AN ABSTRACT OF THE THESIS OF

Noelia L. Volpe for the degree of Master of Science in Wildlife Science presented on March 19, 2014.

Title: Movement and Space Use by the Green Hermit (*Phaethornis guy*) in a Fragmented Landscape in Costa Rica

Abstract approved:

W. Douglas Robinson Matthew G. Betts

Human activities have altered Earth's ecosystems. Most biomes have experienced a 20-50% conversion to human use. Loss of habitat has obvious effects on the persistence of species. Fragmentation, however, may also negatively affect biodiversity for those species that exhibit behavioral responses to changes in habitat configuration. Such behavioral changes include movement, which is influenced by subdividing and isolating habitats through which animals prefer to travel. Ecosystem services that depend on the ability of animals to move through the landscape could be affected by changes in habitat configuration. Pollination is one such process because access of pollinators to flowers is often the key determinant of plant reproductive success. Yet, relatively little is known about how forest fragmentation may influence the flow of pollen carried by forest-dwelling pollinators, such as hummingbirds.

I evaluate how changes in the distribution of pollinators produced by habitat fragmentation in southern Costa Rica affects a pollination web occupied by a generalist

tropical pollinator, the green hermit hummingbird (*Phaethornis guy*). I used radio-telemetry to measure patterns of space use by green hermits living in forested areas with different levels of fragmentation. I first characterize patterns of space use by green hermits at three scales: point, path and home range. I found that green hermits have marked preference for locations in forested areas with high density of *Heliconia* plants and canopy cover; prefer paths close to streams that minimize crossing large stretches of non-forested matrix; and establish their home ranges in areas with high forest amount. In addition, home range area was negatively related to the amount of forest within it and positively related to fragmentation per se. Average resource density within the home range appeared to be unrelated to the area covered by the green hermits. My observations indicate that while the presence of green hermits in an area is mainly determined by the amount of forest available, the way they *move* through a landscape will be strongly affected by habitat configuration. In this context, pollen transfer by green hermits will be limited by the presence of open, non-forested areas owing to matrix avoidance. In landscapes with small discontinuous patches, the total area covered by an individual green hermit is likely to be small so I hypothesize that the genetic variability of pollen it transports may be diminished.

I also assess the effectiveness of a tool commonly used to study the effect of habitat fragmentation on animal movement: translocation experiments. Such experiments are purported to have important advantages of being time efficient and standardizing across individuals the ‘motivation’ to move. Yet, we lack tests of whether movement behavior of translocated birds reflects natural behavior of unmanipulated birds. I

compared the routine movement behavior of green hermits to that of experimentally translocated individuals. Behaviors documented during translocation experiments reflected those observed during routine movements. Both translocated and non-translocated birds showed similar levels of preference for mature tropical forest at the point level and avoided moving across non-forested matrix while selecting streams as movement corridors at the path level. Movement rates (distance covered per unit time) 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. My results show that movement behavior of birds during translocation experiments is similar to natural movement behavior of birds. Therefore, translocation experiments may be reliable tools to address effects of landscape structure on animal movement.

Movement and Space Use by the Green Hermit (*Phaethornis guy*) in a Fragmented Landscape in Costa Rica

by
Noelia L. Volpe

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APPROVED:

Co-major Professor, representing Wildlife Science

Co-major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Noelia L. Volpe, Author

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CONTRIBUTION OF AUTHORS

Dr. W. Douglas Robinson and Dr. Matthew G. Betts contributed to study design, interpretation of data, and writing of chapters 2-3. Dr. Adam Hadley provided data on translocation experiments and contributed in writing of chapter 2.

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DEDICATION

To my parents. Thanks for making me learn English.

CHAPTER 1: INTRODUCTION

Human activities, particularly during the last two centuries, have had a great impact on Earth’s ecosystems, with most of world’s biomes having experienced a 20-50% conversion to human use (Collinge 2009). The consequent modification of the landscape has greatly affected organisms living within and around the modified areas. Landscape structure is defined by two elements (Turner 1989): landscape composition (type and amount of habitat) and landscape configuration (spatial pattern of landscape elements). Changes in landscape composition, primarily through habitat loss, are well known to negatively affect biodiversity (Fahrig 2013). On the other hand, the effects of landscape configuration on species diversity and demography seem to be weak, with either positive or negative consequences (Fahrig 2003; Betts *et al.* 2006).

Local extinction is not the only way in which organisms living in a fragmented landscape can be affected, as the disappearance from an area is the last step of a long process of change that involves behavioral alterations in breeding behavior, dispersal and space use (Lindenmayer & Fischer 2006). These behavioral changes, though sometimes less conspicuous, can have important effects on the overall ecosystem, in particular when they lead to changes in species interactions (Taylor & Merriam 1995; Lindenmayer & Fischer 2006). Pollination is one such interspecific relationship that could be affected by habitat fragmentation. Over 90% of plant species depend on pollinators to carry their pollen and maintain gene flow throughout the population (Ashman *et al.* 2004; Ghazoul 2005; Kremen *et al.* 2007). As such, there will be an interconnection between distribution patterns of plants with those of their pollinators (Thompson 2005). Fragmentation of the landscape is known to affect the movement of fauna (Ricketts 2001; Graham 2001; Diekoetter *et al.* 2007; Hadley & Betts 2009; Gillies & St Clair 2010; Lloyd & Marsden 2011) by subdividing and isolating the habitats through which animals prefer to travel. If the movement of pollinators is constrained by habitat configuration the routes through which pollen moves are likely to become restricted as well (Kremen *et al.* 2007), potentially leading to inbreeding depression due to reduced gene flow (Husband & Schemske 1996; Brown & Mitchell 2001; Bell *et al.* 2005; Taki *et al.* 2010). Having a clear knowledge of how habitat configuration affects pollinators' movement patterns is thus vital for generating and testing hypotheses about the effect of fragmentation on pollen flow.

This thesis is a first step towards understanding how the changes in the distribution of pollinators produced by habitat fragmentation can affect pollination webs, by providing information on how fragmentation affects space use by a generalist tropical pollinator, the green hermit hummingbird (*Phaethornis guy*). Hummingbirds of this genus have been seen to persist in disturbed landscapes in which forest cover has been reduced to scattered patches interspersed in an agricultural matrix (Stouffer & Bierregaard 1995). Even when this persistence can be interpreted as an indicator that forest fragmentation has no effect on the species, there is evidence that this species' movement patterns are being influenced by the presence of non-forested gaps in the areas they are travelling through (Hadley & Betts 2009). The green hermit is a particularly important pollinator in tropical areas, as it is involved in the transport of at least 13 different types of pollen (Borgella *et al.* 2001). Thus, changes in its movement patterns are likely to have a broad effect on the local plant community. Despite the importance of green hermits as pollinators, basic information on space use, such as home range size and habitat preferences, does not yet exist. I will contribute to basic knowledge on this species by making the first characterization of its home range size as well as its overall space use preferences.

In this research, I used radio-telemetry to assess the patterns of space use by green hermit hummingbirds living in forested areas with different levels of fragmentation. I used the information on the locations where the birds were detected to answer questions regarding the effects of forest amount and configuration on their movement behaviors.

In my first chapter, I characterize the patterns of space use by the green hermit hummingbird at three scales, which should relate to the pollination web in three different ways. At the point level, I study the characteristics that determine the presence of the hummingbird at a certain location, which will influence the likelihood of pollinator-plant interactions (Johnson & Bond 1992; Herrera 1995; Everaars *et al.* 2011). At the path level, I study the factors that affect the selection of particular routes to move between two points. This allows the identification of the determinants of pollinator movements between feeding locations, enabling the development predictions about the routes of pollen flow (Tewksbury *et al.* 2002; Townsend & Levey 2005; Van Rossum & Triest 2010). At the home range level, I analyze which landscape elements were influencing the overall area covered by the hummingbirds. This is likely to be affecting how far away the pollen of a particular plant can travel, which provides knowledge about typical pollen transport distances and therefore the likelihood of genetic exchange between distant populations (Law & Lean 1999; Wikelski *et al.* 2010).

