

**PREDATOR PLAYBACK, FORAGING HEIGHT, AND PHYLOGENY AFFECT GAP CROSSING BEHAVIOR IN TROPICAL FOREST BIRDS**Jessie L. Williamson^{1,2} · Matthew E. Fagan³¹ Middlebury College, Department of Biology, Middlebury, VT 05753, USA.² Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131-0001, USA.³ Department of Geography and Environmental Systems, University of Maryland, Baltimore County, Baltimore, MD 21250, USA.

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Abstract · The effects of fragmented landscapes on tropical bird movements remain poorly understood, partly due to a dearth of experimental tests of gap crossing behavior. To learn more about the factors involved in gap crossing behavior, we used predator-playback experiments on four species of understory-insectivore birds (Chestnut-backed Antbird *Poliocrania exsul*, Black-crowned Antshrike *Thamnophilus atrinucha*, White-breasted Wood-wren *Henicorhina leucosticta*, Stripe-breasted Wren *Cantorchilus thoracicus*) at La Selva Biological Station, Costa Rica. We sought to understand species- and family-level differences in gap crossing behavior, specifically: (1) the effect of forest-opening (gap) width, and (2) the effect of perceived risk of predation. A total of 39 treatment (predator playback) and 39 control (silent playback) trials were conducted at gap sites ranging in width from 2.8 to 12.6 m. Predator playback decreased the number of times that birds crossed study gaps, increased latency time in all but one species, and increased the closest distance that birds approached the playback speaker. Gap width affected only latency time: as gap width increased, latency time increased. We observed strong differences in behavioral response between families and species of different foraging heights. In the statistical models, family (Thamnophilidae and Troglodytidae), foraging height (low or mid-story), and trial type (silent control or predator treatment) consistently emerged as strongest predictors of bird behavior. Our results indicate that small linear gaps (< 12.6 m) do not impede movement for these four focal species, but that risk of predation may hinder bird movement even at small gaps.

Resumen · Playback de aves de presa, altura de forrajeo y filogenia afectan el comportamiento de aves insectívoras al cruzar claros de bosque en Costa Rica

Se conoce poco sobre los efectos de los paisajes fragmentados sobre el movimiento de las aves tropicales, debido en parte a la escasez de experimentos sobre la renuencia de diferentes especies a cruzar los claros de bosque. Para aprender más sobre los factores involucrados en el comportamiento de aves al cruzar los claros de bosque, se utilizaron llamadas grabadas de un Gavilán Común (*Leucopternis semiplumbeus*) en experimentos de 'playback' sobre cuatro especies de aves insectívoras (Hormiguero Dorsicastaño *Poliocrania exsul*, Batará Pizarroso Occidental *Thamnophilus atrinucha*, Cucarachero Pechiblanco *Henicorhina leucosticta*, Cucarachero Pechirrayado *Cantorchilus thoracicus*) en la Estación Biológica La Selva, Costa Rica. Se trató de entender las diferencias en el comportamiento de cruzar claros de bosque a nivel de especie, específicamente: (1) el efecto de la anchura del claro y (2) el efecto del riesgo percibido de depredación. Se realizaron 39 experimentos con playback de gavilán (tratamiento) y 39 experimentos con playback de silencio (control) en sitios de claros de bosque con una anchura de 2,8 a 12,6 m. El playback del gavilán disminuyó el número de veces que las aves cruzaron los claros de bosque, aumentó el tiempo que tardaron en iniciar el cruce en tres de las cuatro especies estudiadas y aumentó la distancia más cercana que acercaron el altavoz. La anchura del claro de bosque afectó sólo el tiempo que las aves tardaron en iniciar el cruce: el tiempo que tardaron en iniciar el cruce aumentó con el aumento de la anchura del claro de bosque. Observamos diferencias fuertes en respuestas entre familias y especies de diferentes alturas de forrajeo. En los modelos, familia (Thamnophilidae y Troglodytidae), la altura de forrajeo (bajo o medio del dosel) y el tipo de playback (control de silencio o playback de gavilán) constantemente emergieron como predictores fuertes. Nuestros resultados indican que los claros de bosque pequeños y lineales (< 12,6 m) no impiden el movimiento de las cuatro especies estudiadas, pero que el riesgo de depredación tal vez dificulte el movimiento de aves aun en claros de bosque pequeños.

Key words: Fragmentation · Gap crossing · Insectivore · Predation · Thamnophilidae · Troglodytidae

Receipt 22 December 2016 · First decision 22 March 2017 · Acceptance 18 July 2017 · Online publication 20 July 2017

Communicated by Kaspar Delhey © The Neotropical Ornithological Society

INTRODUCTION

Gap crossing, or movement by animals across habitat with no canopy (Grubb & Doherty 1999), is critical to understanding the long-term effects that habitat loss and fragmentation will have on Neotropical specialists like understory insectivorous birds. Detrimental effects of habitat fragmentation on bird populations include reduced structural connectivity, reduced habitat area, isolation from other suitable habitats, and habitat-edge phenomena, such as changes to temperature, humidity, and light levels (Hagan et al. 1996, Germaine et al. 1997, Stratford & Robinson 2005, Robertson & Radford 2009, Ibarra-Macias et al. 2011, Visco et al. 2015). While the impact of interior forest openings, or gaps, on bird movement is reasonably well-studied in the temperate zone (St. Clair et al. 1998, Desrochers et al. 2002, Harris & Reed 2002), the effects of fragmentation and mechanisms that drive bird gap crossing behavior in the tropics are much less well understood (Stratford & Robinson 2005, Robertson & Radford 2009, Thinh et al. 2012).

Conclusions drawn from extensive temperate and boreal gap crossing research do not necessarily apply to tropical studies, due in part to the unusually specialized lives of tropical birds (Stratford & Robinson 2005). Presence of gaps < 30 m is thought to have little overall impact on temperate forest generalists and specialists (Desrochers & Hannon 1997). Rail et al. (1997) found that boreal forest specialists (*Catharus ustulatus*, *Regulus satrapa*, *Setophaga virens*) showed no significant decrease in their probability of response up to 100 meters (m) through continuous forest. Black-capped Chickadees (*Poecile atricapillus*) have been known to cross gaps as large as 200 m when no other choice existed (St. Clair et al. 1998). In contrast, many tropical species are strongly affected by the slightest changes in environmental variation; they do not range widely, do not disperse far from their natal territories, and avoid unsuitable habitat due to physical or behavioral limitations (Laurance & Gomez 2005, Van Houtan et al. 2007). Due in part to these factors, forest specialists, including the generally dispersal-limited understory insectivores, are declining disproportionately in fragmented forests worldwide (Stratford & Robinson 2005, Ferraz et al. 2007, Kennedy & Marra 2010, Visco et al. 2015).

