The Condor 114(3):639–644

ROAD CROSSING BY BIRDS IN A TROPICAL FOREST IN NORTHERN VIETNAM

Vu T. Thinh[1,3], Paul F. Doherty Jr.[1], Trinh H. Bui[2], and Kathryn P. Huyvaert[1,4]

[1]*Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523-1474*
[2]*Institute of Forest Ecology and Environment, Forestry University of Vietnam, Xuan Mai, Chuong My, Ha Noi, Vietnam*

Abstract. In continuous forests, roads may function as barriers to dispersal by forest wildlife. By testing responses to recorded calls, we compared bird movement over a paved road with movement within forest-interior plots in Cuc Phuong National Park, northern Vietnam, in summer 2007. We focused on two mid-story species, the Striped Tit-Babbler (*Macronus gularis*) and Rufous-throated Fulvetta (*Fulvetta danisi*), and two ground-feeding species, the Puff-throated Babbler (*Pellorneum ruficeps*) and Buff-breasted Babbler (*P. tickelli*). The probabilities of mid-story species' approaching the recording at the road sites were similar to those at the forest-interior sites. The probabilities of the terrestrial species' approaching the recording were lower at the road sites than in the forest interior. For all species, the delay in response was slightly longer at the road sites than at forest-interior sites. Our results indicate that narrow forest roads may inhibit dispersal by understory birds but are less important barriers for mid-story species.

Key words: Fulvetta danisi*,* Macronus gularis*,* Pellorneum ruficeps, Pellorneum tickelli*, playback, road crossing, Vietnam.*

Cruce de Rutas por Aves en un Bosque Tropical en el Norte de Vietnam

Resumen. En el bosque continuo, las rutas pueden funcionar como barreras para la dispersión de la vida silvestre del bosque. Usando la reproducción de cantos previamente grabados, comparamos los movimientos de aves sobre una ruta pavimentada con los movimientos adentro de parcelas del interior del bosque en el Parque Nacional Cuc Phuong, al norte de Vietnam, en el verano de 2007. Nos enfocamos en dos especies del estrato intermedio del bosque, *Macronus gularis* y *Fulvetta danisi*, y en dos especies que se alimentan sobre el suelo, *Pellorneum ruficeps* y *P. tickelli*. Las probabilidades de que las especies del estrato intermedio se acerquen a los emisores de los cantos en los sitios de la ruta fueron similares a las de los sitios del interior del bosque. Las probabilidades de que las especies terrestres se acerquen a los emisores de los cantos fueron más bajas en los sitios de la ruta que en el interior del bosque. Para todas las especies, el retraso en la respuesta fue ligeramente más largo en los sitios de la ruta que en los sitios del interior del bosque. Nuestros resultados indican que las rutas estrechas que atraviesan el bosque pueden inhibir la dispersión de las aves del sotobosque, pero que son barreras menos importantes para las especies de los estratos intermedios.

INTRODUCTION

In forested landscapes, roads can have adverse effects on a diversity of wildlife species (Forman and Alexander 1998, Forman et al. 2003, Spellerberg 1998, Taylor and Goldingay 2010). The effects of roads in forests can include increased habitat fragmentation, changes in species composition, increased noise, and invasions by exotic plant and wildlife species (Reijnen et al. 1995, Forman et al. 2003, Taylor and Goldingay 2010). In the near term, some species may be attracted to habitats near roads because of enhanced foraging or other features of the altered habitat at road edges (Spellerberg 1998), while a large number of studies report road-associated mortality and the potential for longer-term population reduction in animals ranging from large ungulates and small mammals (e.g., Smith-Patten and Patten 2008) to amphibians (e.g., Mazerolle 2004) and birds (e.g., Gottdenker et al. 2008).

