



Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations

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ABSTRACT

Maintaining animal movement in fragmented landscapes depends upon the levels of connectivity among habitat patches, which in turn may depend upon the landscape matrix. Little is known about how the matrix affects dispersal abilities, in part because few experimental tests have been conducted. We experimentally translocated 142 migratory American Redstarts (*Setophaga ruticilla*) and resident Jamaican Todies (*Todus todus*) 0.6–4 km from their territories across landscapes fragmented by peri-urban development and bauxite mining and continuous forest. Redstarts returned more rapidly and with greater success than todies across all landscapes, with 95% of redstarts returning in an average of 2.5 days versus 60% of todies in >20 days. Return success was best predicted by translocation distance for redstarts and by sex for todies, with a trend of fewer birds returning when released in bauxite landscapes. Return time was strongly affected by matrix type, with both species returning more rapidly in a forested relative to a bauxite matrix and intermediately in a peri-urban matrix. These findings provide strong experimental evidence that land cover surrounding forested habitat influences species mobility.

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1. Introduction

Understanding how forest loss and fragmentation reduce functional connectivity across landscapes (sensu [Bélisle, 2005](#)) is essential for predicting species extinctions and ultimately patterns of distribution and abundance across human disturbed ecosystems. As forests become fragmented and converted to human-dominated habitats, natural movement patterns may become disrupted, leading to a loss of population connectivity (e.g., [Fahrig, 2003](#)). Until recently, studies of fragmentation have predominately focused on the effects of patch size and the isolation of forest remnants on extinction and colonization processes, while often failing to account for the role of intervening land cover (termed the “matrix”) ([Ewers and Didham, 2006](#); [Kupfer et al., 2006](#)). The ability of species to re-colonize habitat patches that have been locally extirpated (a process critical for regional population persistence) (e.g., [Hanski, 1998](#)), however, may be largely contingent upon the structure and composition of matrix habitats ([Bender and Fahrig, 2005](#); [Revilla et al., 2004](#); [Ricketts, 2001](#)).

Despite their potential importance, the effects of the landscape matrix on animal dispersal and movement patterns still remain poorly understood. Even for well-studied taxa like birds, little is

known about movement responses to forest fragmentation, with information on bird dispersal capabilities lacking, particularly in the tropics ([Paradis et al., 1998](#); [Walters, 2000](#)). The majority of research on bird movement has been conducted in landscapes of varying amounts of forest cover (e.g., [Bélisle et al., 2001](#)) or landscapes solely dominated by an agricultural matrix (e.g., [Bayne and Hobson, 2001](#); [Castellon and Sieving, 2006](#); [Gillies and St. Clair, 2008](#); [Hadley and Betts, 2009](#)). These studies reveal that mobility of forest-dependent birds is generally greater in landscapes with an increasing amount of forest cover, and that certain species avoid venturing into open pasture even at an energetic cost of greater travel time. Few studies, however, have compared bird movement in other human-modified matrix types or in multiple matrix types in a single setting. Further, when alternative matrix types have been considered, the effects of habitat amount and configuration could not be disentangled from effects due to other matrix features (e.g., [Gobeil and Villard, 2002](#)). Given that the trajectory of land conversion in many regions of the world is from agriculture to increasing urbanization ([DeFries et al., 2004](#)), a better understanding of how forest fragmentation impacts bird movement in more intensively developed landscapes is essential.

Our aim was to determine whether matrix type influences movement abilities of two insectivorous bird species – a habitat generalist, Nearctic–Neotropical migrant, the American Redstart (*Setophaga ruticilla*); and a resident forest specialist, the Jamaican Tody (*Todus todus*). We targeted insectivorous birds because they

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are disproportionately declining in fragmented forests worldwide, with Neotropical–Nearctic migrants (e.g., Askins et al., 1990; Robbins et al., 1989) and Neotropical residents (e.g., Sigel et al., 2006; Sodhi et al., 2004; Stouffer et al., 2009) particularly impacted. Dispersal limitation is increasingly identified as a dominant mechanism underlying their demise (Lampila et al., 2005; Stratford and Robinson, 2005). We experimentally translocated 142 birds from their territories across three landscape treatments: landscapes fragmented by residential (peri-urban) development (i.e., peri-urban matrix), landscapes fragmented by bauxite mining (i.e., bauxite matrix), and landscapes comprising continuous forest (i.e., natural “matrix”). Experimental manipulations, particularly translocations, are essential to measure landscape permeability for vagile species like birds (Bélisle et al., 2001), because they allow for movement motivation to be standardized across individuals, for probable return pathways to be predicted, and for landscape features of interest to be isolated (i.e., matrix types) (Bélisle, 2005).

We tested whether the probability with which birds returned (i.e., return success) or the time it took for them to return (i.e., return time) to territories differed between landscape matrix types and species. We predicted that birds would return at higher frequencies and more rapidly through continuous forest relative to fragmented landscapes, with intermediate return success and return time in peri-urban landscapes. We expected bird movement to be enhanced in peri-urban landscapes compared to bauxite mining landscapes because matrix areas contained greater vegetation cover that could act as stepping stones to aid movement while bauxite matrices lacked this vegetation structure (see Section 2.1). Tropical non-migratory specialists, particularly understory insectivores, are expected to be more dispersal-inhibited than temperate generalist birds (e.g., Harris and Reed, 2002; Paradis et al., 1998; Stratford and Robinson, 2005); thus, we predicted that the

American Redstart would have greater return success and quicker return time than the Jamaican Tody across all landscape types.

Additional factors beyond landscape structure can influence both site fidelity and movement ability and may in turn impact homing propensity (i.e., return of birds). Female birds are typically more dispersive than males (e.g., Greenwood and Harvey, 1982). Birds inhabiting lower quality habitats may be less site-tenacious (e.g., Holmes et al., 1996), and individuals in reduced condition may be less prone to return to territories (e.g., Marra and Holmes, 2001) or less able to withstand physiological costs associated with translocation. Because homing abilities of our study species are unknown, we investigated the potential influence of sex, body condition, and territory habitat quality on return patterns.