Many hypotheses have been proposed about why gaps hinder the movement of tropical understory birds and possible factors behind gap avoidance behavior include light sensitivity, risk of predation (perceived predation risk is higher in open vs. forested areas), gap width (larger gaps present a greater barrier than smaller gaps), and physiological tolerance or metabolic constraints (Turcotte & Desrochers 2003, Stratford & Robinson 2005, Ibarra-Macias et al. 2011, Fagan et al. 2016). Most species exhibit a ‘threshold’ distance, whereby a small change in distance produces an abrupt reduction in the probability of movement (Harris & Reed 2002). Little is known about gap crossing thresholds of tropical species, how

canopy openness and light levels affect species’ perception of gaps, nor about how predators might constrain some species but not others, and ultimately affect how species move across their home ranges. Since these species do not have an evolutionary history in open gaps, it would be expected that the light level would affect their perceptual range, or how far they can perceive the landscape matrix (Lima & Zollner 1996, Ibarra-Macias et al. 2011, Pollock et al. 2015). Additionally, greater gap widths may be perceived as riskier, particularly due to presence of diurnal raptors (Laurance et al. 2004, Castellón & Sieving 2006, Awade & Metzger 2008, Lees & Peres 2009, Robertson & Radford 2009, Kennedy & Marra 2010). Even many strong-flying tropical generalists avoid crossing open matrix in favor of longer forested detours (Hadley & Betts 2009).

An understanding of why gaps hinder movement is a key for understanding the effects of fragmentation on biodiversity and movement. Using playback experiments, we examined whether understory insectivores in Costa Rica are inhibited by gaps of different widths inside continuous forest and to what extent perceived risk of predation affects gap-crossing behavior. Conspecific call stimuli were used to incentivize birds to cross gaps to defend home-range territories, while predator call (hawk) playback was used to test whether presence of a likely predator would hinder gap crossing in light of a simulated territorial intrusion. We tested two predictions: (1) birds are more likely to cross smaller gaps than larger gaps; and (2) perceived risk of predation will reduce bird willingness to cross gaps to defend territories. Additionally, we aimed to estimate gap crossing threshold distances for our four focal species.

METHODS

Study sites. This study was conducted at La Selva Biological Station, Heredia Province, Costa Rica (10°26’N, 83°59’W) from June to July 2012 (Figure 1). La Selva is located on the Caribbean slope of the Cordillera Central and contains 1611 ha of lowland tropical rainforest, ranging in elevation from 34–110 m a.s.l. (Sigel et al. 2006). Average annual rainfall is nearly 4000 mm (McDade et al. 1994) and mean monthly temperature ranges from 24.7°C in January to 27.1°C in August (Sigel et al. 2006). Approximately 73% of the La Selva reserve is old-growth lowland rainforest; the remaining 27% is a mix of secondary forest, cleared pasture, and abandoned plantation (Sigel et al. 2006). The station is plotted on a 50 x 100 m grid, with trails markers visible every 50 m. There are 64 km total of trails, 16 km of which are paved.

For the purposes of this study, a forest gap was considered any long linear forest opening, defined as habitat with no canopy (e.g., pathways, trails, roads), bordered on either side by continuous forest (secondary forest, primary forest, and abandoned tree plantations). Our study was conducted along both paved and dirt trails, as well as gravel and dirt roads in the

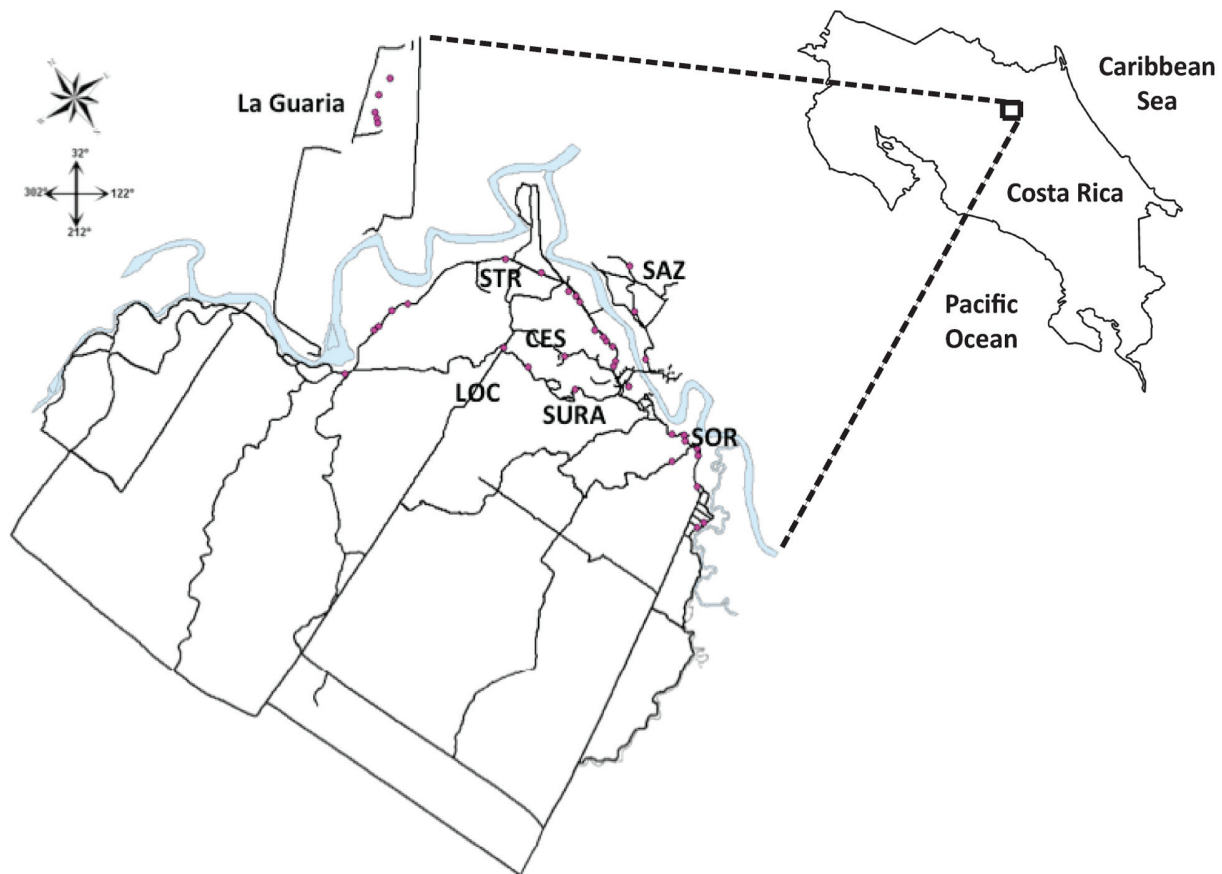


Figure 1. Study sites at La Selva Biological Station, Costa Rica, located along dirt and paved trails in the Old La Selva property, the Las Vegas Annex, the Sarapiquí Annex, and the La Guaria Annex. Additional sites were sampled at Hotel Hacienda Sueño Azul (not depicted), a private reserve south of La Selva Biological station. Labels indicate trail names.