While some bird species may frequent roadside habitats, roads in forests may instead serve as linear, inhospitable gaps that inhibit bird movement through the forest (Forman et al. 2003, Harris and Reed 2002). Gap crossing has been studied worldwide, and birds of both temperate-zone (e.g., Desrochers and Hannon 1997, Grubb and Doherty 1999, Creegan and Osborne 2005) and tropical (e.g., Laurance and Gomez 2005, Van Houtan et al. 2007, Lees and Peres 2009) forests have been shown to be reluctant to cross gaps. Reluctance of forest birds to cross gaps may be related to (1) increased predation risk in areas with less concealed habitat such as along forest edges (Lima and Dill 1990, Lima 2009), (2) problems perceiving habitat availability or suitability on the other side

Manuscript received 13 October 2010; accepted 3 January 2012.
[3]Current address: Wildlife Department, Forestry University of Vietnam, Xuan Mai, Chuong My, Ha Noi, Vietnam.
[4]E-mail: Kate.Huyvaert@ColoState.edu

The Condor, Vol. 114, Number 3, pages 639–644. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2012.100199

of the gap (Lima and Zollner 1996), (3) physical ability to sustain flight across gaps (e.g., Moore et al. 2008), (4) behavioral barriers to movement such as competition (Harris and Reed 2002), or (5) a species' habitat sensitivity when faced with a novel habitat (e.g., Gillies et al. 2011).

Studies of the responses of tropical rainforest birds to narrow gaps in continuous forest have been largely limited to the neotropics. Develey and Stouffer (2001) used playback experiments to evaluate reluctance to cross gaps by flocks of Amazonian birds. Similarly, Lees and Peres (2009) showed that a species' occurrence in fragmented Brazilian forest was related to its propensity to cross gaps. To our knowledge, gap crossing by birds has not been studied in tropical southeast Asia. Nevertheless, information on birds' biology in southeast Asia is critically important given the area's many endemic species, a large proportion of which are considered threatened (Sodhi et al. 2006). The region's growing economy has led to unprecedented rates of conversion of forest to agriculture and logging (Sodhi et al. 2004) and so to increased construction of roads and power lines, emphasizing the need for information on how these sorts of linear corridors influence bird movements.

Using recordings of territorial calls, we examined whether forest birds in Vietnam are inhibited from crossing a road by comparing their movement over a narrow paved road with movement within the forest interior. We focused on four species of the family Sylviidae: two mid-story species, the Striped Tit-Babbler (*Macronus gularis*) and Rufous-throated Fulvetta (*Fulvetta danisi*), and two ground-feeding species, the Puff-throated Babbler (*Pellorneum ruficeps*) and Buff-breasted Babbler (*P. tickelli*). We tested two predictions: (1) birds are not as likely to cross a road to investigate the source of a recording as they are in the forest interior, and, (2) when birds do respond to recordings, the duration from the start of the recording to the bird's approaching it will be longer along the road than in the forest interior.

METHODS

STUDY AREA

Our study site was in the 22 000-ha Cuc Phuong National Park, Vietnam, located 100 km south of Hanoi (20° 14′–20° 24′ N, 105° 29′–105° 44′ E) within the provinces of Ninh Binh, Hoa Binh, and Thanh Hoa. Typical limestone forest constitutes the majority of habitat, and the highest elevation in the park is 700 m. Because the park has been well protected, the forest remains essentially intact with canopy heights reaching 40–50 m.

The park's climate is tropical with two distinct seasons caused by monsoon winds. The hot and rainy season is from May to November, the cool and dry season from December through April. The average year-round temperature is 20.6 °C, the annual minimum temperature is 0.7 °C, and the maximum temperature reaches 39 °C. The park receives ~2100 cm precipitation each year, and relative humidity averages 90%.

We broadcast the four species' calls along a 20-km paved road extending north–south through the park. The road is 6–8 m wide with a 5-m paved surface and is covered by forest canopy forming frequent, narrow gaps along the length of the road. The forest understory on both sides of the road has not been disturbed, and the park is managed primarily for tourism and forest conservation; about 30 vehicles use the road per day (V. T. Thinh, pers. obs.). Our reference sites were located in interior forest at least 200 m from the road.

STUDY SPECIES

In natural forest, the four focal species are relatively abundant, generating a large sample size for the study. The Striped Tit-Babbler weighs 10–12 g, lives in small flocks, and usually frequents the mid-story, typically at heights from 4 to 10 m (V. T. Thinh, unpubl. data). The Rufous-throated Fulvetta weighs 16–18 g, lives in small flocks, and is usually found in the understory and mid-story, up to about 6 m, in old-growth forest. The Puff-throated and Buff-breasted Babblers weigh 26–28 and 16–18 g, respectively, live solitarily or in pairs, and are usually found feeding on the ground or in the understory.