2. Methods

2.1. Study area

We conducted our experiments in Manchester and Clarendon Parishes in central Jamaica, an area that was once covered in predominantly wet limestone forest. Less than 30% of native forest currently remains; forests are now largely restricted to small hill-top remnants on limestone outcrops, with low lying areas converted for agriculture (i.e., historically for cultivation of cash crops, and later for cattle pasture) (Eyre, 1987) and more recently for residential development and mining for bauxite (Evelyn and Camirand, 2003). Locations and extent of forest fragments in this region are similar among landscapes subject to these different land-use pressures and have remained fairly stationary in recent time but are embedded in a changing matrix. This setting provided a unique opportunity to investigate the influence of matrix habitats on movement patterns of forest-dependent birds.

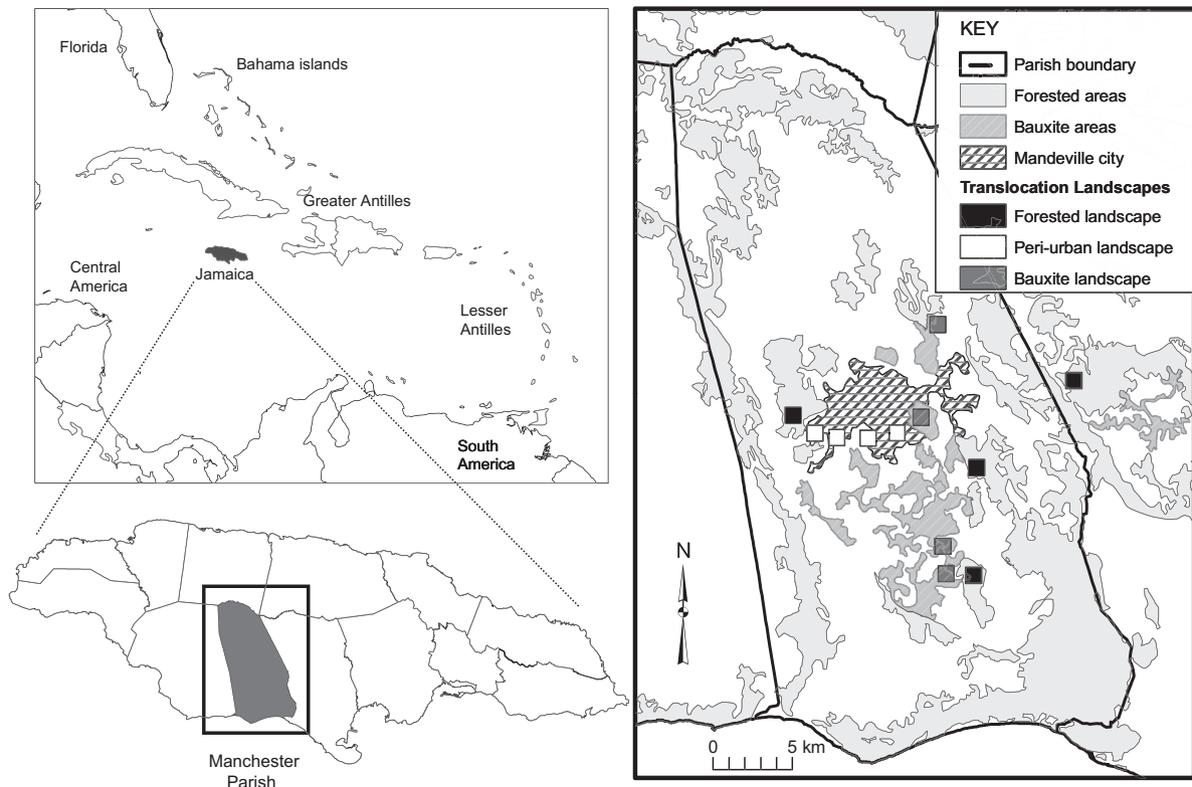


Fig. 1. Locations of the 12 landscapes where experimental translocations were performed as shown in the context of the West Indies (latitude: 17° 56' 44"–18° 05' 36" N; longitude: 77° 23' 19"–77° 34' 18" W). Landscapes are delineated by 1-km² areas centered around capture sites for geographic reference.

We targeted three landscape types: (1) landscapes in which forest has been fragmented by peri-urban development, (2) landscapes in which forest has been fragmented by bauxite mining, and (3) landscapes comprising continuous forest (i.e., peri-urban, bauxite, and forest treatments, Fig. 1). Open areas surrounding forest patches differed substantially in peri-urban versus bauxite matrices. Forest remnants in peri-urban landscapes were surrounded by low-density housing, ornamental gardens, abandoned woodlots, and roadside secondary growth. Bauxite landscapes were former agricultural lands that had been converted to mining within the past 10 years. Relative to bauxite landscapes, peri-urban

matrices contained greater foliage cover and vertical complexity (Kennedy et al., in press).

2.2. Target species

We translocated the Jamaican Tody and the American Redstart (hereafter tody and redstart). Both species are common insectivores in the region. The former species is endemic to Jamaica and the latter species is a migrant that winters in Jamaica from late August through mid-May (Marra and Holmes, 2001). The tody occurs in several forest types, but it is most abundant in mid-elevation