In my second chapter I assess the effectiveness of a tool commonly used to study the effect of habitat fragmentation on animal movement: translocation experiments. This technique consists of displacing an animal away from its home areas and monitoring its return to the capture point to evaluate how landscape structures affect movement behavior. Translocations rely on the assumption that the behavioral patterns observed are representative of the natural behavior of un-manipulated birds. To evaluate the validity of this assumption, I compare the translocation data obtained by Hadley & Betts (2009) with the data on routine movements I gathered during my radio-telemetry study to see if both types of datasets provide the same answer to the question: how is space use of the green hermit affected by habitat fragmentation? I conducted the comparison at both the point and path scales. At the point scale, I assess if both types of studies indicate the same type of relationship between forest amount and presence of the bird at particular locations. At the path scale, I analyze if habitat selection while moving through the landscape is the same for both studies. In addition, I evaluate the effect of forest amount on movement rate.

In chapter four I discuss the findings of the previous chapters as well as future areas of research.

CHAPTER 2: EFFECTS OF FOREST FRAGMENTATION AND HABITAT LOSS ON SPACE USE OF A TROPICAL POLLINATOR

Abstract

Modifications of landscape structure (composition and configuration) affect both persistence and movement patterns of animals. Pollination is an ecosystem service likely to be affected by these changes, as pollen flow depends on the ability of pollinators to move between flowers. To assess what the potential consequences of landscape modification on pollen flow are, I studied the space use of the green hermit hummingbird (*Phaethornis guy*) living in forest remnants in Costa Rica. I conducted a radio-telemetry study and analyzed habitat selection patterns at three spatial scales (point, path and home range). At the point scale, there was a marked preference for forested areas with high density of *Heliconia* plants and canopy cover. At the path scale, step selection functions showed green hermits avoid paths that cross large stretches of non-forested matrix: gaps as small as 50 m diminishes the odds of movement by 50%. In addition, green hermits preferred to move near streams, which highlights the importance of the presence of riparian corridors in the landscape. At the home range scale, forest amount inside the home range, but not connectivity, was larger than what was available within other areas of the same size. Home range area was negatively related to the amount of forest within it but positively related to fragmentation per se. Resource availability within the home range had no effect on home range size. My observations indicate that while the presence of green hermits in an area is mainly determined by amount of forest available, the way

hermits *move* through a landscape will be strongly affected by habitat configuration. In this context, I hypothesize that pollen transfer by green hermits will be limited by their behavioral avoidance of open areas between forest patches. In particular in landscapes with small discontinuous patches, the total area covered by an individual green hermit is likely to be small, and the genetic variability of pollen it transports may be diminished.

Introduction

Humans convert and fragment natural habitats to extract natural resources and produce goods for socio-economic systems. These modifications of habitat lead to transformed landscape structure which, in turn may have further influences even on the untransformed fragments which remain (Collinge 1996). Landscape structure is defined by two elements (Turner 1989): landscape composition (i.e. the type and amount of habitat) and landscape configuration (i.e. the spatial pattern of landscape elements). Changes in landscape composition, primarily through habitat loss, are well known to negatively affect biodiversity (Fahrig 2013). Changes in landscape configuration, on the other hand, often have weak effects (either positive or negative) on species diversity and demography (Fahrig 2003, Betts *et al.* 2006; but see Hadley *et al.* In Press).

Although a species may persist in a fragmented landscape regardless of its configuration, individuals of that species may still show behavioral responses to the size, shape and arrangement of the habitat remnants (Smith & Hellmann 2002). Thus, it is at the level of individual organisms where we are more likely to see immediate effects of landscape configuration. The decisions of individuals as they move through landscapes in search of resources and to avoid predators scale up to influence the landscape-level distribution of species (Lima & Zollner 1996) These fine-scale movement decisions accumulate to generate emergent properties at broader scales including the roles that individuals and species play in ecosystems as seed dispersers or pollinators (Heinrich & Raven 1972; Farwig *et al.* 2009; Gillies *et al.* 2011).

Pollination is one of the ecosystem services hypothesized to be influenced by landscape configuration (Hadley & Betts 2012). Most (>90%) plant species depend on animal pollination (Ghazoul 2005; Kremen *et al.* 2007); this strategy allows more directed flow of pollen among conspecifics than do other pollen vectors (e.g., wind, water) (Ashman *et al.* 2004). Thus, access of pollinators to flowers is often the key determinant of plant reproductive success (Kremen *et al.* 2007). Fragmentation of the landscape is known to affect animal movement (Ricketts 2001; Graham 2001; Diekoetter *et al.* 2007; Hadley & Betts 2009; Gillies & St Clair 2010; Lloyd & Marsden 2011). Dividing once-continuous habitats into patches potentially restricts how far individuals can travel, as the non-habitat surrounding the native patches is often avoided (i.e. the matrix, Ricketts, 2001). The influence of the matrix is therefore likely to have a strong effect on pollen flow, as the routes through which pollen moves will become restricted (see Kremen *et al.* 2007 for examples). Plants living in isolated patches completely surrounded by inhospitable matrix could be in a particularly detrimental position, as pollinator visits can potentially be reduced to a minimum, leading to reduced available pollen quality (Hadley & Betts 2012). The structure of plant-pollinator networks, in which specialized plant species are visited by generalist pollinators and *vice versa*, is thought to buffer pollination against changes in landscape configuration (Memmott *et al.* 2004; Bascompte *et al.* 2006). In particular, when plants have multiple pollinators the disappearance of a specific pollinator can be compensated by the existence of other species that can fulfill that role (Bascompte *et al.* 2006). However, several studies have recently shown that such observations do not necessarily correspond to actual fitness benefits conferred to a plant by a pollinator because some pollinators may be inefficient pollen carriers or could transport low quality, highly-related (Aizen & Harder 2007; Brosi & Briggs 2013). If pollinators are restricted by fragmentation to small patches, the likelihood of transporting pollen among genetically related individuals is high. Thus, the mere presence, or even abundance of a pollinator species at a flower or within a patch does not necessarily imply successful transfer of long-distance high-quality pollen. Having a clear knowledge of how habitat configuration affects pollinators' movement patterns is thus vital for generating and testing hypotheses about the effect of fragmentation on pollen flow.

Hummingbirds are vagile pollinators that persist in fragmented tropical landscapes and populations appear to be robust to anthropogenic disturbance– at least in landscapes characterized by regenerating forest matrix (Stouffer & Bierregaard 1995). Nevertheless, the *movement* of even generalist species of tropical hummingbirds appears to be influenced by landscape structure (Hadley & Betts 2009). The green hermit (*Phaethornis guy*) is a forest interior species which inhabits tropical forests from Costa

Rica to western Colombia and southeastern Peru (Stiles & Skutch 1989). This species is a particularly important generalist pollinator in tropical forests, as it is involved in the transport of pollen from at least 13 different plant species (Borgella *et al.* 2001). The green hermit is also the primary pollinator of *Heliconia tortuosa* – a keystone herb in the study system (Borgella *et al.* 2001). Previous work by Hadley *et al*. (In Press) has found evidence that this species is pollen limited in fragmented landscapes, i.e., its seed production is limited by the availability of pollen (Knight *et al.* 2005). Yet, the mechanism for this remains unknown. One potential mechanism for reduced reproduction in *H. tortuosa* is inadequate pollen flow, negatively affecting pollen *quality* by reducing outcrossing between individuals

Space use by pollinators can be studied at three scales (point, path and home range), each of which informs on different aspects of the relationship between pollinator space use and pollen movement. The study of point-level space use provides information about the local conditions influencing the likelihood of pollinator-plant interactions (Johnson & Bond 1992; Herrera 1995; Everaars *et al.* 2011). Studies at the path-level allow identification of the determinants of pollinator movements between feeding locations, which enables predictions about the routes of pollen flow (Tewksbury *et al.* 2002; Townsend & Levey 2005; Van Rossum & Triest 2010). Finally, home range-scale studies provide information on the ‘area of influence’ of individual pollinators, which provides knowledge about typical pollen transport distances and therefore the likelihood of genetic exchange between distant populations (Law & Lean 1999; Wikelski *et al.* 2010).