GAP-CROSSING TRIALS

Our study extended from May to August, 2007. We ran the trials from 06:00 to 10:00 in the morning and from 15:00 to 18:00 in the afternoon, when the birds were most active, and only during favorable weather (not in rainy or windy weather). As have previous studies (e.g., Sieving et al. 1996, Develey and Stouffer 2001), we used a playback of a territorial call of the targeted species to elicit the birds' directional movement . We played the calls, from Scharringa (2005), on a Sansa 150c Mp3 player with a directional SME-AFS amplified-playback field-speaker system.

At the road sites, three people walked along the road detecting birds. When a bird was detected, one person entered 5 m into the forest on the side of the road opposite the target bird and played the recording until the bird crossed the road or for a maximum of 10 min. The two other people hid in locations where they could track and record the movement of the focal bird. At the reference site (forest interior), the procedures were the same as for the road sites at similar distances from the focal bird. We defined a positive response as a bird crossing the road to approach the recording. For the forest trials, we recorded the response as positive when the target bird came within 5 m of the speaker. For species that live in flocks, we treated the flock as the sampling unit and terminated a trial when the first bird in the flock was observed to approach the recording's source closely.

We timed the duration from the beginning of the broadcast until the bird crossed the road, defining it as the response delay time. Except in 59 cases in which we clearly distinguished two birds as different when they were 50–200 m apart, all trials were conducted at least 200 m from each other to assure their independence. We chose this distance after consulting published studies of home ranges of small understory birds in other tropical forests (Jansen 1999, Dale and Slembe 2005). We used a directional amplifier to broadcast the calls, so nearby non-target birds were less likely to respond to them.

Several studies have shown that the probability of success of attracting birds with broadcast of territorial calls is close to 1.0 in forest interior (Sieving et al. 1996, Develey and Stouffer 2001). An earlier pilot study also indicated a high propensity for birds to approach our playback in the forest interior. Using information from the pilot study, we estimated that a sample of 48 trials each for our "treatment" (road) and reference (forest interior) groups was sufficient to detect an effect size of 20% with a power of 80% and $\alpha = 0.05$ (Zar 1999).

STATISTICAL ANALYSES

To analyze data on presence and absence of responses we used Proc LOGISTIC (SAS Software, version 9.00, SAS Institute. 2002). To evaluate the idea that forest birds near roads are less likely to cross the gap imposed by the road than are birds traveling in the forest interior, we constructed eight models including one with no effect, three with single main effects (road, foraging height ["height"], and species), and four with additive and interactive combinations of road with height and road with species. We grouped species by foraging height: the Striped Tit-Babbler and Rufous-throated Fulvetta, which forage in the mid-story, in one category, the Puff-throated Babbler and Buff-breasted Babbler, which feed on the ground, in the other. Because of complete dependence between species and foraging-height covariates, we did not construct models containing both species and foraging height.

For trials in which birds responded, we analyzed data on the duration from the start of the playback to the bird's approaching the playback (response delay time) with Proc MIXED (SAS) to investigate whether response delay time was related to proximity of the road, feeding habits, and species. We constructed eight models, one with no effect, three with single main effects (road, foraging height ["height"], and species), and four with additive and interactive combinations of road with height and road with species. Again, because of complete dependence between species and foraging-height covariates, we did not evaluate models containing both species and foraging height.

We used Akaike's information criterion corrected for small sample size (AIC_c) to rank models by the factors that influenced both species' responses and their response delay time. Additionally, we used Akaike weights (w_i) and cumulative Akaike weights (Σw_i) to assess the strength of a given model and covariate in explaining the data (Burnham and Anderson 2002). However, the road factor appeared in the models more often (five times) than did the height and species covariates (three times each), so we used an adjusted cumulative Akaike weight (3/5 of Σw_i) for the road factor. The adjusted cumulative Akaike weights helped to reduce the bias in ranking the covariates resulting from differences in the number of times covariates appeared in the model set. Parameters of interest were averaged across the entire model set if multiple models had nontrivial Akaike weights (Burnham and Anderson 2002).

RESULTS

The numbers of independent trials along the road and in the forest interior, respectively, were 46 and 81 for the Striped Tit-Babbler, 36 and 54 for the Rufous-throated Fulvetta, 42 and 38 for the Puff-throated Babbler, and 46 and 77 for the Buff-breasted Babbler. All species responded strongly to the calls. Striped Tit-Babblers were detected in flocks of 2–5 individuals, Rufous-throated Fulvettas in flocks of 2-4 birds, and Puff-throated Babblers and Buff-breasted Babblers solitarily or in pairs. Most individuals were initially detected by their songs or calls.

