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Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species

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Abstract. Translocation experiments, in which researchers displace animals and then monitor their movements to return home, are commonly used as tools to assess functional connectivity of fragmented landscapes. Such experiments are purported to have important advantages of being time efficient and of standardizing “motivation” to move across individuals. Yet, we lack tests of whether movement behavior of translocated birds reflects natural behavior of unmanipulated birds. We compared the routine movement behavior of a tropical hummingbird, the Green Hermit (*Phaethornis guy*), to that of experimentally translocated individuals. We tested for differences in site selection patterns during movement at two spatial scales (point and path levels). We also compared movement rates between treatments. Behaviors documented during translocation experiments reflected those observed during routine movements. At the point level, both translocated and non-translocated birds showed similar levels of preference for mature tropical forest. At the path level, step selection functions showed both translocated and non-translocated hummingbirds avoiding movement across non-forested matrix and selecting streams as movement corridors. Movement rates were generally higher during translocation experiments. However, the negative influence of forest cover on movement rates was proportionately similar in translocation and routine movement treatments. We report the first evidence showing that movement behavior of birds during translocation experiments is similar to their natural movement behavior. Therefore, translocation experiments may be reliable tools to address effects of landscape structure on animal movement. We observed consistent selection of landscape elements between translocated and non-translocated birds, indicating that both routine and translocation movement studies lead to similar conclusions regarding the effect of landscape structure and forest composition on functional connectivity. Our observation that hummingbirds avoid non-forest matrix and select riparian corridors also provides a potential mechanism for pollen limitation in fragmented tropical forest.

Key words: corridors; fragmentation; functional connectivity; Green Hermit hummingbird; landscape; Las Cruces Biological Station, Costa Rica; matrix avoidance; movement behavior; *Phaethornis guy*; pollinators; step selection function; translocation experiments.

INTRODUCTION

Gene flow, dispersal from natal areas and migration, as well as key ecological processes (e.g., nutrient flow, seed dispersal, and pollination) all depend on the capacity of animals to move across landscapes. Landscape fragmentation has long been known to affect animal movement behavior (Arnold et al. 1993, Bennett 1993, Bélisle et al. 2001, Ricketts 2001). By dividing once-continuous habitats into patches, habitat fragmentation may restrict how far individuals can travel and what routes they take—particularly if they select certain land cover types to move through while avoiding others. Changes in the spatial configuration of preferred habitat

can lead to changes in animal movement routes and, consequently, in the spatial distribution of ecological processes associated with them (Cranmer et al. 2012). The degree to which a landscape facilitates or impedes animal movements between resource patches is known as the landscape’s “functional connectivity” (Taylor et al. 1993), a concept that goes beyond the classical structural definition of connectivity (i.e., the degree to which landscape elements are physically linked to each other). Functional connectivity varies among species, because it is influenced by factors such as vagility, tolerance to stress, perception of risk, and susceptibility to competition and predation. Accepting that connectivity depends on the perception of individuals and their responses to landscape characteristics allows for a more realistic view of the potential influences of landscape structure on animal movement (Bélisle 2005), which influences dispersal, habitat selection, and the spatial distribution, genetic structure, and viability of populations (Hanski 1998, Baguette and Van Dyck 2007). Thus, understand-

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ing functional connectivity is of great importance in both landscape ecology and conservation planning.

Translocation experiments have been used extensively to improve our understanding of how behavioral processes influence movements of a wide range of species, including mammals (Bowman and Fahrig 2002, Bakker 2006, Smith et al. 2011, Lawes et al. 2013), temperate and tropical birds (Gobeil and Villard 2002, Ibarra-Macias et al. 2011, Vergara et al. 2013), reptiles (Stanley 1998, Gruber and Henle 2004), amphibians (Mazerolle and Desrochers 2005, Nowakowski et al. 2013), fish (Turgeon et al. 2010, Shima et al. 2012), and insects (Berggren et al. 2002, Soderstrom and Hedblom 2007). These experiments involve capturing individuals and releasing them across gradients in habitat loss and/or fragmentation. Parameters such as homing (return) time, probability of successful return (Gillies and St Clair 2008, Kennedy and Marra 2010, Smith et al. 2011, Lawes et al. 2013), or total distance traveled (Hadley and Betts 2009) are then used to assess how landscape structure influences movement behavior. In general, low probabilities of return and long homing times or travel routes are associated with landscapes of low functional connectivity. Experimental translocations have been assumed to standardize motivation across individuals so that researchers can effectively compare behavior across a range of landscape structures (Bélisle 2005). The alternative—simply monitoring the movement of individuals using a nonexperimental approach—raises the question as to whether certain landscape features are infrequently crossed because they are true barriers, or whether there is simply no motivation to move (e.g., individuals may have sufficient resources without needing to cross these features). Translocations are also more logistically efficient because they allow researchers to randomly or opportunistically place animals directly in landscape contexts of interest.

In previous studies, translocated individuals have consistently shown high return rates, indicating motivation to go back to their capture site (Bélisle et al. 2001, Gobeil and Villard 2002). Translocation experiments have revealed evidence for the importance of matrix type in facilitating movement (Castellón and Sieving 2006, Kennedy and Marra 2010, Lawes et al. 2013), reluctance to move through open areas (Desrochers et al. 2011), utility of stepping stones to increase connectivity (Boscolo et al. 2008), and selection of forest fragments while traveling (Hadley and Betts 2009, Gillies et al. 2011, Ibarra-Macias et al. 2011). The use of translocation experiments is likely to increase in the near future due to three developments (Betts et al. 2014): (1) advances in tracking technology, (2) growing realization of the usefulness of functional connectivity to predict population and genetic parameters, and (3) the increasing awareness of the importance of matrix structure in determining species' response to habitat fragmentation. The likely increase in the popularity of translocation

experiments underscores the importance of addressing potential biases of this technique.