Old La Selva property (667.7 ha), the Las Vegas Annex (65.7 ha), the Sarapiquí Annex (505.1 ha), and the La Guaria Annex (110.9 ha; Figure 1). Study sites were located along forest trails that passed through known focal species territories and were chosen on the basis of meeting width classification parameters. Additional study sites were sampled at Hotel Hacienda Sueño Azul, a 1000 ha private reserve and hotel (10°35'N, 83°97'W) south of Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica. The reserve encompasses areas of primary forest, secondary forest, and abandoned tree plantations. Our study was conducted along a 3 km gravel road that passed through secondary forest, tree plantation, and some pasture areas.

Focal species. Terrestrial understory insectivores, a distinct guild that includes leaf-tossers (Furnariidae), antbirds (Thamnophilidae), antthrushes (Formicariidae), antpittas (Grallariidae), tapaculos (Rhinocryptidae), and wrens (Troglodytidae), are found in most lowland Neotropical forests (Stouffer 2007). They forage almost entirely on arthropod prey taken from the leaf litter, defend large territories, and travel alone, in pairs, or in mixed-species flocks (Willis & Oniki 1972, Stouffer 2007). Due to low abundance, large territories, and specialization to forest floor and

understory environments, this guild is highly sensitive to habitat alteration (Laurance et al. 2004, Sigel et al. 2006, Kennedy & Marra 2010). They suffer from high dispersal limitation and have been found to decline in number with closer proximity to roads (Laurance et al. 2004, Kennedy & Marra 2010).

In this experiment, we studied four species from two families: focal species in the family Thamnophilidae included Chestnut-backed Antbird (*Poliocrania exsul*) and Black-crowned Antshrike (*Thamnophilus atrinucha*); in the family Troglodytidae, we studied the White-breasted Wood-wren (*Henicorhina leucosticta*) and Stripe-breasted Wren (*Cantorchilus thoracicus*). All focal species are highly territorial, abundant in both primary and secondary forest, responsive to playback, and well-studied at La Selva Biological Station (Fagan et al. 2016).

Playback trials. To find and attract focal species, the investigator walked at a steady pace along trails in primary and secondary forest near known focal species' territories (Visco & Sherry 2015, MEF unpubl. data.), broadcasting conspecific 'lure' calls with a portable speaker. The purpose of this was to simulate a territorial intruder to attract birds to the vicinity of trail gaps (Robertson & Radford 2009). Once target birds vocalized in response to the call, the investiga-

tor stopped and initiated repeated playback of the selected species call. Birds were given 10 min to respond to playback by approaching within 5 m of the forest edge. If they did not respond after 10 min, the trial was considered a failure and no data were collected. If the target bird did respond, the experimental trial began after their arrival. The trial starting point was determined by the location of the first responding individual. No more than one playback trial per day was executed for each target bird.

Upon response of the target bird to 'lure' calls, equipment was set up at forest edges (Figure 2). For all playback trials, the side of the trail gap where birds arrived was designated the 'origin', the other side as the 'destination' (Awade & Metzger 2008). In both treatment and control trials, the speaker used to attract the target bird (speaker A) remained at the forest edge on the origin side, continuing to broadcast the conspecific call for a maximum of 10 min. While speaker A played, the investigator crossed the gap and placed a second speaker (speaker C) 10 m from speaker A on the destination side of the forest. Speakers A and C were connected to 50 m audio cables that allowed the investigator to quietly switch between the two speakers from a distance. Upon setting up speakers A and C, the investigator moved approx. 40 m down the path to place a third speaker (speaker B), perpendicular to the others (Figure 2).

Once the speakers and wires were in place, a playback trial commenced by turning off the conspecific playback call from speaker A during a pause in calling, and starting playback from speaker B (either predator call or silent control, depending on trial type). Trials involved two types of playback: predator call treatment trials and silent control trials. In the treatment trial, a Semiplumbeous Hawk (*Leucopternis semiplumbeus*) call was broadcast from speaker B for 20 s to simulate predation risk, followed by a period of 10 s of silence. Following the silence, the conspecific call was broadcast for 10 min from speaker C on the destination side of the gap. This sequence was intended to induce target birds to cross gaps to investigate and potentially defend their territory against conspecific intruders. We chose to use the call of *L. semiplumbeus* for predator playback because this bird is a common raptor species at La Selva Biological Station that tends to hunt at lower levels of the canopy in interior forest.

Control trials were designed to measure target bird response to conspecific intruders in the absence of predator calls. The control trial consisted of a period of 30 s of silence (equivalent in duration to 20 s predator call and 10 s silence in treatment trial), followed by the target bird conspecific call broadcast from speaker C on the destination side of the gap. Each trial lasted exactly 10 minutes. If a predator or other antagonistic bird interrupted the experiment, the trial was stopped and the site was revisited on a different day.

Playback trials were conducted between 05:30 and 09:30 h and between 16:00 and 18:00 h, avoiding rainy and windy days (Desrochers et al. 2002, Turcotte & Desrochers 2003, Sieving et al. 2004, Awade & Metzger 2008). On two occasions, it began raining sufficiently during trials that the experimenter would not have begun them otherwise; because rain interrupted the trials partway through, they were followed through to completion. We alternated gap sizes sampled each day and randomized treatment for each gap site per day. In accordance with paired sampling design, individuals were revisited on different days to test their responses to control and treatment trials (individual ID was inferred from location). Playback trials were spaced at least 250 m from conspecifics and > 50 m from other birds. Throughout playback trials, human interference was minimized by remaining concealed and silent near playback speaker B (perpendicular to the trial), and by taking care not move after the trial commenced.

For all trials, calls were broadcast at a constant volume, ranging from 70–80 dB at 1 m. Focal species songs were taken from the Birds of Costa Rica MP3 sound collection (Boesman 2011). Tracks were mixed in Apple Garageband to produce 10 min loops consisting of 1.5 min of conspecific call followed by 30 s of silence. Playback was clearly audible 25–30 m through continuous forest, a range exceeding the widest forest gap studied. Calls were broadcast from speakers A, B, and C with handheld Altec Lansing iM227 Orbit speakers connected to an Apple iPod Touch. Speakers A and C were connected to the Apple iPod Touch using 50-m long and 35-mm wide audio extension cables, while speaker B was connected to the iPod by a speaker cable.