In this study, I examine habitat selection of green hermits at three spatial scales (point, path and home range) in an effort to answer the question: how do tropical forest loss and fragmentation influence the behavior of a generalist pollinator species? Habitat selection is defined as adaptive disproportionate use of a particular habitat type in relation to available alternatives that are known to be available (Jones 2001). By understanding the elements that define the presence of green hermits, we will be better prepared to assess the potential consequences of landscape disturbance. The selected spatial scales correspond to Johnson's (1980) third order selection (i.e., usage of habitat components within the home range area) and second order selection (i.e., selection of home range area).

At the point scale, I tested the hypothesis that the green hermit was selecting forested areas. To do this, I compared the amount of forest around locations where the bird was observed with the amount available in surrounding areas. If this species is forest dependent, there should be a higher than expected amount of forest at used locations. In addition, I tested the hypothesis that green hermits selected for areas that provided the most cover and food resources. I predicted the levels of canopy cover and resource availability would be higher at used than random locations.

At the path level, I hypothesized that birds moving between points should evidence a preference to stay inside forest, reflecting point-level preferences. If this was true, I predicted that the birds would select movement paths that minimize exposure to open areas (Wilson *et al.* 2007; Bosschieter *et al.* 2010; Aben & Adriaensen 2012). Under the hypothesis that depressed rates of reproduction in *H. tortuosa* in small, isolated patches (Hadley *et al.* In Press) are due to restricted pollinator movement, green hermit movement should be restricted by gaps in forest.

Finally, I evaluated whether the characteristics of green hermit home ranges and home range size is related to landscape structure. If forest amount is a driver of home range selection, the proportion of forest within the home range should be larger than available in the broader landscape. I also tested whether non-forested matrix is avoided by green hermits; I predicted that this species would select areas with high levels of connectivity, independently of habitat amount, as this would minimize the likelihood of gap crossing. Lastly, under the expectation that pollinators attempt to maximize energetic returns for the amount of foraging effort (Heinrich & Raven 1972), I tested the degree to which hummingbird home range size is associated with fragmentation and accessibility of food resources. First, all things being equal, there should be an inverse relationship between the availability of resources within the home range and its size (Hixon *et al.* 1983, Ford 1983, Larter and Gates 1994, Anderson *et al.* 2005). Second, because flower resources are concentrated within forest in this system (Hadley *et al.* In Press) home ranges in continuous forest areas should be smaller than in fragmented landscapes (i.e., there is less need to move long-distances to acquire resources). However, if fragmentation strongly limits movement, the reverse should be true, regardless of resource availability. These alternative hypotheses have important implications for pollen transport. In the former case, plant genes would be *more* likely to travel long distances in fragmented landscapes (Côrtes *et al.* 2013). In the latter, fragmentation would result in limitations to gene flow and subsequent inbreeding depression (Richards *et al.* 1999).

Materials and methods

Study site

The study was conducted in a 20,600 ha area surrounding the Las Cruces Biological Station, Costa Rica (8º 47’ N, 82º57’ W; *ca*. 900 - 1280 m elev.). The reserve comprises 235 ha of primary and secondary forest. The surrounding landscape was previously forested, but now is predominately agricultural, comprised of pasture (>90%), mixed coffee-banana plantations (~5%) and family garden plots. Scattered throughout this agricultural landscape are remnant fragments of Pacific premontane humid forest (1–82 ha) and forested riparian corridors (10 – 40 m wide) (Borgella 2001, Hadley & Betts 2009).

Data collection

Focal species

The green hermit hummingbird is a tropical, forest interior species which ranges from western Colombia and southeastern Peru to Costa Rica (Stiles & Skutch 1989). Green hermits do not defend territories but instead are thought to exhibit ‘traplining’ behavior, moving relatively long distances to feed from nectar-rich flowers (particularly *Heliconia* sp.) (Stiles 1975). This propensity for long-distance daily movements, together with the ability to persist in fragmented landscapes, makes the green hermit an excellent study species for the analysis of movement behavior between modified and intact landscapes. This species is a particularly important pollinator in tropical areas (Borgella *et al.* 2001). Thus, changes in its movement patterns are likely to have a broad effect on the local plant community. Despite the importance of the green hermit as pollen carrier, basic information on its space use, such as home range size and habitat preferences, does not yet exist.

Capture and transmitter attachment

I captured 20 individuals (8 male, 12 female) at forest fragments chosen to represent a gradient in patch size (1.47 – 800 ha) and forest amount (16 – 78 %) within a 1 km buffer from the focal patch. This 1 km distance corresponded to the potential maximum movement distance by green hermits within their home range, based on pilot data. With this sampling design, I aimed to tease apart the effects of landscape composition and landscape fragmentation. I followed individual birds continuously for tracking periods that lasted from 3 – 8 hours per day (mean = 4 days / individual). Green hermits were captured with mist-nets set near food sources (mainly *Heliconia* sp. and *Centropogon* sp.), and with hull traps containing a hummingbird feeder. Each individual was fitted with radio-telemetry units (<0.25 g, Blackburn Transmitters), using eyelash glue for attachment bare skin on their lower backs. Green hermits are relatively large hummingbirds (5.8 ± 0.09g), so transmitter mass was <5% of their body mass. The transmitters generally remained attached for about two weeks. The attachment of transmitters did not appear to affect the behavior of tagged individuals as radio-tagged birds were observed carrying on normally with their reproductive behavior (chasing competitors, lek display, nesting and feeding). The birds' foreheads were marked with nail-polish to allow identification through binoculars.

Radio-tracking

I radio-tracked green hermits from March to May, 2012 – a period which corresponds to the last months of the breeding season (Snow 1977). I obtained location points by following the birds as closely as possible on foot using radio receivers and handheld Yagi antennae. Based on trials with known transmitter distances, I assumed that a bird was 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 when I could detect the signal using the attenuator. Signal was lost when birds were more than 200 m from the observer.

I gathered a total of at least 6 hours of observations per bird (mean 14.41 h, SD: 3.88) over a period ranging from 2 to 8 days. The combined number of sampling hours amounted to 288 h, during which 2428 individual locations were recorded. For the analyses, I only worked with data that were taken from within a 30 m distance from the bird, as these were the records with higher level of certainty (n = 1561). At each point, the observers registered their UTM coordinates (using a GPS device), UTM coordinates of the bird (when visually detected), estimated distance from observer to bird (based on the reading of the receiver), azimuth (of the direction where the signal was stronger), time of arrival and departure from the point by the bird, and cover type (i.e. forested patch or matrix). The final UTM coordinates of birds were calculated *a posteriori* based on the estimated observer-bird distance and the azimuth of the hummingbird location (Appendix A).