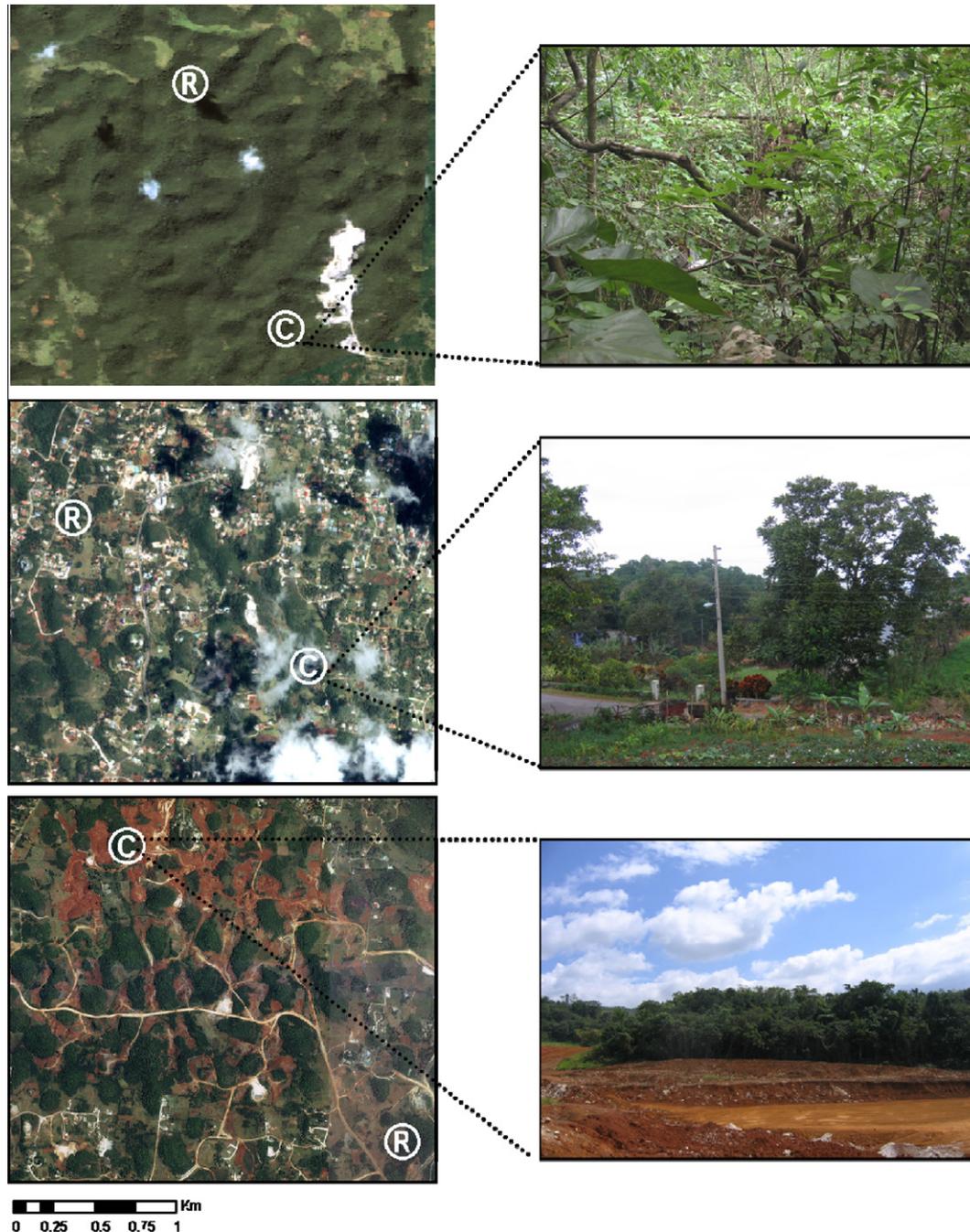


Fig. 2. Three landscape treatments where birds were translocated: (1) landscapes comprising continuous forest (top), (2) landscapes fragmented by peri-urban development (middle), and (3) landscapes fragmented by bauxite mining (bottom). Capture (©) and release (®) locations of one example translocation is overlaid on IKONOS imagery (left panel), juxtaposed with photographs taken in the field near capture patches (right panel). All birds were captured and released in limestone forest patches. Forest cover is surrounded by ornamental lawns, gardens, roadside vegetation, roads, and houses in peri-urban landscapes, and exposed bauxitic soil and early growth of ferns and *Acacia* stands in bauxite mining landscapes.

limestone forests (Raffaele et al., 1998). It is an understory forest specialist that forages commonly <5 m from the ground, taking large insects from leaf undersides (Lack, 1976). The redstart is a habitat generalist that is found in forest, woodland, and non-forested habitats in the Caribbean, where it forages for a wide variety of insect prey on a diversity of substrates (Sherry and Holmes, 1997).

The biology of the Jamaican Tody has yet to be rigorously studied but it is known to breed and hold territories between December and July (Raffaele et al., 1998, C.M. Kennedy, unpublished data), similar to congeners in Puerto Rico (*Todus subulatus*, *Todus angustirostris*, and *Todus mexicanus*) (Kepler, 1977; Latta and Wunderle, 1996). Redstarts return annually to the same territory on their non-breeding, wintering grounds in Jamaica; both males and females vigorously defend independent and exclusive territories (Holmes et al., 1989; Marra, 2000). Given their ease to detect and capture and presumed similar motivation to return to territories, todies and redstarts were ideal species for our translocation experiment.

2.3. Capture and release sites

We captured birds from 12 forest fragments embedded in 4 peri-urban landscapes, 17 forest fragments embedded in 4 bauxite landscapes, and 21 sites in 4 spatially independent and intact forest landscapes (Fig. 1). Capture patches in fragmented landscapes were similar in forest area (mean \pm 1 SD: peri-urban: 4.24 \pm 2.21 ha; bauxite: 3.10 \pm 2.23 ha) and isolation (31.76 \pm 26.74 m and 48.88 \pm 31.33 m to nearest fragment >0.5 ha and 2280.00 \pm 1681.63 m and 2139.47 \pm 1036.11 m to >100 ha fragment in peri-urban and bauxite landscapes, respectively) as determined from an object-based classification of 2001–2002 multispectral IKONOS imagery (1-m resolution, 89% overall accuracy), with measurements conducted in ArcGIS 9.3 (ESRI, 2008) (Kennedy, 2009). Patches were also embedded in landscapes with a similar proportion (34.21 \pm 4.26) and spatial configuration of forest cover (i.e., shape complexity, inter-patch connectivity) (Kennedy et al., in press).