No single model explained the probability of approaching the playback adequately (Table 1). A model in which probability of approach was influenced by an additive combination of road and species had the strongest support, with $w = 0.36$. The second best model, which included

TABLE 1. Ranking of eight candidate models describing the probability of a bird's approaching the source of territorial calls broadcast in Cuc Phuong National Park, Vietnam, in 2007. Models are ranked in ascending order by their AIC_c differences (ΔAIC_c) relative to the best model in the set. Akaike weights (w_i) quantify the probability that a particular model is the best model in the set, given the data.

Model[a]	K[b]	ΔAIC_c	w_i
Road + species	5	0.00[c]	0.36
Road + height	3	0.62	0.27
Road + species + road × species	8	1.68	0.16
Road + height + road × height	4	2.36	0.11
Height	2	3.82	0.05
Species	4	3.93	0.05
Road	2	15.29	0.00
Intercept only	1	19.38	0.00

[a]Model covariates included whether the trial was conducted at the road or in the interior of the forest (road), the species of bird in the trial (species), and whether the species in the trial forages on the ground or in the mid-story (height). The model set included models with no effect (intercept only), a single effect, or additive (+) or interactive (×) combinations of road and species or road and foraging height.
[b]Number of parameters.
[c]AIC_c of the top model = 334.21.

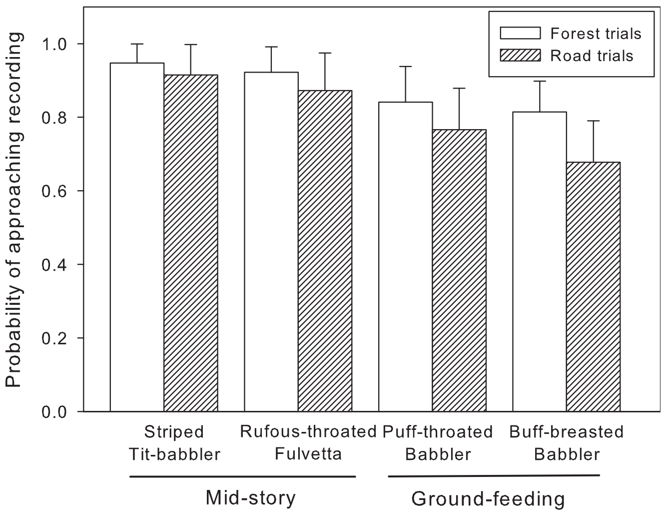

FIGURE 1. Model-averaged probabilities (with 95% confidence intervals) of four species of birds (grouped by foraging height) approaching recordings of territorial calls along a road and in the forest interior, Cuc Phuong National Park, Vietnam.

TABLE 2. Ranking of eight candidate models describing the response delay time before a bird approached the source of territorial calls broadcast in Cuc Phuong National Park, Vietnam, in 2007. Models are ranked in ascending order by their AIC_c differences (ΔAIC_c) relative to the best model in the set. Akaike weights (w_i) quantify the probability that a particular model is the best model in the set, given the data.

Model[a]	K[b]	ΔAIC_c	w_i
Time = road + height[b]	3	0.00[c]	0.33
Time = height	2	0.57	0.25
Time = road + height + road × height	4	1.24	0.18
Time = road + species	5	1.99	0.12
Time = species	4	2.24	0.11
Time = road + species + road × species	8	7.09	0.01
Time = road	2	10.97	0.00
Time = intercept only	1	11.65	0.00

[a]Model covariates included whether the trial was conducted at the road or in the interior of the forest (road), the species of bird in the trial (species), and whether the species in the trial forages on the ground or in the mid-story (height). The model set included models with no effect (intercept only), a single effect, or additive (+) or interactive (×) combinations of road and species or road and foraging height.
[b]Number of parameters.
[c]AIC_c of the top model = 1596.06.

