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Fine-scale movement decisions of tropical forest birds in a fragmented landscape

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Abstract. The persistence of forest-dependent species in fragmented landscapes is fundamentally linked to the movement of individuals among subpopulations. The paths taken by dispersing individuals can be considered a series of steps built from individual route choices. Despite the importance of these fine-scale movement decisions, it has proved difficult to collect such data that reveal how forest birds move in novel landscapes. We collected unprecedented route information about the movement of translocated forest birds from two species in the highly fragmented tropical dry forest of Costa Rica. In this pasture-dominated landscape, forest remains in patches or riparian corridors, with lesser amounts of living fencerows and individual trees or "stepping stones." We used step selection functions to quantify how route choice was influenced by these habitat elements. We found that the amount of risk these birds were willing to take by crossing open habitat was context dependent. The forest-specialist Barred Antshrike (*Thamnophilus doliatus*) exhibited stronger selection for forested routes when moving in novel landscapes distant from its territory relative to locations closer to its territory. It also selected forested routes when its step originated in forest habitat. It preferred steps ending in stepping stones when the available routes had little forest cover, but avoided them when routes had greater forest cover. The forest-generalist Rufous-naped Wren (*Campylorhynchus rufinucha*) preferred steps that contained more pasture, but only when starting from non-forest habitats. Our results showed that forested corridors (i.e., riparian corridors) best facilitated the movement of a sensitive forest specialist through this fragmented landscape. They also suggested that stepping stones can be important in highly fragmented forests with little remaining forest cover. We expect that naturally dispersing birds and species with greater forest dependence would exhibit even stronger selection for forested routes than did the birds in our experiments.

Key words: animal movement; Campylorhynchus rufinucha; *corridors; Costa Rica; fencerows; generalized linear mixed model; habitat connectivity; individual route choice; step selection function;* Thamnophilus doliatus; *tropical dry forest.*

INTRODUCTION

Land use change, which typically involves habitat loss and fragmentation, is expected to be the primary driver of biodiversity loss in the coming century and this may be exacerbated by climate change (Sala et al. 2000). Much of this loss will result from agricultural expansion, particularly in developing countries where both human populations and food demands will increase most rapidly (Cincotta et al. 2000, Tilman et al. 2001). Agriculture is expected to expand in two ways: becoming more intensive on land where it is already present and expanding into new areas that were once forest or other primary habitat (Green et al. 2005).

Both forms of agricultural expansion threaten many of the world's bird species (Green et al. 2005). Agricultural intensification primarily affects the matrix outside of the forest. Removal of forest remnants and isolated trees impacts the potential for forest regeneration (Galindo-González et al. 2000), makes the matrix less suitable for inhabitation or foraging by forest species (Fischer and Lindenmayer 2002, Hughes et al. 2002), and can impede movement of forest species among forest patches (Castellón and Sieving 2006, Stouffer et al. 2006). Expansion of agriculture clears forest habitat and further isolates remaining habitat, increasing the role of the matrix for movement among patches. Indeed, the ability of sensitive forest birds to move through the matrix is the primary determinant of their persistence in forest fragments (Lens et al. 2002, Şekercioğlu et al. 2002).

Movement by forest birds through the agricultural matrix is impeded by gaps between forested patches (Desrochers and Hannon 1997, St. Clair et al. 1998, Develey and Stouffer 2001, St. Clair 2003, Castellón and Sieving 2006, Awade and Metzger 2008). For many forest bird species, these open habitats represent areas of

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high predation risk (Rodríguez et al. 2001, Turcotte and Desrochers 2003) and this may be the reason that forest birds generally avoid them (Lima and Dill 1990). Response to risky habitats probably affects where birds choose to travel in the habitat they encounter. These fine-scale movement decisions can affect the broader pattern of movement (Bowne et al. 1999, Levey et al. 2005), correlate with extinction history and distribution (Moore et al. 2008) and, in simulations, can have impacts that scale up to population dynamics (Russell et al. 2003).

Despite the importance of movement to the conservation of birds, the behavioral decisions of free-moving forest birds are almost completely unknown (Harris and Reed 2002). This stems primarily from the difficultly of tracking moving birds (Desrochers et al. 1999, Bélisle 2005), but it may also stem from a traditional emphasis on habitat selection at points of occurrence over path selection. Indeed, where there is detailed information about the location and habitat use of birds or other vertebrates, analyses typically consider only characteristics of the location (Boyce and McDonald 1999) or the area around the location (e.g., Johnson et al. 2002). More recently, some authors have developed techniques to assess the characteristics of the path segment between successive locations (e.g., Fortin et al. 2005, Whittington et al. 2005, Coulon et al. 2008). Fortin et al. (2005) developed step selection functions (SSF), which are similar to resource selection functions (RSFs; Manly et al. 2002), to compare used path segments to randomly generated "available" segments. Like RSFs, these step selection functions are flexible enough to examine the effects of complex covariates, including situations in which an animal's response to a covariate varies with habitat availability (Hebblewhite and Merrill 2008).