Variables measured. In each trial, we measured four response variables: whether the bird crossed the gap (yes or no), the number of times the target bird crossed the gap (movement from origin to destination side counted as one crossing, back and forth counted as two crossings, and so on), the time it took for birds to initiate gap crossing (latency), and the closest distance the bird approached speaker C (distance to speaker).

If multiple birds arrived during a trial, number of gap crossings was measured by taking the number of the most-crossed individual. For each trial conducted, we noted start time, end time, and gap width. Gap width was measured with graduated tape by taking a measurement from origin side vegetation line (nearest tree or shrub at tree line) to destination side vegetation line at both the location of the placed speakers, as well as at the location where the bird crossed the gap (if relevant). Light level was measured with a Skye SKR 110 sensor, which reports light at 660 and 730nm in $\mu\text{mol m}^{-2} \text{s}^{-1}$, and we used these readings to calculate the red to far-red (R:FR) ratio (Capers & Chazdon 2004). This ratio allowed us to assess relative shadiness independent of the amount

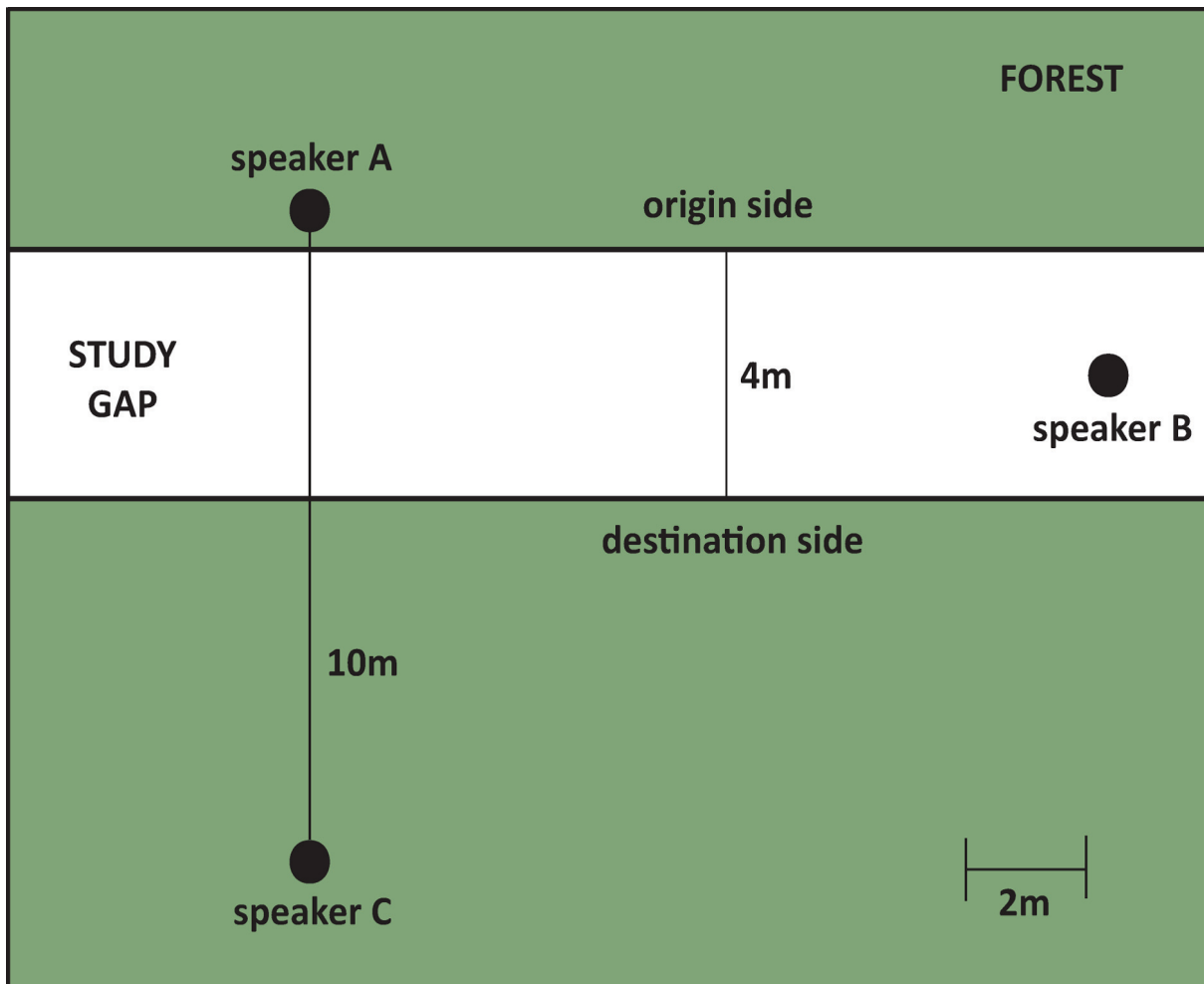


Figure 2. Experiment setup and equipment position during playback trials of gap crossing behavior of four species of lowland rainforest birds at La Selva Biological Station, Costa Rica. Both treatment and control trials followed the same sequence: (1) speaker A broadcast the conspecific call that attracted individuals to the study site; (2) speaker B (approx. 40 m from speakers A and C) broadcast treatment (hawk) or control (silence) call; (3) speaker C broadcast conspecific playback to induce the target bird to cross the gap. The conspecific playback used at speakers A and C was identical. Gap widths sampled ranged from 2.8–12.6 m across.

of light from sun elevation; high light levels are even ratios.

On 14 occasions, control and treatment trials for the same individual were measured at different gap widths (differences ranged from 0.1–2 m in width). We were unable to measure light level at three La Guaria Annex sites, so an average R:FR ratio of 0.55 was used for these localities. Foraging height data was taken from published natural history accounts of our study species (Tarwater & Kelley 2010, Woltmann et al. 2010, Vargas et al. 2011, Flesher 2015), or, when unavailable, from published accounts on foraging behavior of members of the same genus (Zimmer & Whittaker 2009). Our focal species included two low foragers (< 3 m; *P. exsul* and *H. leucosticta*) and two mid-story foragers (3.1 to approx. 20 m; *T. atrinucha* and *C. thoracicus*), with one low and one mid-story forager in each family.

Statistical analyses. Pearson Chi-square and Kruskal-Wallis ANOVAS were used to evaluate the effect of

time of day on all response variables. Data collected from morning and afternoon sampling efforts were pooled (Sigel et al. 2006), as time of day was not a significant predictor of bird behavior and has been shown to have no influence on results in the tropics (Hadley & Betts 2009).