To standardize the stimulus for emigration, we also released birds in forest patches of similar size (mean \pm 1 SD: peri-urban ($N = 17$): 2.01 \pm 1.99 ha; bauxite ($N = 24$): 2.92 \pm 3.49 ha) and isolation (112.46 \pm 61.50 m and 103.49 \pm 47.69 m to nearest fragment >0.5 ha and 2866.20 \pm 1410.43 m and 2456.92 \pm 2309.91 m to >100 ha fragment in peri-urban and bauxite landscapes, respectively). Thus, the landscape matrix was the primary difference among experimental translocations. Release locations were predetermined from imagery, land-cover maps, and previous field research, such that individuals were translocated in one of three landscape treatments: peri-urban matrix ($N = 46$: 35 todies and 11 redstarts), bauxite mining matrix ($N = 50$: 25 todies and 25 redstarts), or forested “matrix” ($N = 46$: 31 todies and 15 redstarts) (see Fig. 2). We captured and released birds in >70 different sites (≥ 100 m in distance) at different time periods throughout the morning hours (see Translocation protocol).

2.4. Translocation protocol

We translocated todies from mid February to early May and redstarts from late February to early April in 2007 (median date: 29 March 2007). Individuals were targeted for translocation after three to six visits, during which we confirmed territorial status based on repeated presence of redstarts and the interaction of a pair of todies, territorial displays (e.g., agonistic displays, fighting, and chasing behavior), and/or tody courtship or nesting behavior. We used the same protocol for pre- and post-translocation surveys (see below) to estimate detection probabilities. Redstarts and to-

dies were detected with probabilities of 0.76 (± 0.06 SE) and 0.72 (± 0.04) in forested landscapes, 0.70 (± 0.07) and 0.78 (± 0.04) in peri-urban landscapes, and 0.75 (± 0.04) and 0.74 (± 0.05) in bauxite landscapes, respectively; probabilities did not differ by landscape type ($\chi^2_{\text{tody}} = 1.003$, $\chi^2_{\text{redstart}} = 1.004$, $df = 2$, $P = 0.606$, based on likelihood ratio tests of occupancy models fit in PRESENCE with and without matrix type as a covariate on detection) (Hines and MacKenzie, 2008). Given high detection rates and lack of bias among treatments, we were confident in the reliability of our return estimates for inference. Moreover, we have no reason to expect systematic bias in bird behavior as a function of landscape type even if detectability decreased in response to capture.

Individuals were caught between 0615 and 1220 h (mean: 0838 h) by attracting them into mist-nets via conspecific bird decoys and species-specific vocalizations to increase the capture probability of territory-holders rather than floaters that may fail to exhibit strong site fidelity. Individuals of both species consistently responded to playbacks during the entire capture period, suggesting similar territoriality and return propensity during the experiment. After capture, each bird was measured (body mass, length of tarsus, culmen, and unflattened wing chord) and banded with a unique combination of color and aluminum bands. We targeted male redstarts but also translocated the few females that were caught, given their known fidelity to winter territories. We determined sex of redstarts based on plumage characteristics (Pyle et al., 1987). We were unable to standardize for sex among todies due to a lack of external dimorphism. Sex of todies was determined based on DNA for 73 individuals and based on discriminant function analysis for 18 todies by comparing their tarsus, culmen, and wing chord lengths to those of individuals of known sex (Kennedy, 2009). In total, we translocated 51 redstarts (43 males and 8 females) and 91 todies (67 males and 24 females).

Immediately upon capture, birds were placed in an opaque cloth bag and transported by vehicle to release sites (mean \pm 1 SD: capture-release time averaging 60.90 \pm 17.26 min). Handling time was slightly higher in forested landscapes (69.22 \pm 18.06 min) than peri-urban (56.54 \pm 16.68 min) or bauxite landscapes (57.26 \pm 14.34 min) due to greater road inaccessibility, but did not vary by species (tody: 59.68 \pm 15.42 min; redstart: 63.08 \pm 20.10 min). Individuals were translocated from 560 m to 4 km (mean \pm 1 SD: 1.741 \pm 0.72 km) from the site of their capture. Redstarts were translocated on average 2.34 (± 0.56) km, which was farther than the distance todies were translocated (1.407 \pm 0.56 km). We selected these distances to be sufficiently large to reduce bias due to prior landscape knowledge from daily movements but small enough to reduce bias due to navigation ability during migration events (Bélisle et al., 2001; Bélisle and St. Clair, 2002; Gobeil and Villard, 2002). On non-breeding grounds, redstarts are rarely observed beyond their territory boundaries (P. P. Marra, unpublished data), which are generally ≤ 0.25 ha (Holmes et al., 1989). The size of the Jamaican Tody's home range is unknown, but territories of the congener *T. mexicanus* are an average 0.70 ha with daily movements expanding only ~ 60 m beyond these boundaries (Kepler, 1977); we suspect territories may be even smaller for *T. todus* based on our observations (C.M. Kennedy, unpublished data).