an additive combination of road and foraging height, also had high support (w_i = 0.27 and ΔAIC_c = 0.62; Table 1). Models containing an interaction between road and species also had some support (w_i = 0.16, and ΔAIC_c = 1.68), as did a model with an interaction between road and foraging height (w_i = 0.11, and ΔAIC_c = 2.36; Table 1). The cumulative Akaike weights (Σw_i) provide evidence that variation in the probability of approaching the playback was influenced by foraging height (Σw_i = 0.57), road (adjusted Σw_i = 0.54), and species (Σw_i = 0.43; Table 1 and Fig. 1). The four top models, carrying a total Akaike weight of 0.90, may have similar biological meanings because of the dependence between foraging height and species: two species forage on the ground and two species forage in the mid-story. In sum, the effect of the road on the probability of approaching the playback varied by species and/or foraging height. The effect of the road on bird movement was very small for the mid-story foragers, the Striped Tit-Babbler and Rufous-throated Fulvetta (Fig. 1). The ground-foraging species (Puff-throated Babbler and Buff-breasted Babbler) were more prone to be affected by the road. The reduction in the probability of approaching the playback at the road was greatest for the Buff-breasted Babbler (Fig. 1). A model in which the probability of approaching the playback was similar along the road and in the forest or constant over species or foraging height received no weight and ΔAIC_c = 19.38 (Table 1).

For the trials in which the target individuals did respond, no single model explained variation in response delay time adequately. Models in which the response delay time was influenced by road and foraging height had the highest support (w = 0.33; Table 2). The second best model incorporated foraging height as the explanatory variable (w_i = 0.25, ΔAIC_c = 0.57), while models including interactions between road and foraging height (w_i = 0.18, ΔAIC_c = 1.24) and road and species (w_i = 0.12, ΔAIC_c = 1.99) had some support. These results indicate that the response delay time was influenced mostly by foraging height (Σw_i = 0.76) and to some extent by the effect of road (adjusted Σw_i = 0.39). Variation by species also had some support with a cumulative Akaike weight = 0.24. The response delay time was higher for the ground-feeders than for the mid-story foragers, and the response delay time was slightly higher along the road site than in the forest interior (Fig. 2).

DISCUSSION

Mounting evidence points to the negative effects of rapid development of infrastructure in response to the needs of a growing human population as an important factor diminishing biodiversity. The ecological effects of roads and associated infrastructure cut across ecological scales, from landscape effects such as increased erosion and hydrological changes to community-level effects such as habitat loss. Furthermore, populations and individuals are affected via road-associated mortality or changes in animals' behavior when the gaps formed by roads function as barriers to movement (Forman and Alexander 1998, Trombulak and Frissell 2000, Forman et al. 2003; see Kociolek et al. 2011 for a comprehensive review). For birds of neotropical forests, the gaps caused by

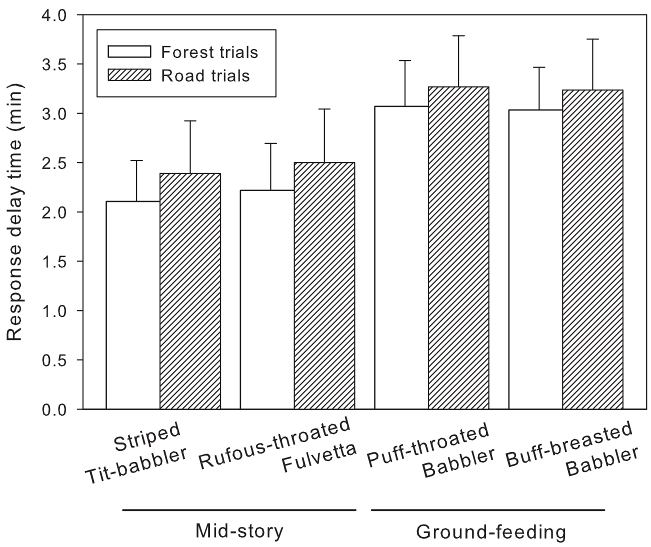

FIGURE 2. Model-averaged response delay times (in minutes, with 95% confidence intervals) of four species of birds (grouped by foraging height) responding to recordings broadcast along a road and in the forest interior, Cuc Phuong National Park, Vietnam.

roads often inhibit movement, and reluctance to cross gaps is related to life-history characteristics such as foraging guild and degree of sociality (Laurance et al. 2004) as well as to aspects of the forest patch and surrounding landscape (Lees and Peres 2009). Nevertheless, no studies, to our knowledge, have examined patterns of gap crossing by birds in the Old World tropics, including southeast Asia.