Among forest birds, tropical species are considered to be particularly sensitive to the effects of habitat fragmentation (Harris and Reed 2002, Stratford and Robinson 2005). We translocated two species of forest bird in highly fragmented tropical dry forest of Costa Rica and used radiotelemetry and GPS technology to collect detailed route information on birds as they moved in novel habitat. We then used SSFs to compare used to available habitat at the scale of single steps to better understand how these birds travel through fragmented habitats.

Methods

Study area

We followed the fine-scale movement of two bird species in an agricultural landscape of northwestern Costa Rica near the town of Liberia. This landscape was once contiguous tropical dry forest, but is now dominated by cattle pasture. Remaining forest is often confined to riparian areas. In addition to forest, there are living fencerows that have been planted at the edges of fields. These are typically a single row of trees with little or no understory. The area also contains individual trees or small patches of trees in the pasture that we term "stepping stones." These are typically remnants of the original forest cover that have been retained as shade for cattle.

Translocations and tracking

We followed moving forest birds in real time at a landscape scale, collecting information about their route and habitat use. We translocated 30 Barred Antshrikes (*Thamnophilus doliatus*, hereafter "antshrikes"; see Plate 1) and 30 Rufous-naped Wrens (*Campylorhynchus rufinucha*, hereafter wrens). Both are common insectivores that hold territories year-round, but antshrikes are forest specialists, typically being found only in the understory of the most intact forest in this region, whereas wrens are forest generalists, being found in a wider range of habitats (Stiles and Skutch 1989). The wrens are also cooperative breeders (Stiles and Skutch 1989). Birds were moved away from their territories in one of three treatments: along riparian corridors, along fencerows, and through pasture. One bird from each species was translocated in each of the three treatments at each of 10 distances (0.7–1.3 km in 0.1-km intervals, then 1.45, 1.6, and 1.9 km). We conducted translocations from June to August 2000 and January to June 2002. All individuals were caught by 09:40 hours local time (mean capture time 06:59 hours ± 65 minutes) by attracting them into a mist net with a playback of a conspecific song. We moved male antshrikes and both male and female adults of the monomorphic wrens. Using eyelash adhesive, we attached a radio transmitter to trimmed feathers on the backs of translocated individuals. Birds were captured in forest and released in fencerow or forest habitat. Due to the rarity of fencerows in the study area, the same fencerow was used for two treatments (one of each species) on three occasions. Thus, 17 fencerows were used for 20 translocations. In these three fencerows that were used twice, we moved an individual of each species differing distances in the same fencerow, which resulted in 10 unique fencerows for each species. Most wrens (23 of 30) were sexed by extracting DNA from a whole tail feather (Griffiths et al. 1998). The remaining individuals were sexed by comparing their body mass, tarsus length, and exposed culmen length to measurements of individuals of known sex using a discriminant function analysis.

Following release, we recorded with radiotelemetry and handheld GPS units the location of each translocated bird approximately every 15 minutes (14.8 ± 8.2 min, mean ± SD) during the day for up to 4 days and daily thereafter for 10 days or until they returned, whichever was earlier. Two observers closely followed individuals by simultaneously triangulating their location from a mean distance of 27 m ± 13 m (SD). More than 96% of locations were taken from $\geq$10 m away. In more open habitat, observers increased their distance to the bird to minimize the chance that their presence