Upon release of each bird, at least one observer remained at the site in a concealed location to ensure that each bird exhibited normal flight capability. An additional observer returned to the capture site within 5 h post-release and monitored for the potential return of the color-banded individual at the vicinity of its territory and surrounding areas (>1 ha). If individuals were not detected to return on the release day, an observer returned to the capture site every day for the first 5 days, followed by day 7, day 10, day 14, with visits thereafter at weekly intervals for up to 3 months or until the target individual was observed on its original territory. Dur-

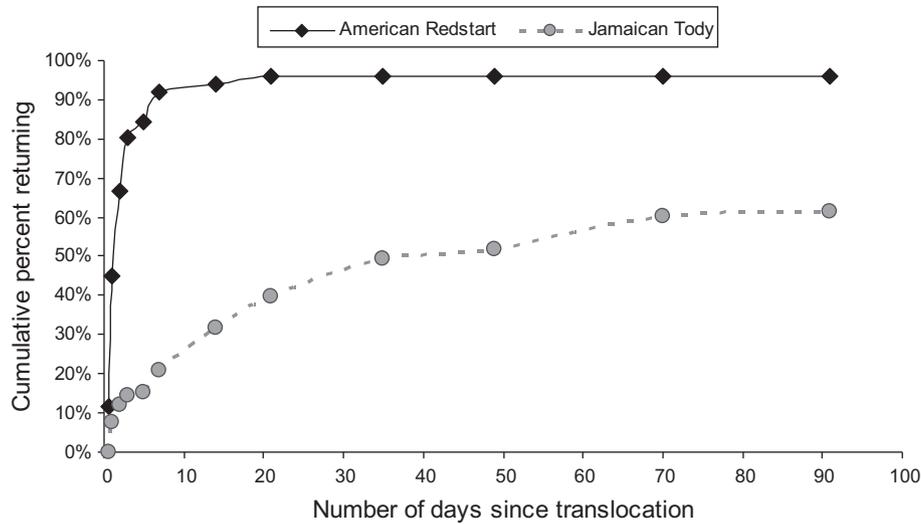


Fig. 3. Cumulative proportion of the number of American Redstarts ($N = 51$) and Jamaican Todies ($N = 91$) detected to return to their territories as a function of the number of days since translocation.

ing each visit, we patrolled the territory grounds for ≥ 1 h, searching passively for the first 30 min followed by broadcasting playbacks at 5-min intervals for the final 30 min.

2.5. Covariates on return success and time

Besides our primary interest in matrix type, we considered four variables that we predicted would most influence species return patterns: sex, body condition, territory habitat quality, and translocation distance. To account for variation in body condition of translocated birds, we estimated body mass corrected for the structural size of each bird (after Marra et al. (1998)). To quantify territory habitat quality, we measured 12 vegetation variables in a 10-m radius plot centered at each capture location: tree diameter, basal area, canopy height, leaf area index, leaf litter depth, abundance of woody and herbaceous vines, and percent herbaceous cover (0–0.5-m height class), low shrub (0.5–2 m), tall shrub (2–6 m), trees (>6 m), and open canopy (Appendix A). We conducted a principal component analysis (PC) on these variables, and used PC axis 1 score as a proxy for vegetation structure. This metric indicates territory habitat quality, given it has been identified as an important determinant of extinction rates for todies (Kennedy, 2009), with similar measures linked to habitat quality for redstarts on their wintering grounds (Marra and Holmes, 2001).

Translocation distance was determined based on the Euclidean distance between capture and release locations for each bird based on measurements taken with a hand-held global positioning system (≤ 10 -m accuracy). Landscape treatment was defined categorically as to whether birds were translocated in a forest, peri-urban, or bauxite matrix. Given the extent of forest fragmentation was similar between peri-urban and bauxite landscapes, matrix treatment served as a surrogate for composition and structure of matrix habitats.

2.6. Modeling of return success and return time

We determined whether return success and return time differed by species over the entire observation period based on univariate models with species as the only covariate. We tested whether return success was influenced by all variables (as listed above), and return time by all variables except territory habitat quality given we had no *a priori* information to predict that this covariate would directly impact homing time. Given that the rela-

tive importance of environmental factors might vary between species, we fit models separately for redstarts and todies. We analyzed return success (i.e., return versus no return) at a 3-day threshold for redstarts and a 35 day threshold for todies. These thresholds represented the timeframe when territories were most frequently visited (i.e., daily for redstarts and at least weekly for todies), and when the majority of returns for each species occurred (84% of redstarts and 80% of todies). Additionally, we analyzed return success when closest to 50% (after Bêlisle et al., 2001), which was at 1-day and 2-week time frames for redstarts and todies, respectively, to estimate homing success by a sizable proportion of birds. Results for both the majority and the 50% thresholds were consistent; thus, final models are presented for the 3-day and 35-day post-translocation time periods only.

To assess the influence of covariates on return success and return time, we used generalized linear models with a binomial error distribution (logit link function) and Cox proportional hazards regression models, respectively. We analyzed return time (i.e., days since translocation) using survival analysis, which compares time-to-failure curves, where “failure” represented the detected return of a bird to its territory. We excluded birds that did not return to territories in Cox regressions to prevent confounding movement with other mechanisms (i.e., philopatry and mortality). Model fitting was conducted using forward step-wise likelihood ratio estimation (Harrell, 2001), in which variables were added that produced the most significant change in the model chi-square ($P < 0.10$), with variables considered statistically significant at $\alpha = 0.05$. Variables significant at $\alpha = 0.10$ were not included in final models, but we discuss associated covariates because they may indicate ecologically important trends. Final model significance was determined via the likelihood ratio test and the significance of coefficients via Wald statistic with posthoc comparisons among groups based on Tukey’s HSD. Each translocation was treated as an independent event in models given that each individual bird was translocated only once and >90% of birds were captured and released at different locations. To investigate the potential for spatial dependence, we conducted preliminary analyses in which we modeled capture and release patches as the only covariate on return success and time. For both species, each individual patch failed to be a strong predictor for either return success ($P > 0.50$) or return time ($P > 0.10$).

Statistical analyses were performed in the R statistical system (R Development Core Team, 2008) using the ‘stats’ package for gen-

Table 1

Variables that significantly influenced the return success and the return time (at $P < 0.05$) of the American Redstart and the Jamaican Tody when translocated ~550 m to 4 km from their territories in three landscape treatments (peri-urban development, bauxite mining, and forested matrix) in central Jamaica. Return success was modeled via generalized linear models (with binomial errors) and return time via Cox regression models.