Measurement of Vegetation Characteristics

I measured vegetation characteristics for a subset of 15 individuals in 20 m radius plots surrounding detection locations. Time limitations prevented me from collecting data on all tagged individuals so this subset should be considered a haphazard sample, but one that still represents a gradient in forest loss and fragmentation. To diminish the likelihood of overestimating resource availability, I selected points >30 m apart, which ensured that the overlap between sampling areas was <10%. Thus, the number of sample plots varied with the spread of the individual movement, ranging from 8 to 18 (mean = 13.4) and covering between 12 and 99% of the estimated home range areas. Each of these locations was paired with a random sample plot located within 500 m of the original observation. This distance is based on observations that green hermits have the capacity to fly at least 500 m in 40 seconds, presumably without stopping (Volpe unpublished data).

In each plot I recorded canopy cover and food resource availability. Canopy cover refers to the area of the ground covered by a vertical projection of the canopy and reflects the dominance of a site by trees (Jennings *et al.* 1999). Canopy cover was measured using an ocular tube following the approach of Kucharcik and Collins (2001) (Appendix B). Resource availability was measured by counting the number of all flowering or fruiting plants within the limits of the plots. The counts included both plants that were known to be food resources for the green hermits as well as those of which no feeding data was available were counted. This was done to prevent underestimating resource availability by ignoring plants that were used by the green hermit even when we did not observe it.

Land cover information

I obtained landscape attributes from GIS data available from Las Cruces Biological Station and 2005 Landsat TM remotely sensed data. Landscape has not experienced any substantial changes since acquisition of satellite images; forest cover in Costa Rica, and in the province where the reserve is located in particular, has remained relatively constant (change between 2005 and 2010 <0.3%) since 2005 (FONAFIFO 2012). I delineated land cover on this raster image using ArcGIS 10.1 (ESRI 2012), classifying it visually as either forest or agricultural matrix. The matrix was later sub-classified into pasture and non-pasture, the latter being composed of unidentified crops and human developments.

Data analysis

Point-level habitat selection

Forest dependency

I compared forest amount at observed locations to the amount present in the area that I expected to be available to each individual. To characterize ‘used’ sites, I generated a 30 m buffer around each recorded point. This size corresponds to the average location error of the records (Manly *et al.* 2002). I used buffers rather than particular location points in order to both account for location error and for the fact that animals select mosaics of habitat rather than particular points in space (Rettie & McLoughlin 1999). Available was defined as the proportion of forest within a 500 m buffer around each recorded point. I used ArcGIS 10.1 to create the buffers and calculate the percentage of forest inside them. To prevent giving excessive weights to location points with multiple records, I only used records separated by >1 m. The final dataset contained 1359 points.

If green hermits select forested areas, the amount of forest within used buffers should be larger than the amount available within randomly located buffers. To test this prediction I applied the linear mixed effects model:

$$Difference = Total\ Forest\ |Individual$$

where 'Difference' corresponds to the difference between observed and available percentage of forest within the buffers. The use of this response allowed me to pair observed and available locations. I used a mixed linear regression instead of a simpler test (e.g., one sample t-test) in order to be able to include the percentage of forest surrounding the area as a predictor variable (hereafter 'total forest'). This was needed to prevent a bias towards observing larger differences between used and available forest for birds living in areas with low overall forest amount. Total forest was defined for each bird as the percentage of forest available inside a single 500 m buffer surrounding all the recorded points. To account for spatial autocorrelation in the residuals, the model included a rational quadratic autocorrelation structure (Zuur *et al.* 2009). I included 'individual' as a random effect to account for potential lack of independence within points selected by each bird.

Resource availability and canopy cover

To test the hypothesis that green hermits prefer locations with high canopy cover and resource availability I ran a logistic mixed-effect regression model that compared 'used' versus 'available' green hermit locations:

$$Presence = \ Resource\ availability + Canopy\ cover\ |\, pair/individual$$

'Presence' indicates if a given point was used or not by a bird at a given time. Resource availability refers to the number of plants within the 20 m radius plot. I included 'pair' nested within 'individual' as random effects in order to both pair the observed-random plots and to account for potential lack of independence within points selected by each bird. The models were run using the '*lme4'* R package.

Given that not all flowering plants are used with the same intensity by the green hermits, I evaluated the influence of different plant species on location choice by generating three groups representing different levels of affinity with the green hermit (Appendix C). This classification was based on field observations and data on pollen loads (Betts & Hadley, unpublished data). An initial assessment showed that when the three groups of plants were included in the analysis, the results did not differ qualitatively from when only plants belonging to the family Heliconiaceae were included. Heliconias are abundant in the study area, being the dominant understory flowering ornithophilous plant. In addition, they have high nectar yields (65 µl/flower/day; Stiles 1975), increasing their attractiveness to hummingbirds. Given that heliconias seemed to be the main resource affecting site choice, only this group was used for subsequent analyses (Appendix C).

Number of plants, rather than numbers of flowers, was used for the analysis because plant detectability did not change during the year, while flower phenology did (Appendix D). This was important because the collection of food resource data was asynchronous with radio-telemetry, taking place over the following 1 to 6 months after it (median = 2 months). The resource availability measurement thus assumes that the number of plants at a location is correlated with number of flowers actually present when the birds were detected. Heliconias are perennial plants with long flowering seasons. The most common of these -*H. tortuosa*- blooms between March and October, with inflorescences that produce flowers for up to 3 months (Stiles 1975). I am thus confident that the plants flowering during movement observations were detected during vegetation surveys.

Path-scale analysis

Path-scale habitat selection

I used a step selection function (hereafter ‘SSF’; Fortin *et al.* 2005) to assess the hypothesis that green hermits actively select forested areas to move between points. This technique compares the straight line connecting two consecutive visited points (‘step’) with other alternative steps that could have, but were not been taken starting at the same origin point (hereafter ‘available’ steps). The model assumes that the environmental characteristics along the lines are correlated with the probability of moving to a particular end point (Fortin 2005). For each bird, I generated alternative random steps based on the frequency distribution of the step lengths and turning angles observed for the *remaining* birds, using the function 'movement.ssfsamples' from the program GME (Geospatial Modelling Environment – Beyer 2012). I generated 20 random steps per observed step. Following Gillies, Beyer, & St Clair (2011). I resampled the data to obtain origin-destination pairs separated by a distance long enough to be able to provide information about the area around them (10 meters) but close enough in time to not be completely unrelated (15 minutes). These constraints resulted in 903 'used' steps. To ensure that the available steps were realistic, I only used those that ended in forest habitat.

I used a mixed matched case-control logistic regression (also termed 'mixed conditional logistic regression'; Duchesne, Fortin, & Courbin 2010) to model the likelihood of an individual hummingbird choosing a particular movement step instead of an alternative available one. To identify the best model, I first identified four 'exposure variables', defined as variables that influence the level of exposure of the individuals to unfavorable conditions along a movement step (Gillies *et al.* 2011). Variables increasing exposure were: number of gaps (i.e., number of times the step line crosses open area), total gap distance (i.e., sum of the lengths of all the gaps along a step) and mean gap size (i.e., average length of gaps in the step). Variables reducing exposure were: step forest amount (i.e., 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 (i.e., length of the step that takes place inside the forest over total step length). To test for the effect of type of matrix on the movement decisions I included an interaction between the exposure variables related to the presence of gaps and the variable ‘mean pasture’. This variable corresponded to the proportion of the linear dimension of a gap that occurred in pasture. I did not include the main effect of this variable because such term would not make sense in cases in which the steps took place only in forest). It is very likely that the non-pasture matrix also influences movement decisions, in particular when it consists of crops that contain food resources. Yet, I did not have precise enough information to evaluate this effect. For this reason, I only included pasture as an indicator of matrix type. I also included a variable I expected to facilitate movement – distance to the nearest stream – because previous observations suggest that this species may use streams as movement corridors.

To decide which variables should be kept in the final model, I built competing candidate models and compared them using Akaike’s Information Criterion corrected for small sample size (AIC_C)**.** Each set of candidate models included a univariate model using a single exposure variable and a full model including the exposure variable, distance to stream and, in the case of number of gaps, mean gaps size and total gap distance, and interaction with mean pasture.