Most translocation studies make two key assumptions: (1) all translocated individuals have a similar level of fidelity to the original capture location and therefore equal motivation to return, and (2) behavioral decisions made after release reflect decisions made during the natural movements of the species. The first assumption is met by selecting individuals that share characteristics likely to affect their willingness to return to the capture point (e.g., territorial mated males), and by randomly assigning landscape treatments in order to minimize bias due to individual variability in the perception of the habitat. The second assumption, on the other hand, is harder to account for because the capture and transport process has the potential to influence subsequent movement behavior by causing stress and perhaps decreasing body condition. Further, such experiments have the potential to overestimate functional connectivity if motivation to return is very high; for instance, individuals might cross gaps that might be barriers (or at least filters) during daily movements. Thus, conclusions about the effect of habitat fragmentation on animal movement based on translocations need to be considered carefully (Haddad 2008, Hadley and Betts 2012). These concerns are relevant to studies using translocation as a proxy for understanding functional connectivity during dispersal (Bélisle and Desrochers 2002), as well as those examining the daily movements (Wilson et al. 2007).

Despite these concerns about the external validity of translocation experiments, no study has yet compared movement behavior of animals during experimental translocations to behavior of “natural” unmanipulated individuals. If movement patterns are altered during translocations, the alteration could be in two possible directions: (1) the novel environmental context could result in greater wariness of the new surroundings (“neophobia”; Greenberg and Mettke-hofmann 2001); or (2) high motivation to return to capture locations would override cautious behavior that would usually result in avoidance of particular areas. Here, we compare the movement behavior of Green Hermit hummingbirds (*Phaethornis guy*) within their normal home range boundaries to that of experimentally translocated individuals. For simplicity, we refer to movements of non-translocated, radio-tracked birds as “routine movements” (Van Dyck and Baguette 2005). We refer to movements of birds displaced from their home territories and radio-tracked as they returned home as “translocation movements.”

We assessed differences in movement behavior between translocated and non-translocated individuals by analyzing patterns of site selection at two spatial scales: individual point locations and movement paths. We also compared movement rates between translocation and routine movements. We expected that if behavior during translocations is affected by neophobia, translocated birds should show (1) stronger preference for forested

areas, (2) greater avoidance of exposed open areas, and (3) slower movement rates. If the motivation to return overrides cautious behavior, we expected to see during translocations (1) a reduced affinity for forested areas, (2) increased likelihood of using open areas, and (3) faster movement rates. If translocations experiments did not affect behavior, we expected to detect no difference between translocation and routine movements.

MATERIALS AND METHODS

Study site

Our study was conducted in a 20 600-ha area surrounding the Las Cruces Biological Station, Costa Rica (8°47' N, 82°57' W). This region is characterized by an agricultural mosaic with scattered remnant fragments of Pacific premontane humid forest (<1 to >1000 ha) and forested riparian corridors (10–40 m wide). The non-forested matrix was previously forested, but now is mainly agricultural, most of which is pasture (>90%) and coffee plantations (~5%) (Hadley and Betts 2009).

Focal species

The Green Hermit hummingbird is a forest interior species that inhabits tropical forests from Costa Rica to western Colombia and southeastern Peru (Stiles and Skutch 1989). Green Hermits do not maintain defended territories, but instead are thought to exhibit “traplining” behavior and typically move over relatively long distances to feed from isolated nectar-rich flowers, particularly *Heliconia* sp. (Stiles 1975). This propensity for long-distance daily movements (maximum recorded = 673 m), together with its ability to persist in fragmented landscapes, makes the Green Hermit an excellent study species for the comparison of movement behavior between modified and intact landscapes. Green Hermit individuals are also faithful to particular breeding leks and have high motivation to return to them (Snow 1974).

We captured Green Hermits with mist nets set near food sources (mainly *Heliconia* sp.) and with traps containing a hummingbird feeder. The individuals were sexed based on their dimorphic plumage (Stiles and Skutch 1989). Each bird was fitted with radiotelemetry units (<0.25 g; Blackburn Transmitters, Nacogdoches, Texas, USA), using eyelash glue to attach these to plucked bare skin on their lower backs. Transmitters generally stay attached for about two weeks. Transmitter attachment did not appear to affect the behavior of tagged individuals (A. S. Hadley and M. G. Betts, unpublished data); we have observed radio-tagged birds conducting normal behavior during foraging and breeding (e.g., chasing competitors, lek display, nesting, and offspring feeding).

Data collection

Radio-tracking.—We radio-tracked Green Hermits January–March 2008 and March–May 2012. In both years, we obtained location points by following the birds

as closely as possible on foot using radio receivers and handheld Yagi antennae. Based on trials under optimal conditions with known transmitter distances, we assumed that tagged birds were within 50 m whenever signal strength was 0.4 (gain less than 1/2), 30 m when signal strength was 0.8, and less than 10 m away when we could detect the signal using the attenuator. At this range, we observed no noticeable difference between signal strength within differing vegetation structures, but points were typically taken when both observer and bird were within forest. Spatial coordinates of bird locations were recorded using a Global Positioning System [GPS] device.