Generalized linear mixed models (GLMMs) with poisson and binomial distributions and a random effect of individual bird (“[1|indivID]”) were used to assess whether family (Thamnophilidae or Troglodytidae), foraging height (low or mid-story), trial type (silent control or predator treatment), gap width, and light level affected measured response variables (whether birds crossed the study gap, how many times birds crossed the study gap, the time birds took to initiate gap crossing (latency), and the closest distance that birds approached the playback speaker). For each response variable we tested four models: the first contained all additive and interactive combinations of family (“family”), foraging height (“forage”), and trial type (“trial”); the second

Table 1. Ranking of models describing predictors of measured behavioral responses during silent control trials and predator playback treatment trials of gap crossing behavior of four species of lowland rainforest birds at La Selva Biological Station, Costa Rica. 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. ¹Model covariates included bird family (“family”; Troglodytidae or Thamnophilidae), species foraging height (“forage”; low or mid-story), the type of trial conducted (“trial”; silent control or predator treatment) the width of the forest opening that the trial was conducted at (“gap”), and light level (“light”). Model sets included models with single main effects, additive (+) effects, and interactive (:) combinations. Asterisk (*) notation indicates that variables expand to include all additive and interactive combinations. ⁰Number of parameters.

Model, by behavioral response ¹	w_i	K^0	ΔAIC_c
Did birds cross the gap?			
Intercept only	0.87	2	0.00
Light + family*forage*trial	0.10	10	4.35
Family*forage*trial	0.02	9	7.13
Gap + family*forage*trial	0.01	10	9.43
Number of times crossed			
Family*forage*trial	0.63	9	0.00
Gap + family*forage*trial	0.17	10	2.60
Light + family*forage*trial	0.17	10	2.61
Intercept only	0.03	2	6.38
Time to initiate crossing (latency)			
Gap + gap:trial + family*forage*trial	1.00	11	0.00
Light + light:family + family*forage*trial	0.00	11	177.31
Family*forage*trial	0.00	9	330.19
Intercept only	0.00	2	1231.70
Closest distance approached to playback speaker			
Light + family*forage*trial	1.00	10	0.00
Gap + family*forage*trial	0.00	10	16.46
Family*forage*trial	0.00	9	16.82
Intercept only	0.00	2	41.76

contained all additive and interactive combinations of family, foraging height, and trial type, as well as the single main effect of gap width (“gap”), and the interaction of gap width and trial type; the third model contained all additive and interactive combinations of family, foraging height, and trial type, as well as the single main effect light level (“light”), and the interaction of light level and family; and the fourth model was a null model, which included only the intercept. The bobyqa optimizer was used for convergence in all models. Species was not included as an effect, as identity could be discerned through interactions of family and foraging height, and gap width and light level were included in separate models to limit redundancy. In constructing model sets, we included only what we believed to be biologically plausible variable combinations using the information-theoretic approach outlined by Burnham and Anderson (2002).

An Analysis of Deviance table (Type III Wald Chi-Square test; package ‘car’) was used to assess model terms, and models were reduced only by removing

the non-significant interactions of gap width and trial type (in the gap model), and light level and family (in the light model). The single main effects of light level and gap width were retained in light and gap models, respectively, to allow for multimodel inference and comparison within model sets (Bolker et al. 2008). We used Akaike’s information criterion corrected for small sample size (AIC_c) to rank models by the factors that influenced species’ behavioral responses. Additionally, we used Akaike weights (w_i) to assess the strength of a given model in explaining the data (Burnham & Anderson 2002, Arnold 2010). We used the ‘lsmeans’ package to compute least-squares means and Tukey’s HSD pairwise contrasts for all significant results in top models (Table 1). Model assumptions were met by verifying normal distribution of residuals and by evaluating goodness-of-fit via R^2 for GLMM (Nakawaga and Shielzeth 2013, Lefcheck 2016).

All statistical analyses were performed in R, version 3.3.1 (R Core Team 2016) with the RStudio interface (RStudio Team 2015), including packages ‘lme4’

Table 2. Species, family, foraging height, sample size (n ; number of birds tested), study gap width range (m), and comparison of mean values \pm SD for each numeric response variable measured during gap crossing playback experiments on four species of lowland rainforest birds at La Selva Biological Station, Costa Rica. Study site gap widths ranged from 2.8–12.6 m. Mean number of gap crossings per trial and mean latency times were calculated only from trials in which birds crossed the gap, while the mean distance that birds approached the playback speaker was calculated from all trials.

Species	Family	Foraging height	n	Study gap width range (m)	Mean number of gap crossings/trial	Mean latency time (s)	Mean distance that birds approached playback speaker (m)
<i>P. exsul</i>	Thamnophilidae	Low	9	3.1–9.6	1.13 \pm 0.35	259.00 \pm 221.12	11.47 \pm 7.36
<i>T. atrinucha</i>	Thamnophilidae	Mid-story	10	3.0–12.6	1.93 \pm 1.33	120.21 \pm 130.53	13.43 \pm 10.06
<i>H. leucosticta</i>	Troglodytidae	Low	11	3.0–9.0	2.29 \pm 2.11	41.29 \pm 62.63	7.35 \pm 8.24
<i>C. thoracicus</i>	Troglodytidae	Mid-story	9	2.8–9.0	4.06 \pm 4.02	53.81 \pm 134.40	5.58 \pm 5.25

(Bates et al. 2015) for GLMM models (function ‘glmer’), ‘AICcmodavg’ (Mazerolle 2016) for AIC_c values and weights, ‘lsmeans’ (Lenth 2016) for Tukey’s HSD pairwise comparisons, ‘car’ (Fox & Weisberg 2011) for Wald Chi-Square Tests, ‘piecewiseSEM’ for R^2 for generalized linear mixed models (Lefcheck 2016), and ‘ggplot2’ (Wickham 2009) for figures.

RESULTS

A total of 39 control and 39 treatment trials were run with paired observations on the same individual for each of the four focal species (Table 2). All species responded to conspecific calls during both silent control and predator playback treatment trials, defined as vocalization in response to the conspecific call, which then initiated the playback trial.

For all model sets except one (whether or not birds crossed the gap), the best-fit model performed substantially better than the null model (Table 1). Residual plots of best-fit models generally showed little skew and normal distributions. Across the majority of model sets, the strongest predictors of bird behavior were family, foraging height, and trial type, as well as the interactions between family, foraging height, and trial type.