As found in other studies using broadcast calls to assess the boundaries of tropical birds' territories (e.g., Develey and Stouffer 2001), the proportion of birds responding to the recordings at our forest-interior sites was very high. Individuals of all four species responded to the playback, typically moving toward the speaker within the first 5 min of the call being played. Anecdotally, birds increased the rate and volume of their songs and calls as they approached the speakers, perhaps in response to the playback's volume or, in the case of territorial males, in response to the perception that the playback was a competing conspecific (e.g., Brumm and Todt 2004, Brumm and Ritschard 2011).

In both of our analyses, foraging height had the strongest influence on the dependent variables of interest and carried the highest cumulative Akaike weight. Presence of the road was the second best variable explaining both the probability of birds approaching the playback and response delay time. The mid-story foragers, the Striped Tit-Babbler and Rufous-throated Fulvetta, were more likely to respond to the recordings than were the two ground-feeding species. These two mid-story species both tend to forage in small single-species flocks, and individuals in flocks may respond more readily to playbacks than do solitary birds because the flock dilutes the risk (Krause and Ruxton 2002) posed by the playback. Additionally, mid-story foragers were as likely to approach the recording along the road as in the forest interior, whereas the ground-feeding species were slightly less likely to approach the recording near the road. This may be explained partially by the better cover over the road at the mid-story height and, hence, a narrower open area to be crossed, as Develey and Stouffer (2001) reported in Amazonia, where mixed-species flocks crossed roads with a closed canopy more than they did roads forming a 10–30 m gap in the vegetation. Our results are also in keeping with the pattern found by Laurance et al. (2004), also in Amazonian rainforest, of solitary understory species crossing roads less often than species foraging higher, in part because the gap imposed by the road forms a forest edge that understory species then avoid.

The response delay times at our forest-interior sites were slightly lower than at the road sites for species foraging at both heights, though the mid-story foragers responded on average more rapidly than did the two ground-feeding species. The longer delay we observed for the understory species may again reflect the propensity for avoiding edges imposed by roads shared by other solitary birds of tropical forest understories (Laurance et al. 2004, Lees and Peres 2009). Or understory birds may be reluctant to approach roads because of indirect effects such as changes in vegetation density or habitat perturbation (Kociolek et al. 2011) at those edges rather than because of the presence of the gap itself. The slower response by understory birds might also indicate predator avoidance (Lima and Dill 1990), the road being perceived as riskier habitat. In this case, closure of the canopy over the road in places may have buffered the mid-story birds from perceiving the road as a strong barrier to avoid, so their response time was on average faster than that of the ground-feeding birds.

In conclusion, lightly used roads of the type that we studied in Cuc Phuong National Park, Vietnam, seem not to affect strongly species that forage mostly in the mid-story because of the relatively slight disturbance of the canopy by the road. At the same time, the two ground-feeding species we studied were less likely to respond and slower to respond to recorded calls at the road interface than in the forest interior, indicating a reluctance to cross the narrow gap the road represented. In the course of economic development, many more linear gaps will be imposed on forest landscapes as roads, powerlines, and accompanying infrastructure are built. On the basis of our results in Vietnam and lessons learned from the neotropics, ecosystems and the avifauna that inhabit them will be affected by this rapid development, so that, if road construction is unavoidable, roads should be designed to minimize edges and gaps and to retain as much canopy closure over the road as possible.

LITERATURE CITED

Brumm, H., and D. Todt. 2004. Male–male vocal interactions and the adjustment of song amplitude in a territorial bird. Animal Behaviour 67:281–286.

BRUMM, H., AND M. RITSCHARD. 2011. Song amplitude affects territorial aggression of male receivers in chaffinches. Behavioral Ecology 22:310–316.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multi-model inference, 2nd edition. Springer, New York.

CREEGAN, H. P., AND P. E. OSBORNE. 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. Journal of Applied Ecology 42:678–687.

DALE, S., AND B. SLEMBE. 2005. Effects of selective logging (50 years ago) on habitat use and ranging behaviour of a forest understorey bird (Red-tailed Bristlebill, *Bleda syndactyla*) in Uganda. African Journal of Ecology 43:114–122.

DESROCHERS, A., AND S. J. HANNON. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11:1204–1210.

DEVELEY, P. F., AND P. C. STOUFFER. 2001. Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. Conservation Biology 15: 1416–1422.

FORMAN, R. T. T., AND L. E. ALEXANDER. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

FORMAN, R. T. T., D. SPERLING, J. A. BISSONETTE, A. P. CLEVENGER, C. D. CUTSHALL, V. H. DALE, L. FAHRIG, R. FRANCE, C. R. GOLDMAN, K. HEANUE, J. A. JONES, F. J. SWANSON, T. TURRENTINE, AND T. C. WINTER. 2003. Road ecology: science and solutions. Island Press, Washington, DC.