In 2008, we captured 19 birds (8 male, 11 female) at leks in the Las Cruces Biological reserve and translocated them across two types of landscape: forested (continuous forest between capture and release points) and agricultural (presence of agricultural land between capture and release points) (Hadley and Betts 2009). Translocation experiments consisted of transporting and releasing individuals at distances ranging from 340 to 1500 m from their capture point and then tracking them on their return to capture locations. We recorded bird locations whenever a position could be determined to within 50 m. Observers followed the birds from the moment of release until they were relocated within 50 m of the capture location, obtaining 133 individual locations (7 ± 2.3 locations/individual, mean \pm SD). Routine movement data were recorded by following individual birds ($n = 13$) continuously for tracking periods that lasted up to 120 min per day (mean = 5 days/individual), gathering a total of 152 individual location points (11.7 ± 5.2 locations/individual).

In 2012, we captured an additional 20 individuals (9 male, 11 female) in forest fragments chosen to represent a gradient in patch size (1.47–800 ha) and forest amount (16–78% within a 1 km radius). This 1 km distance corresponds to the expected maximum movement distance by Green Hermits within their home range (N. L. Volpe, M. G. Betts, and A. S. Hadley, unpublished data). We followed individual birds continuously during tracking periods that lasted from 3 h/d to 8 h/d (mean = 4 days/individual), gathering a total of 1565 individual location points (78.25 ± 5.2 locations/individual \pm 38.4).

Land cover information.—We derived the landscape attributes for analyses from Geographic Information System (GIS) data available from Las Cruces Biological Station and classified Landsat TM remotely sensed data from 2005. We delineated land cover on this raster image using ArcGIS 10.1 (ESRI 2012) as forest or agricultural matrix. Forest cover in this region has remained relatively constant since 2005, with <0.3% change from 2005–2010 (FONAFIFO 2012).

Data analysis

Point-level habitat selection.—Habitat selection is defined as adaptive disproportionate use of a particular cover type in relation to alternatives *that are known to be*

available (Jones 2001). To assess habitat selection at the point scale, we compared observed locations to those we deemed available. We used a 30-m buffer around each recorded point to characterize “used” sites. The 30-m buffers correspond to the average location error of the records (Manly et al. 2002). Buffers also account for the fact that animals select mosaics of habitat rather than particular points in space (Rettie and McLoughlin 1999). “Available” sites were defined as the proportion of forest within a 500-m buffer around each recorded point. The 500 m radius buffers correspond to the area that the bird could potentially access, based on the observation that they can fly at least 500 m without stopping (N. L. Volpe, M. G. Betts, and A. S. Hadley, unpublished data).

We used ArcGIS 10.1 to generate the buffers and calculate forest percentages. To prevent giving excessive weights to location points with multiple records, we did not use records separated by <1 m. Our final data set contained 1799 routine movement points (1349 in 2012; 120 in 2008; $N = 33$ individuals) and 131 translocation points ($N = 19$ individuals).

To test whether point-scale habitat selection behavior differed during translocation experiments, we applied the linear mixed-effects model:

$$\text{Difference} \sim \text{Total Forest} \times \text{Translocation} \quad (1)$$

where “Difference” corresponds to the difference between observed and available percentage of forest. The use of this variable allowed us to pair observed and available locations and to also test for the effect of translocation experiments on habitat selection in the same model. We included an interaction term in order to assess whether bird response to the translocation treatment was mediated by amount of forest in the landscape. In 2012, our sample sites had lower forest amounts at the landscape scale than in 2008. We therefore calculated the percentage of forest (hereafter “total forest”) available inside a single 500-m buffer surrounding all of the recorded points for each bird and included this in our statistical models as a covariate to avoid bias. To account for spatial autocorrelation in the residuals, the model included a rational quadratic autocorrelation structure (Zuur et al. 2009). We included “individual” as a random effect to account for potential lack of independence within points selected by each bird.

Path-level habitat selection.—Selection of a particular cover type (e.g., forest) at the point scale does not necessarily require that alternative cover types (e.g., agriculture) impose barriers to movement; individuals could still be willing to cross through non-habitat to reach a habitat patch. Analysis of habitat selection at the point scale is therefore not informative about broader-scale behaviors. Path-level analysis addresses this issue (Gillies et al. 2011). Step selection functions (SSF; Fortin et al. 2005) allow the analysis of the fine-scale movement decisions of organisms by comparing the straight line

connecting two consecutive points visited (“step”) with other alternative steps that they *could have* taken starting at the same origin point. The model does not assume that the individuals move in straight lines, but that the environmental characteristics along those lines are correlated with the probability of moving to a particular end point (Fortin et al. 2005). In order to make the alternative steps realistic, we generated random draws from the frequency distribution of our observed step lengths and turning angles (Python code is available in the database deposited in Dryad). The random steps associated with any given bird were based on the average distributions of the *remaining* birds. The random steps (20 per observed step) were generated using the function “movement.sfsamples” from the program Geospatial Modeling Environment. Following Gillies et al. (2011), we resampled the data to obtain origin–destination pairs separated by a distance long enough to be able to provide information about the landscape around them (10 m) but close enough in time to not be completely unrelated (15 min). These constraints resulted in 74 “used” steps for translocations and 903 “used” steps for routine movement treatments. To ensure that the available steps were realistic, we only used those that ended in forest habitat, as observed steps ending in open land were rare (~1%).