All the models included a random component that allowed variation among individuals in the selection coefficient for each variable. This addition of individual-level random effects has two advantages: it helps to correct the correlated nature of the data (Gillies *et al.* 2006) and also generates more ecologically sound models, by relaxing the assumption of homogeneous selection among animals (Duchesne, Fortin, & Courbin 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 choice decisions (Gillies *et al.* 2006, 2011). To test these potential factors affecting the selection decisions of individual birds, I ran a linear regression of the individual selection coefficients as a function of broad-scale landscape measures (overall forest availability, connectivity) and individual-specific characteristics (sex). Connectivity was measured using the Landscape Coincidence Probability Index (see below). I expected that birds living in areas with high forest amount and connectivity would show a greater tendency to avoid open areas, because they would have more forested alternatives to use. I applied the mixed conditional logistic regressions in the *mixlogit* module (Hole 2007) in Stata (Statacorp 2011).

Home range scale

Home range estimation

Several reviews and comparisons on the different home range estimators have been published (Hansteen *et al.* 1997; Laver & Kelly 2008; Lichti & Swihart 2011; Powell & Mitchell 2012), but to date there is no consensus on which method is the most appropriate. Following Fieberg and Börger (2012), who suggest that authors should chose a method based on their question and data, I selected for my analyses the Local Convex Hull (hereafter 'LoCoH') approach. The LoCoH method creates increasingly point-inclusive convex polygons that delimit isopleths of varying point density, providing information on intensity of use (Getz *et al.* 2007). For this method, the home range is defined as the area that encloses 95% of the points. I chose LoCoH because it is purported to be sensitive to sharp boundaries in habitat use, such as the ones I observed for green hermit in a forest-pasture system (Fieberg & Börger 2012). LoCoH home range polygons where generated with the '*tLoCoH*' R package, using the *k*-method.

To determine the sensitivity of my results to home range estimation methods, I also generated polygons using. the Brownian Bridge Movement Model (hereafter 'BBMM', Horne *et al.* 2007). I selected the BBMM because it can accommodate autocorrelated data and variability in distance and time lag between successive locations (Fischer *et al.* 2013). In addition, it allows the incorporation of point-specific location errors. The home range limit was defined using the 90% isopleth of the utilization distribution generated by the BBMM (i.e., the area within which there was a 90% chance of finding the animal). My choice of 90% isopleth was based on Börger *et al.* 2006., who argued that it can provide unbiased home range estimates even with few data.

Forest amount

To evaluate the hypothesis that green hermits select home ranges with greater amounts of forest, I rotated the estimated LoCoH home range polygons around their center to simulate potential areas that could have been used and calculated the percentage of forest inside the observed and hypothetical scenarios (hereafter 'rotated alternatives'). As the data were non-normal, I ran a paired Wilcoxon signed rank test comparing the observed percentage of forest versus the mean value for the rotated alternatives. To run the analysis, I excluded the cases in which both the observed and all the rotated alternatives fell completely inside the forest, reducing the sample size to 17. The rotation of home range polygons and estimation of forest amount inside them was accomplished using GME.

Connectivity

To test the hypothesis that matrix avoidance affects home range selection, I compared the degree of connectivity of the forest within the used home range polygons with the connectivity level inside equally shaped 'available' polygons that had the potential to be used. Again, I quantified available home ranges by rotating the observed home range polygons around their center, as described previously, selecting for the comparison those that contained the same amount of forest as the used polygon.

To determine the level of connectivity within each area, I used the Landscape Coincidence Probability approach (Smith *et al.* 2011):

$$CON = \sum_{i=1}^{NC}\sum_{j=1}^{NC}\left(\frac{a_i a_j c_{ij}}{A_L^2}\right) \times 100$$

where NC is the total number of forest patches, a_i and a_j are areas of patches *i* and *j* respectively, c_{ij} is a passibility value which is 0 or 1, and A_L is the total landscape area (including non-forest and habitat patches) (Smith *et al.* 2011). Patches were considered fully connected ($c_{ij} = 1$) if they were within the maximum observed gap-crossing distance (162 m) and unconnected ($c_{ij} = 0$) if they were separated by more than that distance. I chose this metric because it quantifies not only the capacity of the organism to cross between habitat patches but also patch area in relation to the total landscape area. In this way, the maximum levels of connectivity were assigned to those landscapes in which all the habitat is contained in the same patch and this patch occupied a large proportion of the total area. The area of the patches was calculated using GME.

Relationship between home range size and landscape structure

I analyzed the relationship between home range size and four measures of landscape structure which included metrics of landscape configuration (Table 2.1) and habitat amount (percentage of forest). I conducted the analysis at 3 spatial scales: (1) within the home range, (2) within a 500 m radius buffer and (3) within a 1.5 km radius buffer. I ran a principal components analysis (hereafter 'PCA') and selected the most important factors based on the Kaiser criterion (Kaiser 1960): only principal components with eigen-values >1 should be kept for analyses. Finally, I used a simple linear regression with home range size as a response variable and selected components and sex as predictors. Home range area was log-transformed to meet the regression assumptions.

Relationship between home range size and resource density

I estimated the average resource value inside the home area of each bird (R_{HR}) using the formula:

$$R_{HR} = \frac{\sum R_P}{N}$$

where R_P is the resource availability of an individual sample plot and N is the number of points sampled inside the given home range. To analyze the relationship with home range size, I ran a weighted least squares regression in which the observations were weighted by the percentage of the total home range area that was sampled, as estimated by the overlap between sample plots and home range polygons.

$$\log HRarea = R_{HR} + Forest\,\% + MPS + Sex$$

where ‘Forest %’ refers to the proportion of the home range covered by forest and MPS refers to the mean patch size within the home range. These variables were included to account for the influence of landscape structure on home range size. I also tested for an interaction between R_{HR} and MPS to test the hypothesis that the influence of resource density on home range size will be conditioned by forest fragmentation. If that is the case, I would expect a negative interaction between both, in which an increase in fragmentation restricts how much a home range can expand in response to resource availability. Home range area was log-transformed to meet the regression assumptions.

Results

Point-scale habitat selection

Forest dependency

I found that green hermits selected locations at the point scale with an average of 42% more forest than in the surrounding available area (CI 95%: 32.3% to 52.1%, P <0.0001). This strong effect occurred even after controlling for the negative relationship between total amount of forest and difference between observed and available use of forest (-0.28, CI 95%: -0.53 to 0.043, P = 0.02).

Resource density and canopy cover

The presence of green hermits at a given point was positively related to both canopy cover and resource availability (Table 2.2). The addition of one plant to a 0.13 ha plot increased the chances of green hermit visits by a factor of 1.054 (95% CI: 1.020 to 1.090). This translates to about a doubling of the chances of encounter for every increase by 15 plants (or 119 plants/ ha, Fig. 2.1A). Similarly, an increase of 1% in canopy cover increased the likelihood of the bird using a plot by a factor of 1.022 (95% CI: 1.015 to 1.028). A plot with 100% of canopy cover was 8 times more likely to be used that one completely open (Fig. 2.1B). A standardized comparison showed that the canopy cover as the most important variable determining point-level habitat selection (β_{canopy}: 0.84, $\beta_{Resources}$: 0.56).

Path-scale habitat selection

Overall, green hermits selected movement steps that decreased their exposure to gaps in forest cover. 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, while those variables that increased exposure (i.e., number of gaps, mean gap size and total gap length) had negative effects (Table 2.3). However, the strongest predictor was distance to stream; confidence intervals for this variable did not include zero in any of the candidate models. The top model included this variable together with total gap length along the path. The second best model (ΔAICc = 6) included distance to stream, total gap length and the interaction between the latter and the proportion of the gap formed by pasture, though only distance to stream had a significant effect on likelihood of selecting a step (confidence interval did not include zero). None of the interactions between pasture and exposure variables were significant. It is important to note that because most streams in my system are characterized by forest cover, it is difficult to determine, except through large-scale manipulative experiment, the independent effects of these factors.