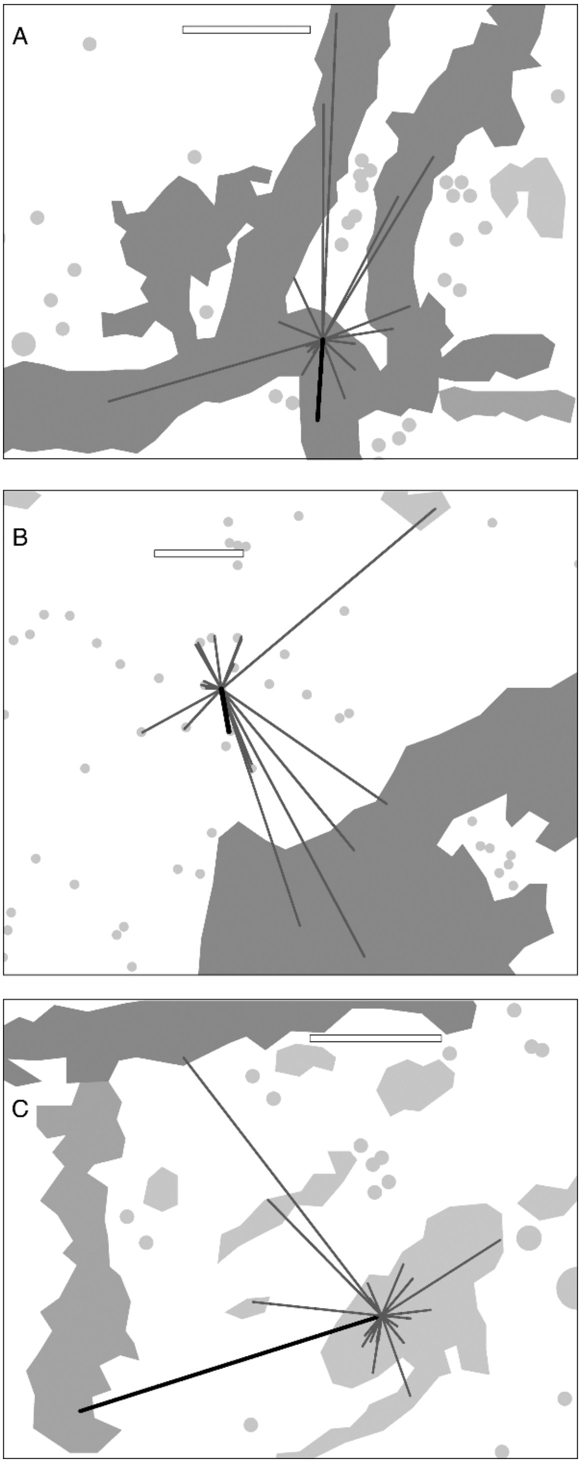

FIG. 1. Examples showing used (thick black) and 20 random (dark gray) steps used in the step selection analysis for (A) an antshrike moving in forest, (B) an antshrike moving among stepping stones, and (C) a wren moving from stepping stone to fencerow habitat. Land cover includes pasture (white), forest (dark gray), fencerow (medium gray), and stepping stone (light gray) habitat. The rectangular bar represents 100 m in each example.

influenced bird movements. These positions provided trajectories of moving birds with unprecedented precision and with which we assessed the habitat used during movement. Even the shortest translocations were well outside the home range of these birds. We calculated home ranges for two antshrikes that returned at 0.58 and 0.30 ha (mean = 0.44 ha, radius if circular = 37 m) and for four wrens at 0.33, 0.31, 0.36, and 1.20 ha (mean = 0.55, radius if circular = 42 m) (Gillies and St. Clair 2010). These are similar to published results for congeners of both species, where home range radius was ~60 m for a congener to the antshrike in Brazil (*T. caerulescens*; Duca et al. 2006) and ~75 m for a congener to the wren in Venezuela (Campylorhynchus *nuchalis*; Yaber and Rabenold 2002). Riparian corridors were typically 50–150 m wide. Fencerows were typically 15–30 m wide with little understory.

Land cover information

Land cover information for the study area was developed from a series of high-resolution (~1-m pixel size) infrared images taken by the Airborne Sensor Facility at the National Aeronautics and Space Administration (NASA) Ames Research Center, Moffett Field, California, USA, as part of the CARTA program during March 2003. Images were orthorectified using a digital elevation model built from 1:20 000 topographic information and the coordinates of known locations in the field with the OrthoBASE package in ERDAS IMAGINE 8 (ERDAS 2002). Land cover was delineated on these images using ArcGIS 9 (ESRI 2005) as pasture, forest, fencerow, or stepping-stone habitat.

To characterize the land cover information influencing bird movement, we developed an extension of the ArcGIS program used by Fortin et al. (2005) for application to these data. We compared observed ("used") steps to a sample of realistic alternative steps, which we call "available" steps, from the same location. Each used step was the straight line connecting two consecutive telemetry locations. We limited our analysis of the used steps to those steps for which the bird moved a minimum distance and the period between successive locations was short enough to have relatively good route information. Thus, we eliminated steps that were <10 m in length and were >35 min in duration. These constraints resulted in 1615 used steps for the antshrikes and 1771 used steps for the wrens. To ensure that the available steps were realistic, we required that these steps end in suitable habitat (i.e., stepping stone, fencerow or forest). Available steps were prevented from landing in pasture habitat because only ~1% of used steps ended in pasture. We made the distributions of step lengths and turn angles for available steps similar to those of the used steps. These distributions were then used to generate 20 available steps for each used step (Fig. 1). Using available steps that were realistic possible steps from the same location helped to ensure that observed differences between used and available steps represented the movement choices of these birds.