For models assessing predictors of whether or not birds crossed the gap (Figure 3), the null effects model (intercept only) had the strongest support ($w_i = 0.87$; Table 1). The second-best model was the light model, which received lower support $w_i = 0.10$ and $\Delta AIC_c = 4.25$, although several main effects were significant (light level, $P = 0.028$; family, $P = 0.0039$; forage height, $P = 0.0099$; and trial type, $P = 0.0084$; all Type III Wald Chi-Square Test). Although the null model received the strongest support, several distinct patterns emerged in the data. All species were more likely to cross gaps during control versus treatment trials ($P = 0.0294$, Tukey’s HSD). Troglodytidae species were more likely to cross gaps than Thamnophilidae species during both control and treatment trials ($P = 0.0109$ and $P = 0.0034$, respectively; Tukey’s HSD); however, there were no differences within Thamnophilidae and Troglodytidae likelihood of crossing between control and treatment trials. Mid-story

foraging species were more likely to cross gaps than low foraging species during playback trials ($P = 0.0081$, Tukey’s HSD). Low foraging species were more likely to cross during control versus treatment trials ($P = 0.0086$, Tukey’s HSD).

For models assessing predictors of the number of times that birds crossed the gap, the model with the additive effects and interactions between family, foraging height, and trial type had the strongest support ($w_i = 0.63$; Table 1). Other models in the set were not well supported (Table 1). Troglodytidae species crossed significantly more times than Thamnophilidae species during both silent control and predator treatment trials ($P = 0.0019$ and $P = 0.0050$, respectively; Tukey’s HSD). There were no significant differences in number of crossings made by low and mid-story foraging species between control and treatment trials; however, mid-story foraging species crossed significantly more times than low foraging species during treatment trials ($P = 0.0016$, Tukey’s HSD).

For models assessing predictors of latency, the top model included the single main effect of gap width, the interaction of gap width and family, and all additive effects and interactions between family, foraging height, and trial type (Table 1). This top model received strong support ($w_i = 1.00$); other models in the set were not well supported (Table 1). Model results showed that for every one-meter increase in gap width, latency time increased by one second (Figure 4). Latency times in predator treatment trials were significantly higher than in silent control trials ($P < 0.0001$, Tukey’s HSD). Thamnophilidae species took longer than Troglodytidae species to initiate gap crossing in both silent control and predator treatment trials ($P < 0.0001$ and $P = 0.0100$, respectively; Tukey’s HSD), and Troglodytidae species took more than double the time to initiate gap crossing during predator treatment trials than during silent control trials ($P < 0.0001$, Tukey’s HSD; Figure 4).

All species showed significantly greater latency times in predator treatment versus silent control trials, with the exception of *P. exsul*, which exhibited higher latency times during silent control trials ($P = 0.0005$, Tukey’s HSD). This trend appears to have been driven by one *P. exsul* individual that crossed

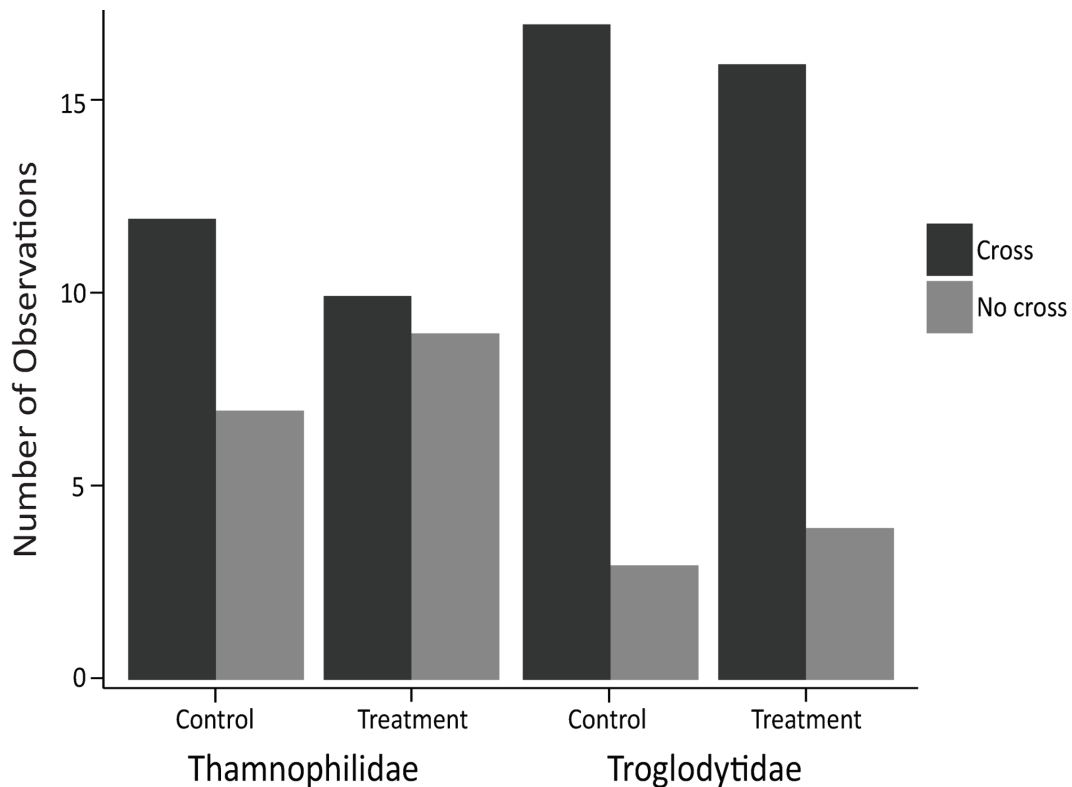


Figure 3. Total cross versus no-cross responses by family during silent control and predator playback treatment trials of gap crossing behavior at La Selva Biological Station, Costa Rica. Family emerged as one of the strongest predictors of bird behavior throughout this study. The two species of Troglodytidae were significantly more likely to cross gaps during both control and treatment trials ($P = 0.0109$ and $P = 0.0034$, respectively; both Tukey's HSD) than the two studied Thamnophilidae species; however, there were no differences in Thamnophilidae or Troglodytidae likelihood of crossing between control and treatment trials.

quickly (latency value of 1 s) during a predator playback trial: when this outlier was removed, model order and weights did not change (Table 1), but *P. exsul* showed the same pattern as the other three species, displaying significantly greater latency times in predator treatment versus silent control trials ($P < 0.0001$, Tukey's HSD). Both low and mid-story foraging species took longer to initiate gap crossing in predator treatment versus silent control trials (both $P < 0.0001$, Tukey's HSD).