Green hermits selected steps that took them closer to a stream and avoided those that involved crossing long stretches of open matrix (Fig. 2.2). All candidate models showed variability among individual birds in the selection coefficients for all the covariates, justifying the use of random terms. (Stream distance: SD = -0.013, Z = -5.66, P <0.001, total gap length: SD = 0.03, Z = 6.22, P <0.001).

None of the bird-specific variables (i.e., sex, total forest available or connectivity) were useful for explaining the observed variability in the strength of selection for distance to stream (Table 2.4). On the other hand, there was a weak negative effect of connectivity on use of large gaps; an increase in the connectivity index increased the avoidance for open areas (β = -0.00052; CI 95%: -0.0003 to -0.0007).

Home range scale habitat selection

Home range characterization

The size of home ranges generated using the LoCoH estimator varied from 0.25 ha and to 6.08 ha (mean = 2.18 ha), being larger for males (mean = 3.12 ha) than for females (mean = 1.50 ha). Mean home range length was 282 m (SD = 179 m, median = 240 m, range =

41 m – 687 m). There was a high proportion of forest inside the home ranges, with a mean of 77% (median = 82%, range = 32% - 100%). These values exclude an outlier whose estimated home range area and length were 153 ha and 2883 m respectively. This was a rare case in the dataset, as no other individual was detected distances longer than 770 m from capture sites. Yet, there were instances in which I lost the signal from the individuals being followed, so I cannot exclude the possibility of a downward bias in home range size and diameter.

Home ranges generated using the BBMM estimator were larger, ranging from 0.96 ha to 26.86 ha (mean = 5.9 ha), while the proportion of forest within them remained relatively constant (mean BBMM = 70.4%, median = 73.9%, range = 29% - 100%). The difference in size could be related to a tendency of BBMM estimators to overestimate areas when the study species have high mobility in relationship to their home range size (e.g.: *Meles meles* Huck *et al.* 2008). A larger amount of points taken within an even smaller time frame is probably needed in order to generate a more precise estimation of home range area with this estimator. LoCoH generated more realistic home ranges estimates than BBMM, producing polygons that adjusted better to the underlying landscape structure, reducing the area that contained unused open matrix. At the same time, it incorporated areas that were known to be used but were excluded by the BBMM (e.g., open areas that were the only possible way through between two patches, Fig. 2.3). Despite the fact that this technique might be underestimating the real home range size (Huck *et al.* 2008) I can feel confident that the area it encompasses is within the limits of the true home range, as it does not go beyond the observed location points. Even when this might be making my estimations of home range size over-conservative, they are still useful as a first approximation of the minimal area of influence of these pollinators. Additional sensitivity analysis regarding regularity of points and the effect of missing data can be found in Appendix E.

Forest amount

I found some evidence that the percentage of forest inside of observed home range polygons was larger than inside available ones (Wilcoxon signed rank test; V = 146, P = 0.0003). The mean difference between observed and rotated alternatives was 10.7%. When excluding the cases where the availability only included forest (n = 4), the difference increases to 13.3%. This selection for forest was independent of home range estimator; repeating the analysis using BBMM home range polygons shielded similar results (mean difference = 8.8%, V = 146, P <0.0001). These results are conservative as the values of forest amount within alternative home ranges were averaged for the comparison, smoothing in this way the potential differences with the used home range. The fact that I detected a difference despite this smoothing would be indicating that selection for forest is strong.

Connectivity

The overall connectivity within the home range polygons, estimated using LoCoH, was significantly higher than connectivity within rotated alternatives (P = 0.001, t = 3.9, df =

19). The connectivity index within observed home ranges was, on average, 13.4% larger than those that were available (CI 95% = 6.1% to 20.6%). However, when I repeated the comparison using only available home ranges that had similar amounts of forest as the observed one (+- 5%), the difference became non-significant (P = 0.78, t=0.28, df = 15). In this case, connectivity within observed home ranges was only an average of 0.12% larger than those available (CI 95% = -0.8% to 1.02%). Thus, the positive effect of connectivity was not independent of forest amount.

On the other hand, when using the BBMM home range estimates, I found a small but statistically significant (P = 0.003, t = 3.36, df = 19) increase in connectivity inside used home range polygons after accounting for forest amount: connectivity index values were 1.46% larger than inside available polygons (CI 95% = 0.55% to 2.37%).

Factors affecting home range size

Landscape structure

At the home range scale, two principal components had high explanatory power for describing home ranges according to the Kaiser criterion, accounting for 77% of the variation of the dataset (Appendix F). The first principal component (PC1) was an indicator of forest availability in the landscape, being negatively associated with landscapes with large forest amount concentrated in large patches. The second principal component (PC2) was an indicator of the level of fragmentation in the landscape, being associated with an increase in patch size and in the continuity of forest fragments. A simple linear regression analysis showed that both components influenced home range size (Fig. 2.4). There was a positive correlation between home range area and PC1 indicating that home ranges were smaller in areas with high forest availability (β_1= 0.19, CI95% = 0.09 to 0.30, P = 0.002). PC2 was also positively correlated with home range area, indicating that an increase in the size and spread of forest patches led to larger home (β_2 = 0.63, CI95% = 0.50 to -0.76, P = <0.001). Home range area was also larger for males than for females (β_3 = 0.43, CI95% = 0.07 to 0.78, P = 0.029). Principal components representing forest amount and fragmentation were not significant at either of the broader spatial scales that I examined (500 m: (PC1 β_1 = 0.012, P = 0.94; PC2 β_2 = -0.011, P = 0.63; Sex β_3 = 0.84, P = 0.18; 1500 m: PC1 β_1 = 0.01, P = 0.90; PC2 β_2 = -0.074, P = 0.74; Sex β_3 = 0.75, P = 0.17; Appendix F).

Resource availability

I found no evidence of resource availability on home range size, neither as a main effect (β= -0.016, CI95%: -0.046 to 0.014, P = 0.29) nor as an interaction (β = 0.046, CI95%: -0.06 to 0.15, P = 0.41). There was evidence of a positive effect of mean patch size on home range size (Fig. 2.5); an increase in of mean patch size by 1 ha was associated to an increase in the median home range size by a factor of 1.9 (CI 95%: 1.4 to 2.7, P = 0.002). Forest amount on the other hand was negatively related to home range size; an increase in one percent in forest amount was associated to a decrease in the median home range size by a factor of 0.06 (CI 95%: 0.02 to 0.14, P <0.001). There was also some evidence for an effect of sex on home range size; the median size of males' home range was likely to be 1.67 times larger than the one of females (CI 95%: 1.06 – 2.61, P = 0.044).

Discussion

Space use by the green hermit was strongly associated with forest amount. At all scales of analysis, there was evidence that the birds selected for forested areas. At the point scale, I saw green hermits were present at locations that had 42% more forest than available alternatives and with a high proportion of canopy cover. At the path level the species selected movement paths that minimized the exposure to non-forested areas. At the home range scale, the amount of forest within the used home range areas was 10% larger than available. The degree of landscape connectivity, on the other hand, appeared to have little effect on home range selection. Thus, persistence in the landscape for this species seems to be dependent only on habitat amount (Trzcinski *et al.* 1999; Desrochers *et al.* 2010; Fahrig 2013).