Data analysis

We used matched case-control logistic regression to generate the step selection function (sensu Fortin et al. 2005). Also known as conditional logistic regression, this analysis compares the characteristics of each used step to the 20 available steps derived from the same starting point. When comparing steps, we expected that birds making route decisions would respond primarily to four variables: the amount of the step that was in the open (proportion in pasture), the amount of the step in forested habitat (proportion in forest), the number of open areas that the bird would have to cross (number of gaps), and the cumulative total distance in gaps that the bird would have to cross (total gap distance). We termed these four related covariates our "exposure variables" as they relate to assumed predation risk, but also to exposure to limited foraging opportunities and unfavorable microclimates. We expected that the degree of exposure would increase with increases in the proportion of a step in pasture, the number of gaps, and the total gap distance crossed. Conversely, exposure would decline with increases in the proportion of the step in forest. Because the four exposure variables were highly correlated, we could not include them all in the same model. Without a priori reasons to choose one exposure variable over another, we built competing candidate models with each exposure variable. Candidate models were built using forward stepwise addition of covariates ($P < 0.1$ for addition). The univariate covariates considered for addition were: the exposure variable, the distance to the capture location (home) from the end of the step, the proportion of the step in fencerow habitat, the proportion of step in stepping-stone habitat, and the habitat at the end of the step (forest, fencerow, or stepping stone). We also considered interaction terms between the exposure variable and the habitat at the start of the step, the habitat at the end of the step, and the distance home at the start of the step. For each exposure variable, we generated a model including only univariate terms and a full model that included the significant univariate terms and interaction terms that were added to the univariate model. We compared the eight candidate models using Akaike's Information Criterion, AIC (Akaike 1973), and Akaike weights (Burnham and Anderson 2002). Once the best model was identified, we added a random coefficient for the exposure variable. This procedure allowed the coefficient for the exposure variable to vary among individuals in the analysis. The use of random coefficients helps to correct for the correlated nature of the data (many steps per individual) to produce more robust coefficients (Gillies et al. 2006).

In addition to generating more robust coefficients for the selection or avoidance of particular habitat elements, the use of random coefficients in these models produces individual-specific coefficients for selection of the exposure variable. These coefficients can then be related to characteristics of the individual to help explain, for example, why some individuals had stronger selection for pasture. This provides an additional layer of information about how the individual responses create the population response. We used linear regression with forward stepwise addition of variables ($P < 0.1$ for addition) to identify relationships between selection coefficients of the individuals and a suite of broader landscape measures. These measures included treatment (riparian corridor, fencerow, or pasture), the mean value of the exposure variable for all of the available steps for that individual, sex (wrens only), and the proportion of forest, fencerow, and stepping-stone habitat in the surrounding area. The calculation of amount of the habitat variables (forest, fencerow, and stepping-stone habitat) for each individual was measured inside an ellipse, with foci on the release and capture points and an eccentricity of 1.4. This ellipse approximated the region in which these birds typically moved while returning. All analyses were performed using Stata 10.0 (Statacorp 2007). The mixed-effects logistic regressions used GLLAMM (Rabe-Hesketh et al. 2004) and the analyses of the individual-specific coefficients used linear regression. Post hoc tests for group membership used the *test* procedure in Stata (Statacorp 2007).

RESULTS

Antshrikes

For the forest-specialist antshrikes, the best model included the proportion of the step in forest as the exposure variable (Table 1). This model fit the data better than the competing models, including the other three exposure variables (proportion of the step in pasture, number of gaps crossed, and total distance of gaps crossed). This model included univariate covariates for the proportion of the step in stepping-stone habitat, the distance home, and steps ending in both forest and stepping-stone habitat (Table 2). The coefficients comparing used to available steps for the three univariate terms that were not part of interaction terms revealed the direction of their effects (Table 2). The antshrikes were more likely to select steps that took them closer to home and that, on average, contained lower proportions of stepping-stone habitat. Relative to availability, antshrikes avoided steps that ended in fencerow. The effect of the proportion of the step in forest in this best-fit model was adjusted by its interaction with three other variables: distance from the home territory to the start of the step, starting the step in forest, and ending the step in a stepping stone.

The interaction terms revealed that selection for forest by antshrikes was context dependent. We explored these interactions by generating linear predictors for each pair of terms from the best model (Table 2, Fig. 2) with the other covariates held constant at their means. The linear predictor is the linear component of the logit equation

TABLE 1. Candidate models for each of the four exposure variables, log-likelihood, AIC values, difference from the best model, and Akaike weights.

Species	Model	k	log L	AIC	ΔAIC	Weight
Antshrikes	Dhome + PF + PSS + EndFR + EndSS	5	−4869	9748.3	32.5	<0.001
	Dhome + PF + PSS + EndFR + EndSS + Dstart × PF + StartFor × PF + EndSS × PF	**8**	**−4850**	**9715.9**	**0**	**0.80**
Best	**Same as above + random coefficient PF**		**−4834**			
	Dhome + PP + EndFR + EndSS	4	−4870	9747.6	31.7	<0.001
	Dhome + PP + EndFR + EndSS + Dstart × PP + EndSS × PP	6	−4853	9718.9	3.0	0.17
	Dhome + TotGap + EndFR + EndSS	4	−4870	9748.0	32.1	<0.001
	Dhome + TotGap + EndFR + EndSS + Dstart × TotGap + EndSS × TotGap	6	−4859	9731.0	15.1	<0.001
	Dhome + Gaps + PSS + EndFR	4	−4869	9745.7	29.9	<0.001
	Dhome + Gaps + PSS + EndFR + Dstart × Gaps	5	−4856	9722.5	6.6	0.03
Wrens	Dhome + PF + PSS + EndFR + EndSS	5	−5355	10 719.3	55.1	<0.001
	Dhome + PF + PSS + EndFR + EndSS + StartFor × PF + EndSS × PF	7	−5331	10 676.6	12.4	0.001
	Dhome + PP + PFR + EndFR + EndSS	5	−5356	10 721.1	56.9	<0.001
	Dhome + PP + PFR + EndFR + EndSS + Dstart × PP + StartFor × PP + StartFR × PP + EndFR × PP + EndSS × PP	**10**	**−5322**	**10 664.2**	**0**	**0.60**
Best	**Dhome + PP + PFR + EndFR + StartFor × PP + random coefficient PP**		**−5312**			
	Dhome + TotGap + PSS + EndFR + EndSS	5	−5354	10 718.4	54.2	<0.001
	Dhome + TotGap + PSS + EndFR + EndSS + Dstart × TotGap + StartFR × TotGap + EndSS × TotGap	8	−5339	10 693.6	29.4	<0.001
	Dhome + Gaps + PSS + EndFR + EndSS	5	−5352	10 713.1	48.9	<0.001
	Dhome + Gaps + PSS + EndFR + EndSS + Dstart × Gaps + StartFor × Gaps + EndSS × Gaps	8	−5325	10 665.0	0.8	0.40