	Variable	Hazard ratio	Coefficient	SE	P-value
<i>Return success</i>					
American Redstart (N = 51)	Constant		5.8825	1.81	0.001
	Translocation distance (m)		-0.0018	0.00	0.008
Jamaican Tody (N = 91)	Constant		-0.8873	0.45	0.048
	Sex-male		1.1576	0.51	0.024
<i>Return time</i>					
American Redstart (N = 49)	Translocation distance (m)	1.00	-0.0006	0.00	0.034
	Landscape-Forest	2.73	1.0029	0.39	0.010
	Landscape-Peri-urban	1.28	0.2431	0.43	0.570
Jamaican Tody (N = 56)	Landscape-Forest	2.92	1.0700	0.39	0.006
	Landscape-Peri-urban	2.09	0.7380	0.37	0.046

The reference category is female for "Sex" and bauxite for "Landscape" variable.

eralized linear models and principal components analysis; the 'MASS' package (v 7.2–44) (Venables and Ripley, 2002) for discriminant analysis; the 'survival' package (v 2.34-1) (Therneau and Lumley, 2008) for Cox regressions; and the 'multcomp' package (Hothorn et al., 2008) for multiple comparisons. We assessed model fit based on plots of residuals versus fitted values, and model assumptions were met (e.g., constant error variance, approximately normal errors, and proportional hazards for Cox regression). Untransformed means ± 1 SE are reported.

3. Results

3.1. Return success

Return success was higher for the American Redstart (96% of 51 individuals) than the Jamaican Tody (62% of 91 individuals) (Fig. 3, $\chi^2 = 24.78$, $df = 1$, $P < 0.001$). For redstarts, the most important determinant of return success was translocation distance, with birds translocated farther having lower return probability ($\chi^2 = 8.26$, $df = 1$, $P = 0.004$) (Table 1). Body condition, territory vegetation structure, and sex did not influence redstart return proba-

bilities at $P > 0.10$. For todies, sex was the only significant predictor of return success, with males more likely to return than females ($\chi^2 = 5.50$, $df = 1$, $P = 0.019$). Sixty-nine percent of male todies versus 42% of female todies were found to return to their territories by the end of the 3-month observation period. Translocation distance, body condition, and territory vegetation structure did not influence return probability for the resident species ($P > 0.10$). Although not significant, there was a trend of lower return success by redstarts ($\chi^2 = 5.72$, $df = 2$, $P = 0.057$) and todies ($\chi^2 = 4.15$, $df = 2$, $P = 0.126$) released in a bauxite matrix relative to peri-urban development and forested landscapes (Fig. 4).

3.2. Return time

Mean time for todies to return to territories was 20.6 (± 2.79) days, which was significantly longer than that for redstarts (2.6 ± 0.49 days) ($\chi^2 = 50.00$, $df = 1$, $P < 0.001$). The return time of redstarts was influenced by the additive effects of matrix type and translocation distance ($\chi^2 = 16.40$, $df = 3$, $P < 0.001$), whereas matrix type was the only significant factor influencing the return time for todies ($\chi^2 = 8.46$, $df = 2$, $P < 0.001$). For both species, individuals returned faster in forested than in bauxite landscapes; return times were intermediate in peri-urban landscapes (Table 1, Fig. 5). Redstarts that were translocated farther from their territo-

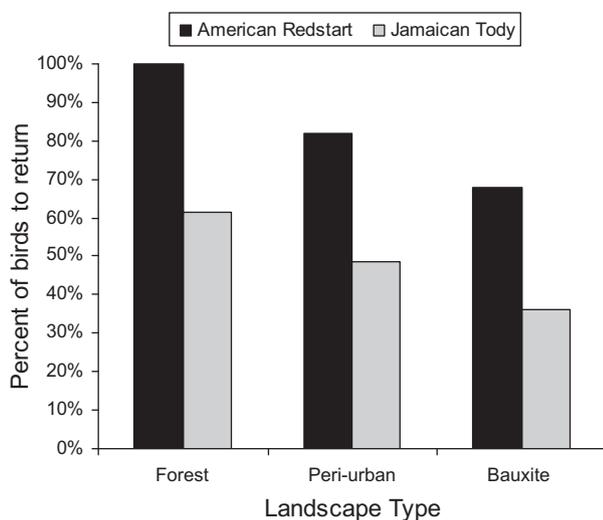


Fig. 4. Return success 3-days after translocation (American Redstart) and 35-days after translocation (Jamaican Tody) in three landscape matrix types (forested: N = 46, 15 redstarts and 31 todies; peri-urban development: N = 46, 11 redstarts and 35 todies; and bauxite mining: N = 50: 25 redstarts and 25 todies). Return thresholds (3-day and 35-day) were chosen to provide comparable percentages of returning birds for the two species. Return success did not differ by landscape treatment at $P < 0.05$ for either species, but differed at $P = 0.057$ for the American Redstart and $P = 0.126$ for the Jamaican Tody.

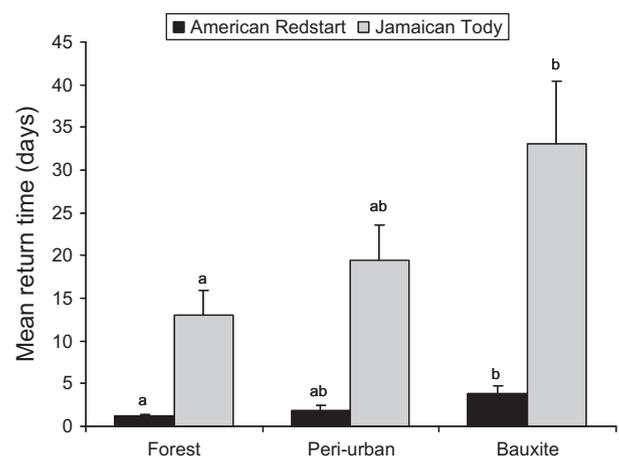


Fig. 5. Mean return time (± 1 SE) by the American Redstart and the Jamaican Tody after translocation in three landscape matrix types (forested: N = 35, 15 redstarts and 20 todies; peri-urban development: N = 32, 10 redstarts and 22 todies; and bauxite mining: N = 38: 24 redstarts and 14 todies). Shared letters indicate no significant difference ($P < 0.05$) among treatments based on Cox regression models and post hoc Tukey's HSD tests. Return time of todies differed at $P < 0.10$ between peri-urban and bauxite landscapes.

ries had slightly longer return times ($P < 0.05$), but translocation distance did not affect return time for todies ($P > 0.10$). Sex and body condition were not important predictors for the return time for either species ($P > 0.10$).