For models assessing predictors of the closest distance that birds approached the playback speaker, the top model included the single main effect of light level and all additive effects and interactions between family, foraging height, and trial type (Table 1). This model received high support ($w_i = 1.00$). Other models in the set were not well supported (Table 1). Both bird families approached the speaker more closely during silent control versus predator treatment trials (Both $P < 0.0001$, Tukey's HSD; Figure 5). Troglodytidae species approached the speaker more closely than Thamnophilidae species during both silent control and predator treatment trials ($P = 0.0042$ and $P = 0.0400$, respectively; Tukey's HSD). There were no significant differences between low and mid-story foraging species in the closest distance approached to the playback speaker between control and treatment trials; however, both low and mid-story foraging species

approached the playback speaker less closely when comparing within groups between control and treatment trials ($P < 0.0001$ and $P = 0.0011$, respectively; Tukey's HSD).

DISCUSSION

Predator playback, foraging height, and family-level differences strongly affected bird behavior. Most notably, we found a strong effect of predator playback on bird gap crossing behavior, indicating that risk of predation may affect movement across small, linear forest openings. This is consistent with previous studies, where perceived risk of predation has been found to be one of the strongest drivers of bird gap crossing behavior (e.g., Sieving et al. 2000, Awade & Metzger 2008, Hadley & Betts 2009, Kennedy & Marra 2010). Typically, factors such as large open spaces and edge effects (Hagan et al. 1996, Stratford & Robinson 2005, Ibarra-Macias et al. 2011) increase perceived risk of predation. Given that the gap widths used in this study did not exceed 12.6 m and were generally found in advanced primary and secondary forest where canopy cover was often dense or the gap was obscured by branches crossing over the path, it is especially striking that bird behavior was affected so strongly by predator playback.

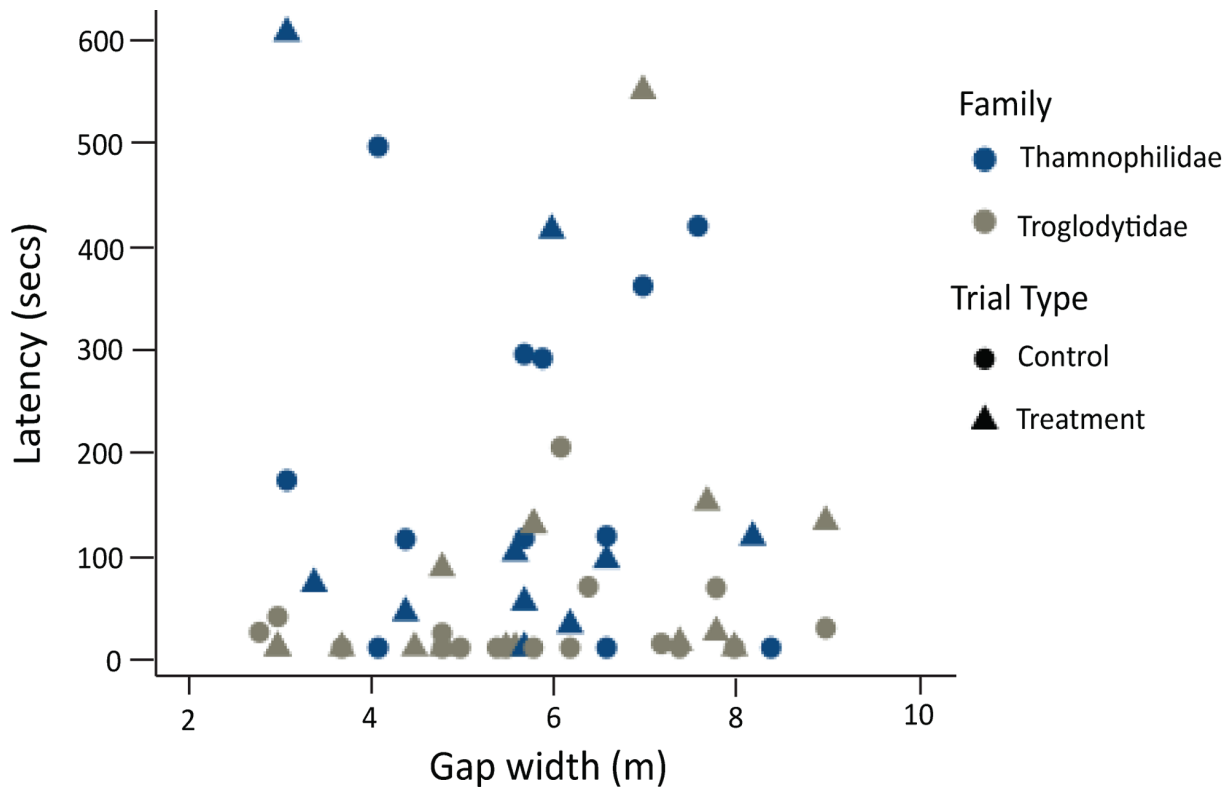


Figure 4. Relationship between gap width and latency time of Thamnophilidae species and Troglodytidae species during silent control and predator playback treatment trials at La Selva Biological Station, Costa Rica. Latency times increased with increasing gap width, and gap width and the interaction of gap width and family emerged as top predictors of latency across latency models (see Table 1). Thamnophilidae species took longer to initiate gap crossing than Troglodytidae species in both silent control and predator treatment trials ($P < 0.0001$ and $P = 0.0100$, respectively; Tukey's HSD).

Our data show an overall strong effect of phylogeny on gap crossing behavior. These results are consistent with those from Ibarra-Macias et al. (2011), who found that gap crossing latency differed significantly by species, with forest-restricted species showing greater latency times than forest-unrestricted species. In the present study, differences among species behavioral responses were strongest between family-level clades. The Thamnophilidae species in this study exhibited more reserved behavior than the Troglodytidae species: both *P. exsul* and *T. atrinucha* crossed gaps less frequently (Figure 3) and did not approach the speakers as closely, independent of whether or not they crossed the gap (Figure 5), as *C. thoracicus* and *H. leucosticta*. Possibly the most notable inter-species differences were found between the mid-story-foraging wren, *C. thoracicus*, and the low foraging antbird, *P. exsul*. *P. exsul* behaved much more cautiously than all other focal species, even more so than *T. atrinucha*, a member of the same family. Although all four species are territorial and highly aggressive, our results show that these behaviors are much more pronounced in both wren species, highlighting between-family differences.