Notes: The two best models for each species are in boldface. Candidate models were built using forward stepwise addition. The four exposure variables are: proportion of the step in forest habitat (PF), proportion of the step in pasture habitat (PP), total amount of gap crossed (TotGap), and the number of gaps crossed (Gaps). Other variables included in the models are: distance home at the end of the step (Dhome), distance home at the start of the step (Dstart), proportion of the step in fencerow habitat (PFR), proportion of the step in stepping-stone habitat (PSS), start in forest (StartFor), start in fencerow (StartFR), end in fencerow (EndFR), end in stepping stone (EndSS). The best model was the model with the lowest AIC plus a random coefficient for the exposure variable minus nonsignificant terms ($P > 0.1$).

predicting relative probability of use. Higher values indicate a greater relative probability of use. Antshrikes selected steps with more forest when they were distant from their territory, but selected steps with less forest when they were close to their territory (Figs. 1A and 2a). There was a similar effect of starting habitat. Antshrikes selected more forested steps when the step started in forest, but selected less forested steps when starting in the non-forest habitat of fencerows and stepping stones (Fig. 2b). Finally, they selected less forested steps when the step ended in a stepping stone, but selected more forested steps when the step ended in fencerow or forest (Fig. 2c). Put another way, given the choice between two steps ending in stepping-stone habitat, they were more likely to choose the step with less forest, but if the step ended in forest or fencerow habitat, they were more likely to choose the more forested step. In addition, the intersection of the lines in Fig. 2c indicates that when the available steps had low amounts of forest cover, antshrikes preferred steps ending in stepping stones

TABLE 2. Final model coefficients, standard errors, significance, and random coefficient variance for the step selection by both species from the best model in Table 1.

Species	Variable	Coefficient	SE	P	Variance
Antshrikes	Distance home at end of step (km)	−4.07	0.47	<0.001	
	Proportion in forest (PF)	−2.40	1.02	0.019	2.51
	Proportion in stepping stone	−0.847	0.422	0.045	
	Step ends in fencerow	−0.536	0.220	0.015	
	Step ends in stepping stone	0.627	0.274	0.022	
	Distance to home at start × PF	1.29	0.64	0.045	
	Step starts in forest × PF	1.78	0.64	0.005	
	Step ends in stepping stone × PF	−2.63	1.00	0.009	
Wrens	Distance home at end of step (km)	−1.58	0.25	<0.001	
	Proportion in pasture (PP)	0.918	0.402	0.022	2.29
	Proportion in fencerow	0.743	0.302	0.014	
	Step ends in fencerow	0.283	0.134	0.035	
	Step starts in forest × PP	−0.939	0.343	0.006	

Note: Each species had only one variable with a random effect included in the model; variance in random coefficients is given for these terms.