Nevertheless, it is important to note that persistence does not necessarily mean indifference; the *movement patterns* of the green hermit are still affected by landscape configuration. I found that green hermits choose to avoid gaps and, when possible, move within the forest. This tendency was more marked in landscapes with high connectivity which allowed more options to move through forest, such as riparian buffers. Riparian buffers tend to increase connectivity between patches by acting as thoroughfares between them (Gilbert-Norton *et al.* 2010). Indeed, green hermits in this study showed a marked preference to move close to streams which highlights the critical importance of these landscape elements -- particularly given that they are some of the last remaining areas of forest cover in agricultural landscapes. Interestingly, preference for streams was observed in non-fragmented areas as well, hinting that there might be additional factors guiding the birds' behavior. Streams may facilitate movement by acting as 'flight-paths' (Snow 1974), offering open pathways through otherwise dense forest. Alternatively, there may be a higher abundance of flower resources or nesting sites in damp areas next to streams (Betts & Hadley unpublished data, Stiles 1975). Regardless, the presence of riparian corridors in fragmented areas is likely to enhance the ability of a green hermit to travel. Corridors do not appear to be a requisite for movement in fragmented landscapes though. Even when the birds tend to avoid gap crossing, they are still capable of moving through the matrix. I observed gap crossing by green hermits traveling between two unconnected forest patches that were 129 to 162 m apart, but also in cases when there was a clearing within the home range (N = 4 individuals). This ability to cross non-forested areas could explain how green hermits are present in small patches completely surrounded by matrix (Hadley *et al.* unpublished data), even more so if one-time dispersal movements are less sensitive to gaps than chronic foraging movements of adults (Van Dyck & Baguette 2005). Nevertheless, it is important to highlight that gap crossing abilities are limited; no birds were seen crossing distances larger than 162 m, and my models indicate that the presence of gaps as small as 50 m substantially diminishes the odds of movement by 50%. Surprisingly, I found no evidence for an effect of matrix type on movement decisions by the green hermit. Pasture appeared to restrict movement no more than other forms of non-forest matrix (e.g., coffee coffee and banana plantation), though admittedly, the resolution of my land cover typing was low.

Home ranges of green hermits are larger in landscapes with a proportionally small amount of forest. The observed tendency could be indicating that the birds have to move longer distances to access the amount of forest they need. In landscapes with similar forest amount, habitat configuration affects home ranges by promoting small home range sizes when patches are small and compact, and large home range sizes when patches are larger and more elongated. This pattern could be reflecting a movement constraint that limits the potential size of home ranges by forcing the birds to stay within the reduced area of small patches. In particular, in areas where the distance between neighboring fragments is large, the birds will not be able to access other patches due to gap avoidance. On the other hand, if the forest remnants are larger and connected by corridors the birds will have more mobility across the landscape.

Implications for pollination systems

Green hermits avoid open areas and move within forest when possible. As a consequence, the configuration of forest remnants in the fragmented landscape will likely determine pollen (i.e. gene) flow. For example, plants in two separate patches connected by a corridor will likely have a higher rate of pollen exchange than two patches with no connections (Townsend and Levey 2005, Van Geert *et al.* 2010, Kormann *et al.* In Prep). This does not necessarily mean that ornithophilous plants in structurally isolated patches will be entirely genetically isolated (Lander *et al.* 2010); gene flow likely occurs, though probably at a much reduced rate. Given that the likelihood of moving in a certain direction is reduced by the presence of open areas, it is likely that short gap distances may act as a reproductive filter to plant reproduction.

I found that forest fragmentation has a negative effect on how far away a bird can travel, with landscapes with small mean patch size supporting smaller home ranges. The results are consistent with observations by Hadley *et al.* (In Press) that seed sets from *Heliconia tortuosa* plants are reduced in small forest patches. This could be explained by a reduction of pollen quality due to hummingbirds being forced to move within a smaller area, increasing the likelihood of transporting pollen from closely related plants. A reduction in the local recruitment of Heliconia plants could potentially have a broader impact in the ecosystem, through a cascading effect on local plant communities. The availability of *Heliconia* plants, in particular *H. tortuosa,* was a strong predictor of the presence of green hermits at a given location. I hypothesize that a reduction of the number of *H. tortuosa* – which is considered a keystone food resource (Stiles 1975, Hadley *et al.* In Press) – could lead to a decreased visitation rate by this generalist pollinator (Borgella *et al.* 2001) leading to a "network collapse" (Kaiser-Bunbury *et al.* 2010) associated to the reduction of pollen flow for the other ornithophilous plants present in the area.

The optimal scenario to maximize distance of pollen transport seems to be one with landscapes with a relatively low amount of forest distributed in large, spread patches connected by corridors, as this would force the birds to move longer distances to access the amount of habitat they require to subsist. It must be taken into account though, that even when an increase in the area of influence of an individual pollinator might lead to a higher level of connection between distant plants, it does not necessarily follow that there will be an increase in the genetic diversity (i.e. quality) of the transported pollen**.** If the patch, or group of patches, through which a green hermit has to move is surrounded by large expanses of open area that the bird is not willing to cross, then the genetic exchange of plants will still only take place within a restricted subset of plants that are accessible to the pollinators. In a landscape with continuous forest, which can support a larger number of pollinators (Hadley *et al.* In Press), it is more likely that there will be overlap of pollinator home ranges from the same or different species. I hypothesize that plants growing in these overlapping areas will potentially receive more diverse pollen incorporating new alleles. Thus, even when a single individual might cover a reduced area, the combined effect of multiple individuals moving through a large area will likely increase long term genetic heterogeneity (Fig. 2.6).

Limitations and future directions

One of the main limitations of this study is that it assumes that there are no food resources in the matrix that could affect movement decisions by the green hermit, even when there is evidence that the birds feed from banana plants growing in the agricultural matrix (Betts & Hadley unpublished data). Time restrictions did not allow me to collect data on the distribution of this high-reward food source in the matrix and there no high-resolution satellite imagery yet exists for the study area. The presence of food resources in the matrix could influence the reduced avoidance of gaps in areas with low connectivity. Areas with low connectivity contained large proportions of agricultural land. If this included crops that contained banana plants the birds might have been more willing to enter the matrix than in more connected areas where the main food resources where inside the forest. To address this possible limitation, I suggest that future studies conduct either mensurative or manipulative experiments, following green hermits moving through areas with different combinations of connectivity and resource availability (i.e. connected with and without matrix resources; unconnected with and without matrix resources) and analyze if the probabilities of gap crossing are affected by these variables.

In conclusion, my work provides evidence that space use patterns of a generalist tropical pollinator are influenced both by composition and configuration of the underlying landscape. The amount of available forest will determine the presence of the green hermit within its home range and in the landscape, and thus the plants that will have access to the pollinator. The configuration of the forest fragments will determine the patterns of pollen flow, potentially defining the degree of outcrossing in the plant population. The structure of plant-pollinator networks is expected to buffer pollination against changes in landscape structure (Memmott *et al.* 2004; Hadley & Betts 2012), as the disappearance of a particular pollinator can be compensated by the existence of other species that can fulfill that role (Bascompte *et al.* 2006). Given that the efficiency of pollinators with great sensitivity to fragmentation is expected to diminish quicker than the efficiency of more mobile species that can still access isolated patches (Hadley & Betts 2012), mobile species are likely to have an important role in the buffering process. The fact that the green hermit, a generalist pollinator, is affected by landscape structure despite its high vagility and willingness to enter open areas, hints that pollinator species with reduced mobility and higher forest affinity will be even more affected. If this is true, the effect of forest fragmentation on the pollinator network might be larger than expected. Conservation policies that promote forest connectivity will be vital for the maintenance of healthy ecosystems.

Tables

Table 2.1. Definitions of landscape structure metrics measured in the southern Costa Rican study area. Codes are abbreviations used in Results.