We used a mixed-matched case–control logistic regression (also termed “mixed conditional logistic regression”; Duchesne et al. 2010) to model the likelihood of an individual hummingbird choosing a particular movement step instead of an alternative available one. We followed a strategy similar to that of Gillies et al. (2011) to identify the best model. First, we identified four “exposure variables,” i.e., variables that influence the level of exposure of the individuals to unfavorable conditions (increased predation rate, sub-optimal microclimates) along a movement step. Variables reducing exposure were: step forest amount (percentage of forested area inside a 30-m buffer around the step) and proportion of the linear dimension of a step that occurred in forest (length of the step that takes place inside the forest over total step length). Variables increasing exposure were: number of gaps (number of times the step line crosses open area) and total gap distance (sum of the lengths of all the gaps along a step). All of these variables were highly correlated, so we built competing candidate models to decide which of them should be kept in the final model. We also included a variable that we expected to facilitate movement—distance to the nearest stream—because our previous observations suggest that this species may use streams as movement corridors. Each set of candidate models included a univariate model using a single exposure variable and a full model including the exposure variable and distance to stream. We had no a priori reason to expect interactions among these two variables, so we did not include interaction terms in the models. We compared models using Akaike’s information criterion

corrected for small sample size (AIC_c). All of the models included a random component that allowed the selection coefficient for each variable to vary between individuals. The addition of individual-level random effects not only helps to correct the correlated nature of the data (Gillies et al. 2006), but also results in a more ecologically sound model by relaxing the assumption of homogeneous selection among animals (Duchesne et al. 2010). In addition, the random coefficients inform on how each individual responds to model covariates, and can be used to assess how individual-specific factors affect selection decisions (Gillies et al. 2006, 2011). In order to test for these potential correlates of selection decisions, we ran a linear regression of the individual selection coefficients as a function of broadscale landscape measures (overall forest availability) and individual-specific characteristics (sex). Finally, we tested the hypothesis that selection of habitat path characteristics differed between translocations and routine movements by including translocation treatment (translocated/non-translocated) as a predictor. We applied the mixed conditional logistic regressions in the mixlogit module (Hole 2007) in Stata (Statacorp 2011).

Movement rate.—Existing translocation studies often use “movement rate” as a metric of functional connectivity (e.g., Bélisle et al. 2001, Smith et al. 2011). We therefore tested whether the average movement rates during translocations differed from those of nonexperimental individuals by applying the linear mixed-effects model:

$$\text{Speed} \sim \text{Time Interval} + \text{Translocation} \times \text{Step Forest}. \quad (2)$$

“Time interval” corresponds to the time (seconds) passed between consecutive points. This variable was included because an exploratory analysis of the data showed a strong negative correlation between length of time interval and observed movement rate ($\beta = -0.82$, 95% CI = -0.86 to -0.78 ; $P < 0.001$). This implies that long time intervals between points are less accurate than short ones; during long intervals, individuals have more time to move to areas that we were not able to detect, leading to an underestimation of distance traveled and associated speed. Regardless, this does not constitute a bias in our study because the same effect occurred for both translocated and non-translocated birds. We also included an interaction term to test if forest amount at a 30-m scale around each movement path (hereafter “step forest”) affected the speed of translocated vs. non-translocated birds differently.

We log-transformed both speed and time intervals in order to meet assumptions of regression models that residuals be normally distributed. Due to the fact that the speed value at each point was influenced by the time interval used to calculate it, we could not average all of the values per bird, but rather had to include all of the individual points in the model. We restricted the data points to those that were separated by 20 min or less, in order to diminish the effect that long time intervals had

on overall speed. This restriction reduced the sample size for this analysis to 1244 points (29 birds) for routine movement in 2012, and 83 points (18 birds) for translocations. The final model included “Date” nested within “Individual” as a random effect.

Model selection and spatial autocorrelation.—In all analyses, we performed mixed-effects models to account for the lack of independence between points belonging to the same bird. To identify top-ranked models in linear regressions, we followed the top-down approach of Zuur et al. (2009), which has three stages: (1) identify the optimal error structure (using AIC_c); (2) identify the optimal fixed-effect structure for the given random-effect structure (using likelihood ratio tests); (3) check final model assumptions (heterogeneity, normality, and independence of residuals). We used restricted maximum likelihood estimation (REML) as the likelihood estimator of the final models, as it is considered to be a less biased estimator (Zuur et al. 2009). The mixed-effects models were run using the R package nlme (R version 3.0.2; R Development Core Team 2013). We generated correlograms (R package ncf; R version 3.0.2) of the models’ residuals to check for spatial autocorrelation. In cases where we detected spatial autocorrelation (Moran’s $I > 0.1$), we accounted for it using model error structures that reflected these dependencies. Before combining the routine movement data from 2008 and 2012, we tested for differences in movement patterns between years. The interannual difference (2008 vs. 2012) in the amount of forest cover in “used” locations was small and not statistically significant (mean -4.07% , 95% CI = -12.58 to 4.43 ; $P = 0.34$). However, there was some evidence for a difference in movement rate between years; speed in 2012 was 0.37 times slower than in 2008 (95% CI = 0.01 to 0.6 ; $P = 0.045$). The very minor differences in habitat selection behavior enabled us to justify lumping years in point-level habitat selection analysis. Slower movement rates in 2008 suggest that detection of differences in movement speed between translocation and routine movement could be due either to true differences in movement behavior or to differences attributable to year of sampling.

RESULTS

Point-level habitat selection

Green Hermits used areas with higher percentages of mature tropical forest than was available. This habitat selection behavior was consistent between translocation and routine movement studies (Fig. 1) after controlling for forest amount at the landscape scale (translocated $\bar{x} = 29.08\%$ more forest than available, routine $\bar{x} = 29.09\%$; $t = 0.09$, $P = 0.93$). Confidence intervals around the difference (0.01%) in the percentage of forest selected were small ($\pm 4.4\%$) in relation to the mean values (29.08%), corresponding to a difference of $< 15\%$, which is likely to exclude a biologically meaningful effect. We found no evidence of an interaction between transloca-