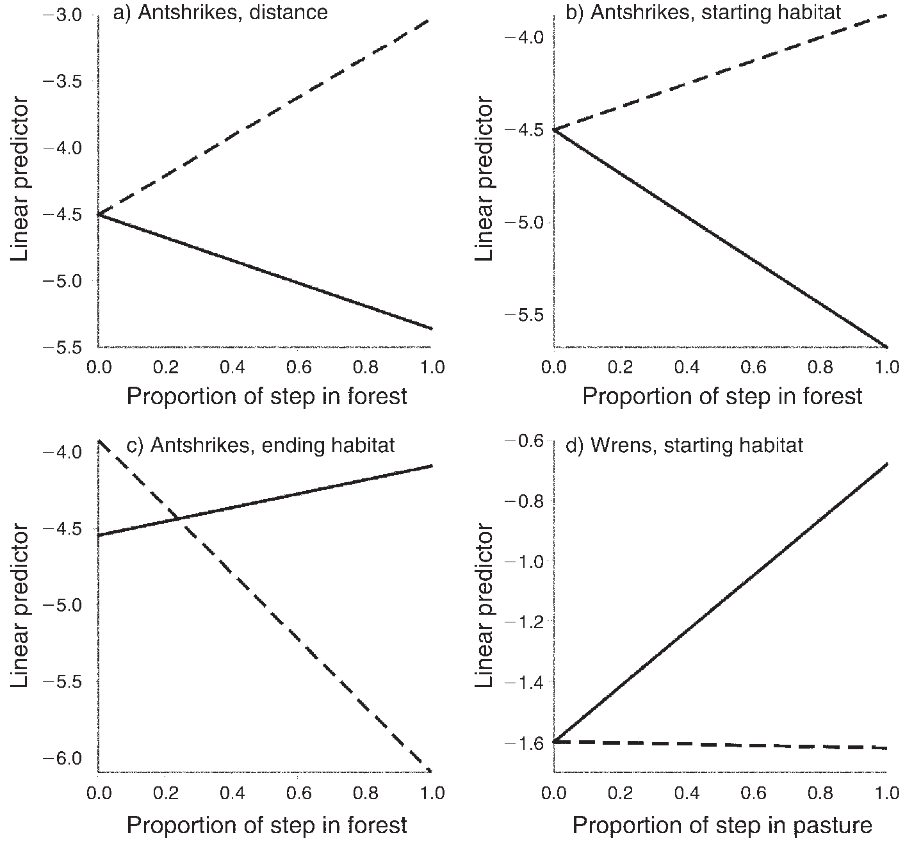

FIG. 2. The linear prediction of the probability of use (a–c) by antshrikes in relation to the proportion of the step in forest and (d) by wrens in relation to the proportion of the step in pasture. Antshrikes selected steps with more forest when distant from their territory (a; dashed line = 2 km), but avoided steps with more forest when close to their territory (a; solid line = 0.2 km). They selected steps with more forest when their step started in forest (b; dashed line) vs. non-forest (b; solid line = fencerow and stepping-stone habitat). They selected steps ending in stepping stones (c; dashed line) at low amounts of forest cover, but selected steps ending in non-stepping-stone habitat at higher amounts of forest cover (c; solid line = forest and fencerow). Wrens selected steps with more pasture when the step started in non-forest habitat (d; solid line = stepping-stone and fencerow habitat), but the proportion of the step in pasture did not affect step choice when the step started in forest habitat (d; dashed line). These values were generated from the best models (Table 2), with the other covariates held constant at their mean.

(e.g., Fig. 1b), whereas when steps had high amounts of forest, antshrikes preferred steps ending in forest or fencerow.

The variance in the random coefficient for the proportion of forest was of a similar magnitude to the coefficient estimate (Table 2), indicating that there was substantial variation among individual antshrikes in their selection for the proportion of the step in forest. However no candidate variables were significant predictors of these individual-specific coefficients (Table 3), suggesting that this individual variation was related to other unmeasured factors.

Wrens

The best model for the forest-generalist wrens included a different exposure variable than the best antshrike model: the proportion of the step in pasture (Table 1). Like the antshrikes, wrens responded to the distance home at the end of the step and the presence of fencerow at the end of the step. Model coefficients revealed that wrens selected steps that took them closer to home, had more fencerow habitat, and ended in fencerows (Table 2). However, their selection for the proportion of the step in pasture was context dependent. When they started from forest, the amount of pasture did not affect their choice of steps. In contrast, when

TABLE 3. Final models predicting the individual-specific coefficients from the step selection functions (SSF) models in Table 2.

Species	Variable	Coefficient	SE	*P*
Antshrikes	Constant	−0.00076	0.223	1.000
Wrens	Sex (males)	1.057	0.433	0.022
	Mean proportion pasture in available steps	4.340	1.844	0.026
	Constant	−1.391	0.499	0.010

Notes: No variables were added to the model for the antshrikes. For wrens, females are the reference category for the effect of sex, so the coefficient given is for the males.

they started from fencerow or stepping-stone habitat, wrens selected steps with more pasture (Figs. 1c and 2d).

As for the antshrikes, the magnitude of the random coefficient variance indicates that there was substantial variation among individual wrens in their response to the proportion of the step in pasture (Table 2). Males selected steps with greater proportions in pasture more strongly than did females (Table 3). Selection for steps with more pasture was stronger in individuals that had available steps with more pasture. In other words, the strength of selection increased with increasing availability of pasture in the landscape. This measure of the mean amount of pasture in the available steps varied from 4% to 42% across the 30 individuals.