GILLIES, C. S., H. L. BEYER, AND C. C. ST. CLAIR. 2011. Fine-scale movement decisions of tropical forest birds in a fragmented landscape. Ecological Applications 21:944–954.

GOTTDENKER, N. L., T. WALSH, G. JIMÉNEZ-UZCÁTEGUI, F. BETANCOURT, M. CRUZ, C. SOOS, R. E. MILLER, AND P. G. PARKER. 2008. Causes of mortality of wild birds submitted to the Charles Darwin Research Station, Santa Cruz, Galápagos, Ecuador, from 2002–2004. Journal of Wildlife Diseases 44:1024–1031.

GRUBB, T. C., AND P. F. DOHERTY. 1999. On home-range gap-crossing. Auk 116:618–628.

HARRIS, R. J., AND J. M. REED. 2002. Behavioral barriers to non-migratory movements of birds. Annales Zoologici Fennici 39:275–290.

JANSEN, A. 1999. Home ranges and group-territoriality in Chowchillas *Orthonyx spaldingii*. Emu 99:280–290.

KOCIOLEK, A. V., A. P. CLEVENGER, C. C. ST. CLAIR, AND D. S. PROPPE. 2011. Effects of road networks on bird populations. Conservation Biology 25:241–249.

KRAUSE, J., AND G. D. RUXTON. 2002. Living in groups. Oxford University Press, Oxford, England.

LAURANCE, S. G. W., P. C. STOUFFER, AND W. F. LAURANCE. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. Conservation Biology 18:1099–1109.

LAURANCE, S. G. W., AND M. S. GOMEZ. 2005. Clearing width and movement of understory rainforest birds. Biotropica 37:149–152.

LEES, A. C., AND C. A. PERES. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. Oikos 118:280–290.

LIMA, S. L. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews 84:485–513.

LIMA, S. L., AND L. M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

LIMA, S. L., AND P. A. ZOLLNER. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11:131–134.

MAZEROLLE, M. J. 2004. Amphibian road mortality in response to nightly variations in traffic intensity. Herpetologica 60:45–53.

MOORE, R. P., W. D. ROBINSON, I. J. LOVETTE, AND T. R. ROBINSON. 2008. Experimental evidence for extreme disperal limitation in tropical forest birds. Ecology Letters 11:960–968.

REIJNEN, R., R. FOPPEN, C. TERBAAK, AND J. THISSEN. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. Journal of Applied Ecology 32:187–202.

SAS INSTITUTE. 2002. SAS software, version 9.00. SAS Institute, Inc. Cary, NC.

SCHARRINGA, J. 2005. Birds of tropical Asia 3: sounds and sights. Bird Songs International, Enschede, the Netherlands.

SIEVING, K. E., M. F. WILLSON, AND T.L. DESANTO. 1996. Habitat barriers to movement of understory birds in fragmented south-temperate rainforest. Auk 113:944–949.

SMITH-PATTEN, B. D., AND M. A. PATTEN. 2008. Diversity, seasonality, and context of mammalian roadkills in the southern Great Plains. Environmental Management 41:844–852.

SODHI, N. S., L. P. KOH, AND B. W. BROOK. 2006. Southeast Asian birds in peril. Auk 123:275–277.

SODHI, N. S., L. P. KOH, B. W. BROOK, AND P. K. L. NG. 2004. Southeast Asian biodiversity: an impending disaster. Trends in Ecology and Evolution 19:654–670.

SPELLERBERG, I. F. 1998. Ecological effects of roads and traffic: a literature review. Global Ecology and Biogeography Letters 7:317–333.

TAYLOR, B. D., AND R. L. GOLDINGAY. 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. Wildlife Research 37:320–331.

TROMBULAK, S. C., AND C. A. FRISSELL. 2000. Ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.

VAN HOUTAN, K. S., S. L. PIMM, J. M. HALLEY, R. O. BIERREGAARD JR., AND T. E. LOVEJOY. 2007. Dispersal of Amazonian birds in continuous and fragmented forest. Ecology Letters 10:219–229.

ZAR, J. H. 1999. Biostatistical analysis, 4th edition. Prentice Hall, Upper Saddle River, NJ.