4. Discussion

Landscape connectivity is commonly evaluated in terms of the amount and spatial distance of remnant habitat in relation to species movement abilities, often without consideration of matrix habitats. Although it is increasingly recognized that land cover surrounding forest fragments can affect the mobility of even vagile taxa like birds, this is one of few experimental demonstrations that bird movement patterns are mediated by the conditions of the landscape matrix (see also Castellon and Sieving, 2006; Gillies and St. Clair, 2008; Gobeil and Villard, 2002), and is unique in detecting this effect even when controlling for patch area and isolation.

4.1. Species traits mediate bird movement

The American Redstart returned with greater success across all landscape types than the Jamaican Tody, with the proportion of redstarts returning to their territories being 1.5 times as high as that of todies. The lower return probability of todies may be explained in part by a greater proportion of female todies (26.4%) translocated than female redstarts (15.7%), which may have been less site-faithful. The age of individuals or their pairing status (e.g., Greenwood and Harvey, 1982; Holmes et al., 1996) may also underlie why fewer todies returned – if we translocated juveniles and/or siblings acting as helpers on territories (this type of communal breeding has been documented for the congener *T. mexicanus*; Raffaele et al., 1998). The ultimate reason(s) todies failed to return to capture sites within the 3-month survey period is thus unknown – whether due to mortality during dispersal (i.e., predation), behavioral decisions to settle in new locations, and/or an inability to orient successfully to territories after displacement. Our experimental evidence suggests, however, that the matrix may have played a role, given fewer returns of both redstarts and todies in bauxite landscapes, but this factor was not significant, perhaps due to insufficient sample size.

An even more striking result was that redstarts returned eight times faster than todies. With an average return time >20 days, the tody displayed relatively poor homing capabilities. Temperate (Bélisle et al., 2001; Bélisle and St. Clair, 2002; Gobeil and Villard, 2002) and other tropical insectivorous birds (Gillies and St. Clair, 2008) have been reported to return to territories within 2–3 days under similar translocation experiments (albeit performed in largely agricultural or forested landscapes). Enhanced homing ability in redstarts may be due to a greater willingness to cross open spaces and to navigate in a wide variety of non-native habitats. This assertion is based on the fact that redstarts commonly use diverse habitats on their wintering grounds (e.g., Confer and Holmes, 1995); thus, they may be less behaviorally inhibited in fragmented landscapes (e.g., Greenberg, 1983). Given they are long-distance migrants, redstarts may have also evolved greater cognitive abilities (e.g., memory and processing of environmental information) that enhance their exploratory and navigational abilities (e.g., Mettke-Hofmann and Gwinner, 2004).

4.2. Landscape matrix mediates bird movement

We found no significant difference in return success among landscape treatments in contrast to our predictions, perhaps due to low sample size or translocation distances that were too short,

but a trend was detected with fewer returns of birds released in bauxite landscapes. The speed of return, however, did significantly differ, with both species returning more quickly in a forested matrix than in a bauxite matrix. Movement rates through peri-urban landscapes were more similar to intact forest relative to bauxite landscapes. This dissimilar permeability is due to differential movement and not to differential mortality, because the pattern is based only on birds that successfully returned. Moreover, we found no differences in the original territory habitat structure of translocated birds or in their initial body condition, further isolating the effects of matrix type as the primary driver of return time.

We propose that the detected differences in landscape permeability are most simply explained by behavioral inhibitions to movement. Bauxite landscapes typically have little vegetation cover in matrix areas. Birds are thus subject to expansive open spaces and are forced to cross wide gaps (often hundreds of meters) when navigating between forest fragments. Previous experiments using song playbacks indicate that many forest-dependent species demonstrate a strong reluctance to cross even small habitat gaps (e.g., <25–50 m) despite their presumed physical capabilities (e.g., Harris and Reed, 2002). Gap-crossing and recent translocation experiments reveal that birds may avoid venturing into open areas and instead preferentially move through landscape features most similar to their optimal habitat at an energetic cost of greater travel time (e.g., Desrochers and Hannon, 1997; Gillies and St. Clair, 2008). A reluctance to cross gaps may be a response to avoid predators (e.g., Lima and Dill, 1990), or the result of limited perceptual range (e.g., Zollner and Lima, 2005) or low motivation (e.g., few suitable resources in the matrix; Bélisle and Desrochers, 2002). Thus, birds in bauxite mining landscapes may have remained longer in release patches (e.g., Castellon and Sieving, 2006), searched a longer time for suitable cover, or taken more circuitous routes back to territories (e.g., Gillies and St. Clair, 2008; Hadley and Betts, 2009). We cannot, however, rule out the potential role of food resources in driving differential homing patterns if birds foraged for longer durations to meet the energetic demands of movement given fewer resources in different matrix types.

Movement (homing) trends detected by this experiment provide essential insight into differential permeability of common Caribbean landscapes, but the specific features that either facilitated or impeded movement remain unknown because bird movement trajectories and differential use of matrix features were undocumented. At the time of the study, radio transmitters that were sufficiently small in size were not readily available to detail movement patterns and behavioral decisions of target birds during their return paths. Recent advances in miniaturized tracking technology are making feasible the more precise tracking of smaller animals (e.g., Hadley and Betts, 2009), which will enhance future research on bird movement behavior.