Discussion

Our results demonstrate that moving forest birds respond to several aspects of land cover as they choose routes through fragmented tropical forest, and that responses differ both within and among species. These results provide some of the first detailed information about the fine-scale movement decisions of forest birds moving at a landscape scale, the scale that is most relevant to conservation (Lima and Zollner 1996). Previous studies of movement behavior using translocations of forest birds either have not followed the return path (e.g., Bélisle and St. Clair 2001, Bélisle et al. 2001, Gobeil and Villard 2002) or have monitored the bird's location too infrequently to get detailed information on route choice (Laurance and Gomez 2005, Castellón and Sieving 2006). To date, detailed information about movement trajectories has been collected only for very small animals and spatial scales (e.g., insects: Crist et al. 1992, Haddad 1999, Schultz and Crone 2001; small mammals: Bakker and van Vuren 2004, McDonald and St. Clair 2004; but see Levey et al. [2005] for an exception with birds) or for large animals at landscape scales (e.g., wolves, *Canis lupus*, Whittington et al. 2004, 2005; elk, *Cervus elaphus*, Fortin et al. 2005; bison, *Bison bison*, Bruggeman et al. 2007). The detailed route information that we have collected for birds moving across highly fragmented landscapes provides a novel opportunity to examine the effects of habitat context on movement decisions for animals and the role of exposure in those decisions.

Of the four exposure variables that we examined (proportion of step in pasture, proportion in forest, number of gaps crossed, and cumulative gap-crossing distance), the proportion of forest was the most important predictor of the movement of the antshrikes, whereas the proportion of pasture best explained the movement of wrens. This suggests that antshrikes view forest habitat as more secure for movement than fencerow or stepping-stone habitat, but the wrens view all three similarly. This matches the habitat selection information for these species (Gillies and St. Clair 2010), which showed that antshrikes preferred forest habitat over fencerow and stepping-stone habitat, whereas wrens selected non-pasture habitats similarly (forest, fencerow, and stepping-stone habitat). The response of our forest specialist to forest habitat was similar to the findings of Sieving et al. (2000) that the availability of understory was the primary predictor of whether forest-specialist birds were willing to travel in treed corridors. A treed corridor without understory would be similar to the fencerows in our study area. Thus, conservation planning for this and possibly other generalist species could consider all of the non-pasture habitats when planning for landscape connectivity. In contrast, planning for the more sensitive forest specialist, and possibly other similar species, would need to be based on the amount and configuration of forested habitat.

An important variable predicting the steps selected by both species was the distance from the end of the step to the home territory. Because birds consistently selected step endpoints that were closer to home than the available choices, it is apparent that they were homing during their paths. We expect this because the majority of the translocated individuals for both species successfully returned (Gillies and St. Clair 2008).

One implication of the differing dependency on forest for movement by the forest generalist vs. specialist is the utility of living fencerows for conservation purposes. An examination of entire return paths (Gillies and St. Clair 2008) showed that fencerows were not effective travel routes for antshrikes, whereas they were often used by wrens. At the finer spatial scale of the analyses here, antshrikes avoided steps ending in fencerow, whereas wrens selected steps that both contained more fencerow habitat and ended in fencerow habitat. The avoidance of fencerows by the antshrikes may be the mechanism causing antshrikes to travel longer paths in forest around fencerows (Gillies and St. Clair 2008). For the wrens, the fencerows may represent a very effective means to travel in their desired direction, covering a small area, but providing mostly continuous tree cover. Living fencerows have been advocated as a means to provide connectivity in fragmented landscapes (Rosenberg et al. 1997, Şekercioğlu et al. 2002); hedgerows, which are similar, but typically have more understory, are used extensively in the United Kingdom with support of agricultural subsidies (Oldfield et al. 2003). These results suggest that the utility of fencerows may be limited to forest generalists. For the specialist that we studied, the structural connectivity afforded by fencerows did not generate functional connectivity (sensu Taylor et al. 1993, Bélisle 2005). The response of these birds to forest and stepping-stone habitat was more complex and was dependent on the context of the step.

The importance of context for step selection was demonstrated in our results by the several significant interaction terms included in best models for both species. Antshrikes selected steps with more forest when they were far from their home territory, when they started the steps in forest, and when they ended steps in

Plate 1. Barred Antshrike *Thamnophilus doliatus* with transistor antenna. Photo credit: Cagan Şekercioğlu.

forest or fencerow. The effect of distance home on selection for forest appears to reflect a change in the perception or response to exposure. Because crossing open habitat exposes forest birds to the risk of predation (Lima and Dill 1990, Rodríguez et al. 2001, Turcotte and Desrochers 2003), a change in gap crossing may mean that birds were more willing to take risks closer to their home territories when the benefit of doing so was more tangible.

In addition to the effect of distance from the capture location, antshrikes were also more likely to select forested steps when they began the step in forest, but they were less likely to select forest when they ended the step in stepping-stone habitat. While in forest habitat, they preferred forested routes for steps that ended in forest to minimize their exposure. Conversely, steps beginning from non-forest habitat or ending in stepping stones probably occurred when the bird was more exposed, crossing non-forest habitat to reach a forested destination. Birds were apparently willing to be more exposed when traveling between non-preferred habitats, perhaps to expedite their travel through these habitats. Wrens exhibited a similar tendency to be more exposed when they were outside of forested habitat by selecting steps with more pasture under those conditions. Both species appeared to exhibit more exposed, and possibly more risky, movement decisions when more secure, forested routes were not available.