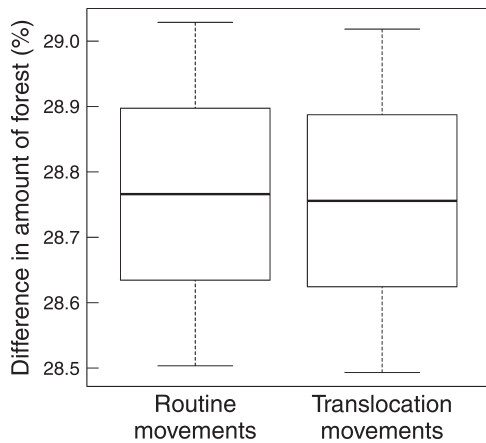


FIG. 1. Predicted difference in the amount of forest inside “used” vs. “available” (random) buffers for Green Hermit hummingbirds (*Phaethornis guy*), including non-translocated birds conducting routine movements vs. movement of birds that had been translocated. Results presented are after accounting for the total amount of forest at the landscape scale. Boxes represent first and third quartiles of the data and horizontal lines are medians. Error bars represent the data range. We used a 30-m buffer (the average location error) around each recorded point to characterize “used” sites. “Available” sites were defined as the amount of forest within a 500-m buffer (the area that the bird could potentially access) around each recorded point.

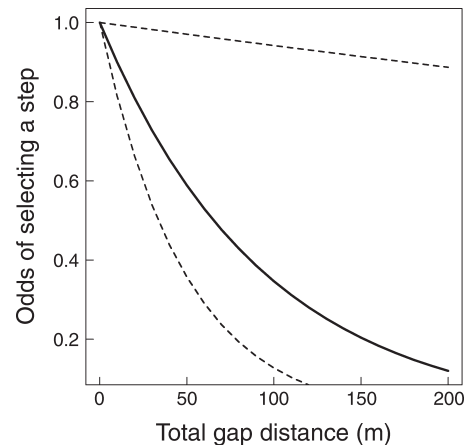


FIG. 2. Effect of total gap distance on the odds of the Green Hermit hummingbird choosing a given step, as calculated from the top step selection function model provided in Table 1. The dashed lines represent the 95% confidence interval for the estimation.

tion treatment and landscape context ($\beta = 0.003$, 95% CI = -0.011 to 0.0175 ; $P = 0.64$).

Path-level habitat selection

Both translocated and non-translocated Green Hermits selected movement steps that reduced exposure. All candidate models showed that variables decreasing exposure (i.e., forest amount, proportion of step in forest) had clear positive effects on the likelihood of

choosing a given path, whereas those variables that increased exposure (i.e., number of gaps and total gap length) had negative effects (Table 1). The top model included total gap length along the path and distance to nearest stream. Green Hermits selected steps that took them closer to a stream and avoided those that involved crossing long stretches of open matrix (Fig. 2). All candidate models showed variability at the individual bird level in the selection coefficients for all of the covariates, justifying the use of random terms. The standard deviations for the random coefficients of the top model were -0.013 for distance to stream ($Z = -4.79$, $P < 0.001$) and -0.02 for total gap length ($Z = -5.41$, $P < 0.001$).

TABLE 1. Model coefficients, standard errors, odds ratios (OR), and AIC_c values for candidate models used to predict observed Green Hermit hummingbird movement steps in study area at the Las Cruces Biological Station, Costa Rica.

Model	Variable	Coefficient	SE	OR	AIC_c	ΔAIC_c
Stream + TotGap	Stream	-0.017***	0.003	0.98	5657	0
	TotGap	-0.011*	0.005	0.99		
Stream + ForAm	Stream	-0.015***	0.003	0.99	5706	50
	ForAm	1.95*	0.775	7.03		
Stream + PropInFor	Stream	-0.016***	0.003	0.98	5710	54
	PropInFor	1.45*	0.709	4.26		
Stream + NumGap	Stream	-0.017***	0.003	0.98	5749	92
	NumGap	-0.33	0.220	0.72		
Stream	Stream	-0.017***	0.003	0.98	5784	127
TotGap	TotGap	-0.015**	0.005	0.98	5785	128
ForAm	ForAm	2.76***	0.788	15.80	5806	149
PropInFor	PropInFor	2.14**	0.755	8.50	5824	167
NumGap	NumGap	-0.55*	0.248	0.58	5870	214

Notes: Green Hermit movement steps were predicted in relation to random unused steps as a function of the following variables: distance to stream (Stream), total gap length along a step (TotGap), percentage of forest inside a buffer surrounding the step (ForAm), proportion of the step in forest habitat (PropInFor), and number of gaps along the step (NumGap). The top-ranked AIC_c model is indicated in boldface.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

TABLE 2. Effect of sex, overall forest availability, and translocation treatment on the selection coefficients for total gap length and distance to stream estimated from our top step selection function model.

SSF variable	Variable	Coefficient	SE	P
Total gap length	Intercept	-0.018	0.0060	0.005
	Overall forest	0.00009	0.0001	0.54
	Translocation	0.003	0.0062	0.68
	Sex (male)	0.027	0.0113	0.022
	Overall forest \times Sex (male)	-0.0004	0.0002	0.046
Stream distance	Intercept	-0.016	0.002	<0.0001
	Translocation	-0.0006	0.003	0.856

None of the bird-specific variables (i.e., sex, total forest available, and translocation treatment) were useful for explaining the observed variability in the strength of selection for distance to stream. On the other hand, males avoided steps that involved large total gap distances more strongly than did females. We found support for a weak interaction between forest amount and sex; males' avoidance of large gaps was amplified as the overall forest amount increased (Table 2). We did not detect a difference between translocated and nonexperimental birds in their selection coefficients for either of our top-ranked variables (Table 2). The multiplicative effect of the translocation treatment on the selection coefficient for total gap length was 1.00 (95% CI = 0.99 to 1.01) and for distance to stream was 0.999 (95% CI = 0.993 to 1.006). The narrow confidence intervals around effect sizes for both variables reduce the possibility that lack of statistical significance was due to low statistical power.