Although it does not appear that birds responding to playback were desensitized to predation risk because of the strong effect of this variable on behavior, on several occasions focal species did vocalize

through predator playback, suggesting that heightened aggression caused them to behave less cautiously. Alternatively, it could very well be the case that territorial defense against conspecific intruders (i.e., the conspecific playback) took precedence over behavioral response in light of perceived predation risk. The focal species studied are highly aggressive and defend year-round territories. If respondents experienced high predation risk while in a heightened state of aggression against a territorial intruder, this risk may have been perceived as less great a threat than the threat of a territorial intruder. Differences in the degree of territoriality could be responsible for apparent differences in crossing behavior. It is also possible that predator playback did not appropriately convey risk because birds perceive predator presence and associated risk using visual cues. However, given that predator playback strongly affected species responses for three of the four measured response variables, this is likely not the case.

The bulk of previous Neotropical studies have focused on bird gap crossing behavior using a range of gap widths much wider than our own 2.8–12.6-m range: Sieving et al. (2000) studied 2.5–50-m wide corridors; Laurance et al. (2004) looked at 30–40-m wide gaps across roads; Awade & Metzger (2008) used 6–115-m gaps between forest

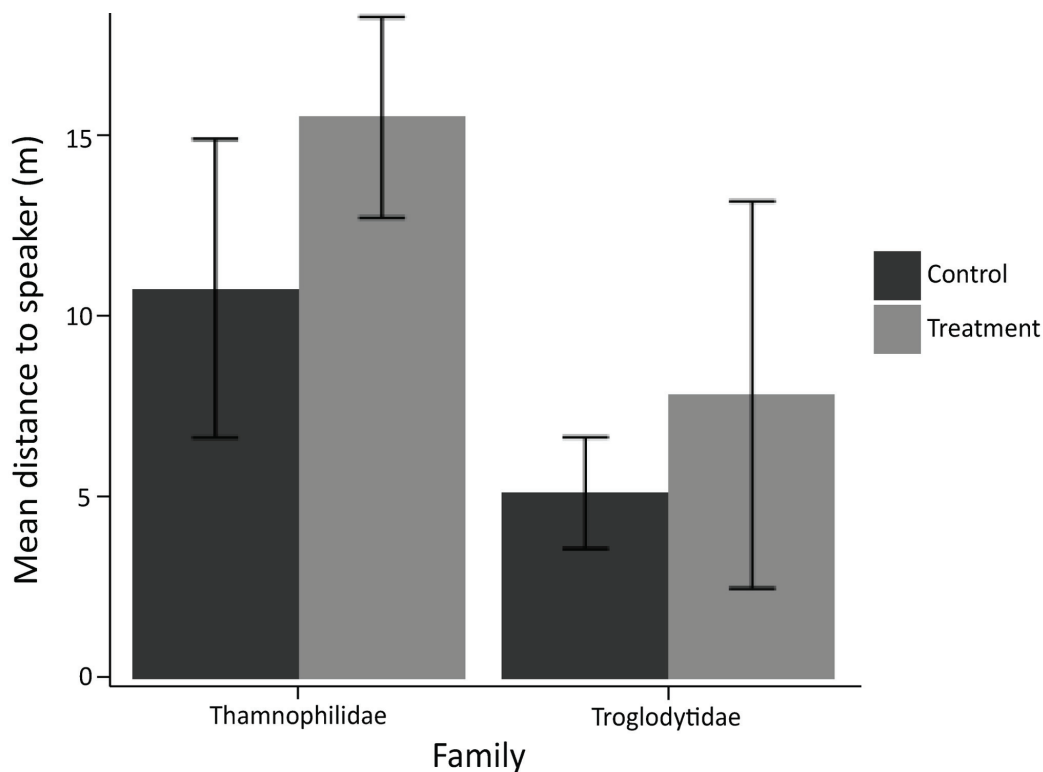


Figure 5. Mean distance (m) \pm SE that Thamnophilidae species and Troglodytidae species approached the speaker during treatment and control trials of gap crossing behavior at La Selva Biological Station, Costa Rica. Troglodytidae species approached the speaker more closely than Thamnophilidae species during both control and treatment trials ($P = 0.0113$, Tukey's HSD).

patches; and Laurance & Gomez (2005) studied farm clearings > 250 m in width. We believe that it was not possible to identify gap crossing threshold distances for the four focal species studied because the widths of study gaps used in this experiment were smaller than these species' gap crossing thresholds. Our results suggest that the gap crossing threshold distances for the understory insectivores studied here fall somewhere between our widest-studied gap width (12.6 m) and the intermediate gap widths previously studied in the literature (estimated 20–40 m). It has been found that forest age within 100 m of the edge greatly affects gap permeability, with understory insectivores more closely linked to more mature forest (Powell et al. 2013). In addition to the study gap widths being fairly narrow, it is possible that because study sites were located in primary and mature secondary forest, edge effects were less pronounced and gaps were not perceived as true breaks in habitat. Additionally, while roads are known to be serious deterrents to bird behavior and movement (Trombulak & Frissell 2000, Develey & Stouffer 2001), our results should be generalized only to rural roads with low levels of disturbance that are of similar sizes as the gaps and forest roads used in this study.

Our study revealed that small linear gaps do not impede crossing rates or birds' seeming willingness to cross gaps, suggesting that gap width may only hinder birds at larger widths (> 12.6 m). However, the strong effects of predator playback suggest that risk of pre-

ation may hinder bird movement even at small gaps that measure several meters in width. This is particularly relevant for low foraging species, which display restricted movement compared to their mid-story foraging counterparts. Our results were consistent with those of previous studies, suggesting that no single model best-predicted bird gap crossing behavior (Think et al. 2012). We recommend that future studies consider the combined effects of foraging height and flight strength on bird movement, as well as incorporation of a visual stimulus (e.g., a hawk or owl model) into playback experiments.

ACKNOWLEDGMENTS

We thank the Organization for Tropical Studies (OTS), La Selva Biological Station, the National Science Foundation Research Experience for Undergraduates (NSF-REU) program (DBI-0851933), and National Aeronautics and Space Administration Earth System Science Fellowship (NNX10AP49H to MEF) for support and funding for this research. We thank La Selva Biological Station, the Puerto Viejo de Sarapiquí fire station, and the Sueño Azul owners for granting site access and permission to conduct research. We are grateful to Pablo E. Allen, Andrew Herberg, Deborah M. Visco, Meghan R. Fitzgerald, Kelsey A. Ream, and students of the OTS 2012 summer REU program for assistance in the field. Christopher C. Witt, Erik B. Erhardt, Jennifer A. Rudgers, Daniel J.

Krofcheck, Anastasiia Kim, Lindsey Pittington, Austin Ritter, Chauncey R. Gadek, Jenna M. McCullough, Andrea N. Chavez, and Joshua Lynn provided helpful feedback and statistical advice on this manuscript. This manuscript was greatly improved by thoughtful comments from Jeffrey A. Stratford and Kaspar Delhey.

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