Behavior in relation to exposure varied not only with the habitat context, but also among individuals. The analysis of the individual-specific coefficients for the exposure variables can relate individual responses to their larger landscape contexts, which included the treatment configuration and habitat availability. Despite plausible effects of these contexts, none of these variables appeared to have a significant effect on the individual variation in selection by the antshrikes. Wrens, however, increased their selection for steps with more pasture as the amount of pasture in the landscape increased. This is a counterintuitive result. We expected that a functional response (sensu Mysterud and Ims 1998) to the availability of pasture in steps would mean that selection would decline with increasing availability. If this were the case, those wrens in landscapes with more pasture would have shown lower selection for pasture to decrease their exposure. Nystrand (2006) observed such an effect in Siberian Jays (*Perisoreus infaustus*), which exhibited less risky foraging when they lived in a riskier landscape. Instead, it appears that the wrens are taking even greater risks in the most fragmented landscapes. This result matches those of Turcotte and Desrochers (2003), in which birds in less forested landscapes took greater risks to forage. Our results suggest that where the loss and fragmentation of habitat creates landscapes with more exposure overall (i.e., more pasture), this forest-generalist species responds by increasing its willingness to use non-forested habitat for movement through the landscape. Subsequent work will be needed to know if this response ultimately lowers bird survival during movement.

The other significant predictor of individual variation for the wrens was their sex. Greater selection for pasture by male wrens may reflect differential fitness consequences of territory loss between the sexes. In birds, females are generally the dispersing sex (Greenwood 1980) and dispersal by a cooperatively breeding congener was also female biased (Yaber and Rabenold 2002). In that species, male reproductive success was higher for individuals that stayed on the territory to inherit a breeding position than those that dispersed, but this was reversed for females (Yaber and Rabenold 2002). Thus, males may be more motivated than females to return to the territory where they probably held a breeding position, because the consequences of loss of that position could be greater for males. Greater motivation could lead to a greater willingness to take risks, yielding stronger selection for steps with more pasture. Breeding females on territories have also been found to cross fewer and smaller gaps than males making extraterritorial movements (Norris and Stutchbury 2001, 2002).

Movement by the forest specialist in low forest cover situations and their use of stepping stones has some important conservation implications. Our results suggest that stepping stones facilitate movement in highly fragmented habitats with low forest cover. Boscolo et al. (2008) found that stepping stones were used by translocated forest birds crossing between isolated forest patches. Others have suggested that stepping stones are also valuable habitat for birds living in agricultural areas (Fischer and Lindenmayer 2002, Şekercioğlu et al. 2007) and as foci of forest regeneration (Galindo-González et al. 2000). Consequently, their conservation has been advocated as a general principle for biodiversity conservation in agricultural landscapes (Fischer et al. 2006, Manning et al. 2006). Unfortunately, the continued presence of stepping stones in the landscape as remnants of the original forest cover is not assured. Interviews with farmers in our study area indicated that some of them planned to intensify their operations, using methods that would require clearing stepping stones to remove obstructions for the use of machinery (C. Gillies, *unpublished data*). Agricultural intensification in Australia, which also occurred to facilitate mechanization, resulted in the loss of up to 70% of stepping stones (Maron and Fitzsimons 2007). Furthermore, because the understory of these trees is now cattle pasture, some of which is regularly burned, new stepping stones do not appear to be recruiting to replace the loss of large trees. These losses may be particularly detrimental to the permeability of this landscape for antshrikes and many other forest-specialist species.

Although our results demonstrated that the forest specialist was generally reliant on forested routes, there are two reasons why we may have underestimated the importance of forest to its step selection. First, we collected movement information from birds motivated by an artificial stimulus (translocation and homing) to be more exposed than a dispersing bird would be. A dispersing bird exploring a novel landscape would not have a specific destination in mind and therefore would not have the need to cross open areas to reach that destination. Second, we constrained the step lengths of the available steps to best compare where the bird went to where it could have gone. If the birds were selecting forested areas on a broader scale than single steps, constraining the available steps to the same starting location as the used steps would undersample the less forested areas in the landscape that were beyond the locations where the available steps could end. Thus, available steps constrained to the location of the bird would yield more forested steps than available steps randomly placed in the landscape. In addition, we may be underestimating the importance of forested routes to forest specialists more generally, because there are many tropical species that are much more forest dependent than our forest specialist. Although the antshrikes are a forest specialist in this environment, terrestrial insectivores, usually from the families Formicariidae and Rhinocryptidae, are very poor fliers and are reported to be some of the most sensitive to habitat fragmentation (Sieving et al. 1996, Laurance et al. 2004).

For conservation planning, forested routes (i.e., corridors) through fragmented landscapes are probably the best option to facilitate the movement of sensitive forest specialists. Fencerow and stepping-stone habitat is unlikely to be enough to conserve these species. However, stepping stones appeared to have particular utility for movement when forest cover was low; this may mean that their conservation will be important in this and other landscapes.

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