Movement rate

We detected significantly faster rates of movement for Green Hermits when homing during a translocation experiment than during routine movements (Fig. 3); the median speed for translocation studies at a given time interval is 4.48 times faster than for routine movements (95% CI = 3.39–6.04; $P < 0.001$). In both cases, the movement rate was negatively related to the amount of forest around a movement step. An increase in 1% of forest amount was associated with a decrease in the median speed by a factor of 0.987 (95% CI = 0.984–0.99; $P < 0.001$). We detected no evidence of interaction between translocation treatment and forest amount (likelihood ratio test, $L = 3.5$, $df = 8$, $P = 0.06$).

DISCUSSION

Translocations vs. routine movements

Our results provide the first evidence that movement behavior of birds used in translocation experiments is similar to movement behavior under natural conditions. Translocated and non-translocated birds consistently selected similar landscape elements when moving, indicating that both routine and translocation movement studies lead to similar conclusions regarding the effect of landscape structure on functional connectivity. In particular, we found evidence that (1) point-level

habitat selection is consistent between translocation and routine treatments, (2) path-level analyses showed avoidance of similar features between treatments (e.g., forest gaps), (3) translocations did not appear to result in neophobia, and (4) decreasing movement rates as a function of mature forest occurred to a similar degree between treatments.

Despite the congruencies that we observed in hummingbird behavior during routine movements and translocations, it is important to note that these similarities may not necessarily hold in other contexts. Importantly, our primary objective in translocation studies was to approximate functional connectivity for adult Green Hermits during their daily movements as pollinators (Hadley and Betts 2009). This is unlike previous efforts that have used translocation behavior as a proxy for functional connectivity during breeding or juvenile dispersal (e.g., Gobeil and Villard 2002). Dispersal behavior could differ fundamentally from the daily foraging movements in the vagility of individuals in the level of motivation to move, as well as the degree of risk-taking behavior. For instance, dispersing individuals might be less motivated than

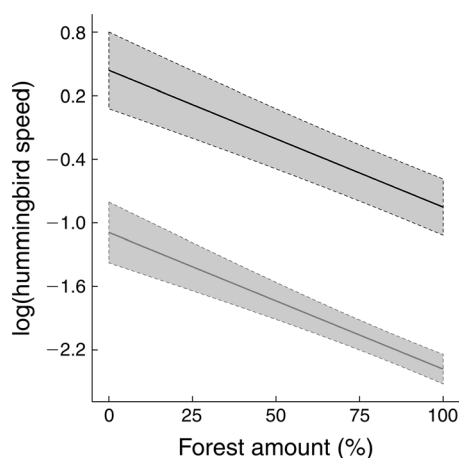


FIG. 3. Predicted effect of forest amount on log-transformed Green Hermit speed (originally measured in m/s) after accounting for time between consecutive points. Regression lines are shown for routine (gray lines, $\beta_0 = -1.1$, 95% CI = -1.38 to -0.8) and translocation movement data (black lines, $\beta_2 = 0.41$, 95% CI = 0.045 to 0.78). Fitted values were calculated using the mean time interval (4.89 min).

translocated individuals to cross inhospitable areas, as the latter have the incentive to return to an area where they have already invested in reproduction (Gillies and St Clair 2010). However, it is interesting to note that >50% of individuals in our study were translocated over distances greater than the size of Green Hermit home ranges. Therefore, it is quite likely that these individuals were experiencing novel conditions, a situation that approximates the new conditions encountered during natal dispersal. Further, our results show that translocated birds do not use open areas with greater frequency than do routinely moving birds; if translocations increase motivation to cross open areas in a substantial way, then we should have seen differences in the observed gap avoidance pattern.

A second major potential criticism of translocation studies is that the treatment itself (i.e., transportation and release of animals in an unknown area) induces a stress that reduces movement capacity. However, we found little support for results of the translocation treatment being affected by stress-induced behaviors. If neophobia or stress affects the results of translocation experiments, we would have expected to see: (1) an increased use of forested areas relative to routine treatments reflecting a need to rest (i.e., perch) often, (2) reduced movement rates, reflecting a wariness about the new environment or stress from handling. However, we found support for neither of these behaviors. On the contrary, we observed increased movement rates in translocated birds that could indicate a reduced wariness of the surroundings due to a strong motivation to return home. Thus, although we observed no differential use of forest at point or path levels for translocated vs. non-translocated birds, higher speeds during homing indicate that for this metric at least, translocations represent a liberal measure of movement capacity.

It is important to note that a large portion of the routine movement data collection took place in different years, which had the potential to introduce treatment \times year confounding interactions (20 out of 33 routine treatments were conducted in 2012). However, this potential confounding would be more likely to have enhanced rather than detracted from our ability to detect differences in hummingbird movement behavior between treatments; we found no statistical differences between treatments, despite the potential for inter-year variability in movement decisions and habitat selection. As noted previously, movement rates differed between routine and translocated birds, but there is little evidence that this was a function of confounding between treatment and time; the observed difference in movement rates of routine movement studies carried out during different years was small (95% CI is 0.01 to 0.6 times slower in 2012) in comparison to the large difference between routine and translocation movement rates (95% CI is 3.39 to 6.04 faster in translocations).

