observations, although some were recorded in as many as 14 flocks. The number of uncommon species per observation also did not differ among treatments (Table 4; $F_{2,12} = 2.469$, $p = 0.126$). For core, regular, and uncommon species, the mixed-model ANOVA revealed consistent differences among flocks despite the lack of a treatment effect (all $F_{14,424} > 4.770$, $p < 0.001$). This result indicates that our sampling was adequate to detect differences in composition among flocks, but that differences in composition were unrelated to flock location.

Discussion

Our general conclusion is that the open road we studied formed flock territorial boundaries and was a barrier to flock birds, but that it did not lead to systematic changes in flock composition or territory size. These effects were all partially ameliorated by growth of roadside vegetation. Our results are among the most minimal effects that have been shown for roads, as might be expected for a narrow, rarely used road accompanied by no other disturbance (Trombulak & Frissell 2000). Our results also suggest that edge effects on the flocks we studied were less than would be expected from results in forest fragments (or from many temperate-zone studies), illustrating the difficulty in separating edge from area effects (e.g., Murcia 1995; Didham 1997).

Most flock territories were bounded by the road, although two of five flocks used both sides of the road after secondary growth formed a closed canopy over the road surface (Fig. 1). Playback experiments also demonstrated that understory flocks were reluctant to cross the open road (Table 2). Despite the flocks’ strong avoidance of the road itself, proximity to the road did not affect territory size or flock composition. Furthermore, flocks adjacent to the road used the forest to within several meters of the road clearing. These results suggest that the effect of the road was limited to the actual cleared area.

The narrow area of physical disturbance and light traffic along the road we studied appeared not to be associated with increased area requirements or a decrease in the frequency with which birds joined flocks (Tables 1, 3, & 4). Curiously, the density of some temperate-zone species has been shown to be more sensitive to road openings, although most of these studies were conducted with wider and more heavily used roads (Rich et al. 1994; Reijnen et al. 1995; Ortega & Capen 1999; Forman & Deblinger 2000). Even so, studies focusing on birds of the temperate-forest interior have generally shown reduced density near all edges, not just roadsides (e.g., Van Horn et al. 1995; Ortega & Capen 1999). We do not know how the construction of the road affected vegetation structure in the immediately adjacent forest, or how deeply any edge effects on vegetation penetrated into the forest. Tree mortality and vegetation biomass is strongly affected by edges (Laurance et al. 1997), and

Table 4. Mean number of species per observation for core, regular, and uncommon species.

Type	Total species	Treatment*					
		interior		closed		open	
		range	mean \pm SD	range	mean \pm SD	range	mean \pm SD
Core	9	4–9	6.9 \pm 0.6	3–9	6.9 \pm 0.4	4–9	6.6 \pm 0.5
Regular	11	0–8	2.8 \pm 0.8	0–6	2.2 \pm 0.6	0–9	3.1 \pm 1.7
Uncommon	55	0–6	1.5 \pm 0.3	0–12	1.4 \pm 0.5	0–12	1.7 \pm 1.1

*Treatment effects were not significant for any type. Standard deviation (SD) is among flocks.

these changes in forest density might be expected to relate to flock territory size (Jullien & Thiollay 1998). Roadside edges are without corners and are less exposed, so perhaps edge effects are less severe (Murcia 1995). Minimal edge effects on the flocks we studied reinforce observations from fragments, in which flocks leave some fragments to use adjacent tall secondary growth (Stouffer & Bierregaard 1995), a situation similar to flocks crossing the closed road.

In temperate forests, edges of fragments or narrow corridors, such as roads or powerlines, may create ecological traps, attracting predators, parasitic cowbirds, or nonforest birds, especially in heavily fragmented landscapes (Gates & Gysel 1978; Ambuel & Temple 1983; Rich et al. 1994; Robinson et al. 1995). Along the road we studied, we do not know whether the main predators of mixed-species flock birds, probably *Micrastur* forest-falcons, are affected by edges. Cowbirds were rare at our site except in open areas (Cohn-Haft et al. 1997). Although nonforest birds use fragment edges, they rarely penetrate into forest (Stouffer & Bierregaard 1995; Stouffer & Borges 2000). Preliminary data suggest that invasion of nonforest birds along the road is minimal, so competition with edge species is probably not a significant problem for flock species (P.C. S. and P.F.D., personal observation; S. G. Laurance, personal communication). It remains to be seen if differences in prey availability or other factors affect the reproductive success or mortality of individuals living along the road (e.g., Burke & Nol 1998).

Along the open road, *Thamnomanes* occasionally crossed in response to playback, although the road formed the territorial boundary for all five flocks. Once again, this illustrates that birds will sometimes leave their territories in response to playback. Thus, the road serves as a territorial boundary and is generally a barrier to movement, but it is not an absolute barrier. For example, we suspect that dispersing birds sometimes cross the road to prospect for territories on the other side (S. G. Laurance, personal communication). In contrast, open pastures are nearly absolute barriers to movement of flock birds (Stouffer & Bierregaard 1995).

The closed road formed the boundary of the flock territory for three of five flocks. We know nothing of the history of these flocks, but based on our results we can speculate about how the construction of the road approximately 25 years ago and its subsequent maintenance have affected them. Because the flocks were unwilling to cross the road in response to playback, we suspect that the construction of the road probably divided the home ranges of flocks living in the area that was cleared. These flocks either conformed to the new edge, remaining on just one side of the road, or they broke up (for discussion of movements of flocks displaced by fragmentation see Bierregaard 1990). Along the open road, the present spatial organization appeared stable and comparable to territories of flocks in the forest interior. For

these birds, the edge of the road may be treated as the edge of a gap. Understory flocks move around the edges of gaps but do not cross canopy openings (P.F.D. and P.C.S., personal observation).

The closed road approximated the condition of gaps that begin to regenerate. The roadway continued to form the territory boundary for three flocks, even though they could be made to cross the road with tape playback. For these flocks, the road appeared to form a historical boundary. When it was first opened, it was comparable to the open road, and this effect had persisted despite the modification of the physical barrier by succession. One flock was an interesting exception. It used nearly equal areas on both sides of the road, so it probably had persisted in its present location only since regrowth connected the two sides of the road and provided sufficient forest area.

We chose to work with flocking species in part because of the ease with which they could be followed for determination of flock composition and home range. It remains to be seen if other species that have disappeared from small fragments, such as terrestrial insectivores and army-ant followers (Stouffer & Bierregaard 1995; Stratford & Stouffer 1999), are also affected by roads.

Although our results were generally encouraging for birds in forested areas bisected by narrow, rarely used roads, we caution that this situation will not be comparable to roadsides in unprotected areas, where timber extraction and forest clearing radically alter the landscape adjacent to roads. Our results are also unlikely to apply to animals large enough to be hunted, which undoubtedly suffer as a result of the easy access provided by roads.

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