4.3. Conservation implications

Categorizing landscapes into a “matrix” versus “habitat” components and treating all anthropogenically modified lands as a single cover type (i.e., non-habitat) in fragmentation research or conservation planning may lead to erroneous decision-making. Based on our experiments, both the migrant American Redstart and the resident Jamaican Tody display differential movement abilities contingent upon whether once-continuous forest was converted to peri-urban or bauxite mining development. We hypothesize that similar permeability of peri-urban and forested landscapes was due to shrubs and trees in the peri-urban matrix providing some degree of structural connectivity. Residential landscapes have greater tree cover between forested hilltops as a result of ornamental gardens in lawns, abandoned woodlots, and tree-lined roadsides (Kennedy et al., in press). Maintaining matrix veg-

etation cover, even if composed of non-native species and clusters of trees, seemingly facilitates bird movement between otherwise isolated forest patches. Castellon and Sieving (2006) similarly found that the Chucao Tapaculo (*Scelorchilus rubecula*) dispersed as readily in matrix habitat composed of shrubby vegetation as in wooded corridors, with vegetation cover the likely dominant cue over composition. Their study and our data support the utility of restoring and/or maintaining matrix vegetation cover to serve as potential stepping stones for bird movement. Encouraging private land owners to restore trees via native forest regeneration or ornamental plantings may be a more feasible management strategy compared to the creation of corridors, with the latter more costly in restoration efforts and land acquisition but a primary focus of conservation planning.

The persistence of populations in fragmented systems may hinge upon the ability of individuals to disperse successfully through different matrix types to (re)colonize habitats and rescue populations from local extirpation (e.g., Revilla et al., 2004; Wiegand et al., 2005). Lack of vegetation structure in bauxite landscapes may impose great constraints on bird movement. Mined landscapes present an opportunity to test experimentally the importance of tree cover to the maintenance of connectivity for forest-dependent birds in an adaptive management framework. Planting trees in specific spatial arrangements and floristic assemblages, during post-mining restoration, would help to ascertain the relative effect(s) of matrix vegetation configuration, structure, and composition and to identify threshold gap distances (sensu Harris and Reed, 2002) above which the probability of movements become dramatically reduced.

Experimental studies designed to elucidate the relative impact of matrix cover types on species dispersal abilities are needed for further comparison. Given seemingly idiosyncratic responses by species to fragmentation, experimental movement studies are essential for predicting which species/guilds are most threatened by habitat conversion. Our findings build upon emerging empirical evidence that support long-standing hypotheses that certain species may be more susceptible to extirpation in fragmented systems due to dispersal limitation. In particular, specialists appear more at risk than generalists (Gobeil and Villard, 2002; Haddad, 1999; Lees and Peres, 2009), tropical species appear more at risk than temperate species (Moore et al., 2008), and residents appear more at risk than migrants (Bélisle and St. Clair, 2002; Paradis et al., 1998). This study reveals that whether or not these groups of species ultimately decline in fragmented landscapes may depend in large part on the suitability of the intervening matrix.

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Appendix A. Territory vegetation structure

A1. Methods

To quantify vegetation structure of territories, we measured 12 variables in a ten-meter radius plot centered at each bird capture location: tree diameter, basal area, canopy height, leaf area index, leaf litter depth, abundance of woody and herbaceous vines, and percent herbaceous cover (0–0.5 m height class), low shrub (0.5–2 m), tall shrub (2–6 m), trees (>6 m), and open canopy. Each plot was divided into four equal quadrats based on 10-m transects in each cardinal direction. We measured tree basal area using a 10-factor prism at each plot center. Within each quadrat, we measured diameter breast height and canopy height of the largest tree, and we estimated the abundance of herbaceous and woody vines based on a categorical scale (0 = absent, 1 = solitary, 2 = few, scattered individuals, 3 = common, 4 = abundant). At 2-m intervals along each transect, we measured leaf litter depth and foliage structure at various heights. Foliage structure was scored based on foliage touches along a pole at four height classes (0–0.5 m, 0.5–2 m, 2–6 m, >6 m), with percent cover calculated as the percent of all points at a given height interval with ≥ 1 touch (after Schemske and Brokaw, 1981). Percent canopy openness and effective leaf area were estimated based on hemispherical canopy photographs taken at 5-m intervals in two randomly selected transects with a Nikon Coolpix 950 Camera and FC-E8 Nikon Fish-eye lens. Percent canopy openness and effective leaf area (Leaf Area Index Ring 4) (Stenberg et al., 1994) were calculated using the Gap Light Analyzer (GLA) program (v 2.0) (Frazer et al.,

Table A1

Factor loadings from a principal component analysis of plot-level vegetation variables for each sampled forest patch. The first principal component axis (PC1) explained 32.17% of variance in plot-level vegetation structure. All variables were significantly correlated with PC1 scores based on Pearson correlation coefficients at familywise $\alpha = 0.05$.

Vegetation variable	PC1
Leaf area index	-0.3324
Basal area (m/ha)	-0.3228
Tree diameter (cm)	-0.3182
Canopy height (m)	-0.3817
<i>Percent cover (%)</i>	
Open canopy	0.3489
Herbaceous layer	0.2959
Low shrub layer	0.2410
Tall shrub layer	-0.1312
Tree layer	-0.4101
<i>Abundance (scale 0:4)</i>	
Herbaceous Vines	0.2308
Woody vines	0.1115
Litter depth (cm)	-0.1408

1999). All measurements were calibrated between two observers. Repeat measurements across quadrats and transects were averaged to determine plot-level vegetation for each capture location. To distill the variation in the 12 patch-level vegetation variables into fewer non-correlated components, we conducted a principal component analysis (PC).

A2. Results

Territory vegetation structure, as determined by PC1, was strongly positively associated with percent open canopy, herbaceous and low shrub cover and the abundance of herbaceous vines. In contrast, PC1 was strongly negatively associated with the proportion of tree cover, canopy height, leaf area index, tree basal area, tree diameter, and leaf litter depth (Table A1).

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