Hummingbird habitat selection behavior

Our habitat selection analyses revealed that Green Hermits, during both translocation and routine movements, chose to move through regions that reduced their exposure to agricultural matrix. At the point level, the birds selected areas surrounded by proportionally large amounts of forest; at the path level, they avoided movement steps that required crossing open areas. In addition, hummingbirds exhibited strong selection for steps with large amounts of forest. These results are all consistent with our observations that translocated Green Hermits take detours on their way home to stay in forested areas and circumvent the agricultural matrix, even when this leads to a longer return path (Hadley and Betts 2009). This effect sheds light on an important mechanism for pollen limitation in isolated tropical forest fragments (Hadley et al. 2014, *in press*); gaps appear to act as a movement filter, which scales up to influence the long-distance pollen transfer in fragmented landscapes and therefore plant fecundity.

We found that translocated Green Hermits selected paths along streams, a tendency that was also reflected in their routine movements. Interestingly, this tendency is apparent in birds occurring in both fragmented and continuous landscapes. Streams may facilitate movement by offering open paths through otherwise dense forest. Alternatively, there may be a higher abundance of flower resources in damp areas next to streams (M. G. Betts and A. S. Hadley, *unpublished data*). Often the last remaining areas of forest cover in agricultural landscapes tend to be forested buffers next to streams. Therefore, these riparian buffer strips may be particularly important for the maintenance of connectivity in fragmented areas. This finding is consistent with a growing body of evidence showing the importance of forest corridors for maintaining landscape connectivity (Tewksbury et al. 2002, Gilbert-Norton et al. 2010). Previous translocation studies report similar conclusions, both indirectly by finding a negative relationship between homing time and presence of riparian corridors (Ibarra-Macias et al. 2011), or directly by analyzing the homing patterns of radio-tracked individuals (Gillies and St Clair 2008).

We found a negative relationship between movement rate and forest amount for both translocated and non-translocated birds. This could indicate that areas with little forest are used primarily as thoroughfares to move between more heavily forested sites; slower movements in areas with high forest cover suggest that additional time is spent on other activities, such as feeding or perching. Slower movements through areas of high resource quality and lower risk have been reported for species ranging from cougars (Dickson et al. 2005) to crickets (Berggren et al. 2002).

Translocation experiments showed that habitat fragmentation mainly affected Green Hermit behavior by altering movement routes, while classical translocation metrics such as homing time and success remained

unaffected. Hermits are extremely vagile (Moore et al. 2008) and able to persist in highly fragmented landscapes. Given these characteristics, it would be useful to examine these same questions for species expected to experience higher landscape resistance, because potential differences in movement rates and homing success could be more pronounced.

In conclusion, our results showing that translocation experiments reflect “natural” behavior provide preliminary support for the use of translocation experiments as a reliable tool for testing the effect of different landscape types on the movement patterns of organisms. Translocation experiments allow for experimentation in landscape ecology, an approach that has typically been rare in this field. Researchers are able to confront individuals with a full range of landscape structures, thereby facilitating the testing of hypotheses that relate to functional connectivity. In addition, they require a reduced sampling period, making them logistically convenient. Comparative studies similar to ours should be undertaken on different taxa and species expected to be more sensitive to landscape fragmentation, as well as in instances in which dispersal behavior is a central research question.

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LITERATURE CITED

- Arnold, G. W., D. E. Steven, J. R. Weeldenburg, and E. A. Smith. 1993. Influences of remnant size, spacing pattern and connectivity on population boundaries and demography in euros *Macropus robustus* living in a fragmented landscape. *Biological Conservation* 64:219–230.
- Baguette, M., and H. Van Dyke. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology* 22:1117–1129.
- Bakker, V. J. 2006. Microhabitat features influence the movements of red squirrels (*Tamiasciurus hudsonicus*) on unfamiliar ground. *Journal of Mammalogy* 87:124–130.
- Bélisle, M. 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. *Ecology* 86:1988–1995.
- Bélisle, M., and A. Desrochers. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology* 17:219–231.
- Bélisle, M., A. Desrochers, and M. J. Fortin. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82:1893–1904.
- Bennett, A. 1993. Microhabitat use by the long-nosed potoroo, *Potorous tridactylus*, and other small mammals in remnant forest vegetation of south-western Victoria. *Wildlife Research* 20:267–285.
- Berggren, Å., B. Birath, and O. Kindvall. 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metroptera roeseli*). *Conservation Biology* 16:1562–1569.
- Betts, M. G., L. Fahrig, A. S. Hadley, K. E. Halstead, W. D. Robinson, J. Bowman, J. A. Wiens, and D. B. Lindenmayer. 2014. A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography* 37:517–527.
- Boscolo, D., C. Candia-Gallardo, M. Awade, and J. P. Metzger. 2008. Importance of Interhabitat gaps and stepping-stones for Lesser Woodcreepers (*Xiphorhynchus fuscus*) in the Atlantic Forest, Brazil. *Biotropica* 40:273–276.
- Bowman, J., and L. Fahrig. 2002. Gap crossing by chipmunks: an experimental test of landscape connectivity. *Canadian Journal of Zoology* 80:1556–1561.
- Castellón, T. D., and K. E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology* 20:135–145.
- Cranmer, L., D. McCollin, and J. Ollerton. 2012. Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos* 121:562–568.
- Desrochers, A., M. Bélisle, J. Morand-Ferron, and J. Bourque. 2011. Integrating GIS and homing experiments to study avian movement costs. *Landscape Ecology* 26:47–58.
- Dickson, B. G., J. S. Jenness, and P. Beier. 2005. Influence of vegetation, topography, and roads on cougar movement in southern California. *Journal of Wildlife Management* 69:264–276.
- Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* 79:548–555.
- ESRI. 2012. ArcGIS Desktop: Release 10.1. Environmental Systems Research Institute, Redlands, California, USA.
- FONAFIFO (Fondo Nacional de Financiamiento Forestal). 2012. Estudio de cobertura forestal de Costa Rica 2009–2010. Ministerio de Ambiente, Energía y Telecomunicaciones, San José, Costa Rica.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Gilbert-Norton, L., R. Wilson, J. R. Stevens, and K. H. Beard. 2010. A meta-analytic review of corridor effectiveness. *Conservation Biology* 24:660–668.
- Gillies, C. S., H. L. Beyer, and C. C. St. Clair. 2011. Fine-scale movement decisions of tropical forest birds in a fragmented landscape. *Ecological Applications* 21:944–954.
- Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* 75:887–898.
- Gillies, C. S., and C. C. St. Clair. 2008. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences USA* 105:19774–19779.
- Gillies, C. S., and C. C. St. Clair. 2010. Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology* 47:182–190.
- Gobeil, J.-F., and M.-A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98:447.
- Greenberg, R., and C. Mettke-hofmann. 2001. Ecological aspects of neophobia and neophilia in birds. Pages 119–178 in V. Nolan, Jr., and C. F. Thompson, editors. *Current Ornithology*. Volume 16. Springer-Verlag, New York, New York, USA.
- Gruber, B., and K. Henle. 2004. Linking habitat structure and orientation in an arboreal species *Gehyra variegata* (Gekkonidae). *Oikos* 107:406–414.
- Haddad, N. M. 2008. Finding the corridor more traveled. *Proceedings of the National Academy of Sciences USA* 105:19569–19570.

- Hadley, A. S., and M. G. Betts. 2009. Tropical deforestation alters hummingbird movement patterns. *Biology Letters* 5:207–210.
- Hadley, A. S., and M. G. Betts. 2012. The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews* 87:526–544.
- Hadley, A. S., S. J. K. Frey, W. D. Robinson, W. J. Kress, and M. G. Betts. 2014. Tropical forest fragmentation limits pollination of a keystone understory herb. *Ecology* 95:2202–2212.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.
- Hole, A. R. 2007. Fitting mixed logit models by using maximum simulated likelihood. *Stata Journal* 7:388–401.
- Ibarra-Macias, A., W. D. Robinson, and M. S. Gaines. 2011. Forest corridors facilitate movement of tropical forest birds after experimental translocations in a fragmented Neotropical landscape in Mexico. *Journal of Tropical Ecology* 27:547–556.
- Jones, J. 2001. Habitat selection studies in avian ecology: A critical review. *Auk* 118:557–562.
- Kennedy, C. M., and P. P. Marra. 2010. Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations. *Biological Conservation* 143:2136–2145.
- Lawes, T. J., R. G. Anthony, W. D. Robinson, J. T. Forbes, and G. A. Lorton. 2013. Movements and settlement site selection of pygmy rabbits after experimental translocation. *Journal of Wildlife Management* 77:1170–1181.
- Manly, B. F. J., L. McDonald, and D. L. Thomas. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic, Dordrecht, The Netherlands.
- Mazerolle, M. J., and A. Desrochers. 2005. Landscape resistance to frog movements. *Canadian Journal of Zoology* 83:455–464.
- Moore, R. P., W. D. Robinson, I. J. Lovette, and T. R. Robinson. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* 11:960–968.
- Nowakowski, A. J., B. O. Jimenez, M. Allen, M. Diaz-Escobar, and M. A. Donnelly. 2013. Landscape resistance to movement of the poison frog, *Oophaga pumilio*, in the lowlands of northeastern Costa Rica. *Animal Conservation* 16:188–197.
- R Development Core Team. 2013. R version 3.0.2. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rettie, W. J., and P. D. McLoughlin. 1999. Overcoming radiotelemetry bias in habitat-selection studies. *Canadian Journal of Zoology* 77:1175–1184.
- Ricketts, T. 2001. The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158:87–99.
- Shima, J. S., D. McNaughtan, S. W. Geange, and S. Wilkinson. 2012. Ontogenetic variation in site fidelity and homing behaviour of a temperate reef fish. *Journal of Experimental Marine Biology and Ecology* 416–417:162–167.
- Smith, M. J., M. G. Betts, G. J. Forbes, D. G. Kehler, M. C. Bourgeois, and S. P. Flemming. 2011. Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landscape Ecology* 26:709–721.
- Snow, B. 1974. Lek behavior and breeding of Guys Hermit Hummingbird *Phaethornis guy*. *Ibis* 116:278–297.
- Soderstrom, B., and M. Hedblom. 2007. Comparing movement of four butterfly species in experimental grassland strips. *Journal of Insect Conservation* 11:333–342.
- Stanley, M. C. 1998. Homing in the skink, *Oligosoma grande*, within a fragmented habitat. *Journal of Herpetology* 32:461–464.
- Statacorp. 2011. Stata Statistical Software: Release 12. Stata-Corp, College Station, Texas, USA.
- Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican Heliconia species. *Ecology* 56:285–301.
- Stiles, F. G., and A. Skutch. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, New York, USA.
- Taylor, P., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571–573.
- Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, J. Brinkerhoff, E. I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences USA* 99:12923–12926.
- Turgeon, K., A. Robillard, J. Grégoire, V. Duclos, and D. L. Kramer. 2010. Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. *Ecology* 91:3332–3342.
- Van Dyck, H., and M. Bagueette. 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology* 6:535–545.
- Vergara, P. M., C. G. Pérez-Hernández, I. J. Hahn, and J. E. Jiménez. 2013. Matrix composition and corridor function for austral thrushes in a fragmented temperate forest. *Landscape Ecology* 28:121–133.
- Wilson, R. F., H. Marsh, and J. Winter. 2007. Importance of canopy connectivity for home range and movements of the rainforest arboreal ringtail possum (*Hemibelideus lemuroides*). *Wildlife Research* 34:177–184.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.27900>