Code	Name	Definition
PLAND	Percentage of landscape	Percentage of the total landscape that correspond to the habitat type
LPI	Largest Patch Index	Percentage of the landscape comprised by the largest patch
AREA_MN	Mean patch size	Average patch area
AREA_CV	Patch size coefficient of variation	Measurement of uniformity of patch size in the landscape
ED	Edge density	Amount of edge per unit area
GYRATE_AM	Area-weighted mean patch radius of gyration	Average distance an individual can travel inside a patch before reaching its border

Table 2.2. Effect of canopy cover and number of plants from the family Heliconiaceae on the likelihood of a green hermit using a given 20 m radius plot.

	Coefficient	P	SE	OR
Intercept	-1.47	<0.001	0.22	
Number of Plants	0.05	0.0015	0.02	1.06
Canopy	0.02	<0.001	0.003	1.02

Table 2.3. Model coefficients, standard errors, confidence intervals (CI), odds ratios (OR) and AICc values for the candidate models used to predict observed hummingbird movement steps 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), mean gap size (MeanGap), proportion of the gap that takes place inside pasture (Pasture). The top-ranked AICc model is bold.

Model	Variable	Coefficient	SE	Ci	Cs	OR	AICc	ΔAICc
Stream + TotGap	Stream	-0.020	0.003	-0.026	-0.014	0.981	5218	0
	TotGap	-0.019	0.005	-0.029	-0.009	0.981	5218	
Stream + TotGap * Pasture	Stream	-0.0181	0.003	-0.024	-0.012	0.982	5224	6
	TotGap	-0.0097	0.004	-0.018	-0.002	0.990	5224	
	TotGap *Pasture	-0.0053	0.006	-0.017	0.007	0.995	5224	
Stream + MeanGap	Stream	-0.019	0.003	-0.026	-0.013	0.981	5229	10
	MeanGap	-0.020	0.006	-0.032	-0.008	0.980	5229	
Stream + MeanGap * Pasture	Stream	-0.0173	0.003	-0.023	-0.011	0.983	5242	24
	MeanGap	0.0032	0.004	-0.005	0.011	1.003	5242	
	MeanGap *Pasture	-0.0068	0.007	-0.020	0.007	0.993	5242	
TotGap	TotGap	-0.033	0.009	-0.051	-0.015	0.968	5320	101
Stream + PropInFor	Stream	-0.017	0.003	-0.023	-0.011	0.983	5322	104
	PropInFor	0.779	0.501	-0.223	1.781	2.180	5322	
Stream + NumGap * Pasture	Stream	-0.0177	0.003	-0.024	-0.012	0.982	5332	114
	NumGap	-0.2179	0.225	-0.668	0.232	0.804	5332	
	NumGap *Pasture	-0.7258	0.62	-1.966	0.514	0.484	5332	
Stream + ForAm	Stream	-0.021	0.004	-0.029	-0.013	0.979	5333	114
	ForAm	0.353	0.253	-0.153	0.859	1.423	5333	
Stream + NumGap	Stream	-0.018	0.005	-0.028	-0.009	0.982	5334	116
	NumGap	-0.169	0.281	-0.731	0.393	0.845	5334	
MeanGap	MeanGap	-0.042	0.011	-0.064	-0.02	0.959	5338	120
Stream	Stream	-0.018	0.004	-0.026	-0.009	0.983	5358	139
PropInFor	PropInFor	1.702	0.849	0.004	3.399	5.484	5415	197
NumGap	NumGap	-0.539	0.324	-1.189	0.109	0.583	5433	215
ForAm	ForAm	0.523	0.32	-0.117	1.163	1.687	5449	231

Table 2.4. Final models predicting the individual-specific coefficients for total gap length and distance to stream from the step selection functions (SSF) models in Table 2.3. None of the explanatory variables (forest amount, connectivity nor sex) were able to explain the variability observed in the selection coefficients for stream distance, while only connectivity affected the selection coefficients for total gap length.

SSF variable	Variable	Coefficient	SE	P
Total gap length	Intercept	0.01	0.008	0.0925
	Connectivity	-0.00052	0.0001	0.0001
Stream distance	Intercept	-0.017	0.003	<0.0001

Figures

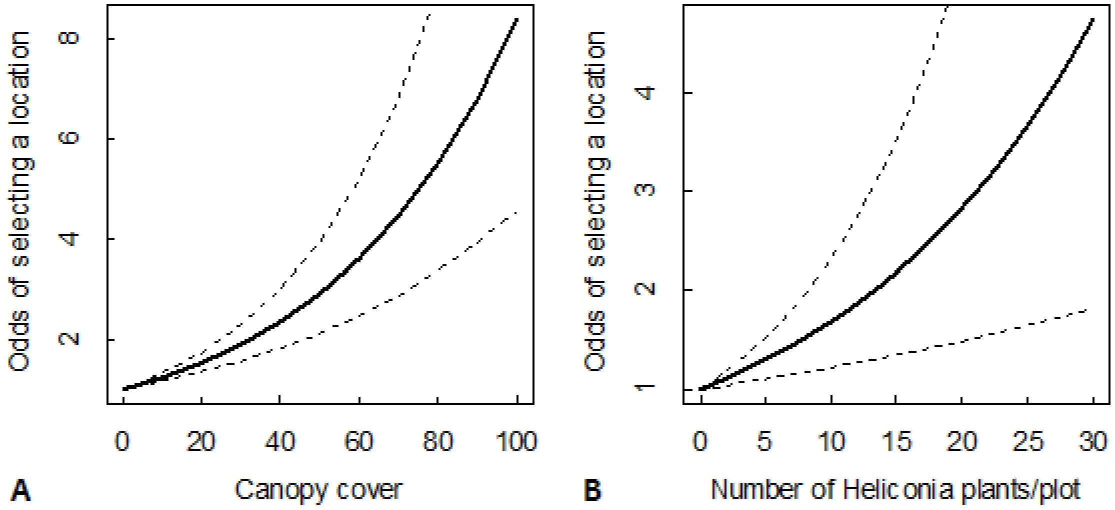

Figure 2.1. Effect of canopy cover (A) and number of Heliconia plants (B) on the odds of the green hermit hummingbird choosing a given location, as calculated from the regression model provided in Table 2.2.

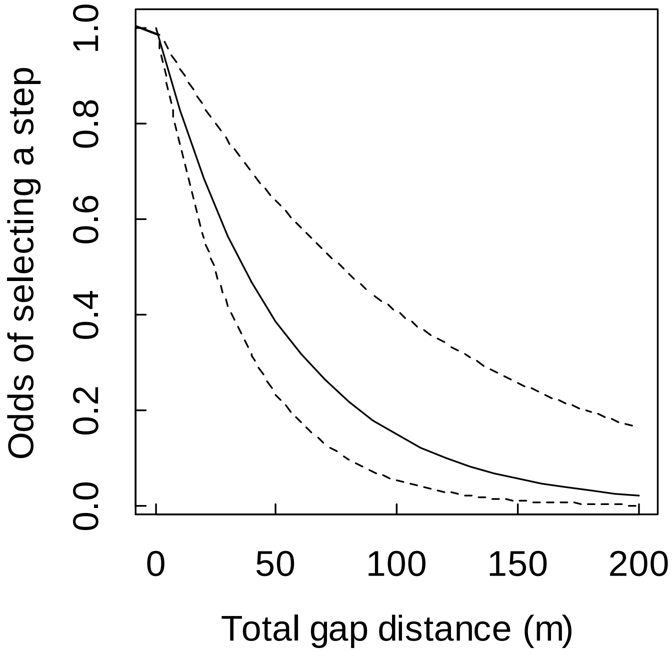

Figure 2.2. Effect of total gap distance on the odds of the green hermit hummingbird choosing a given step, as calculated from the top step selection function model provided in Table 2.3.

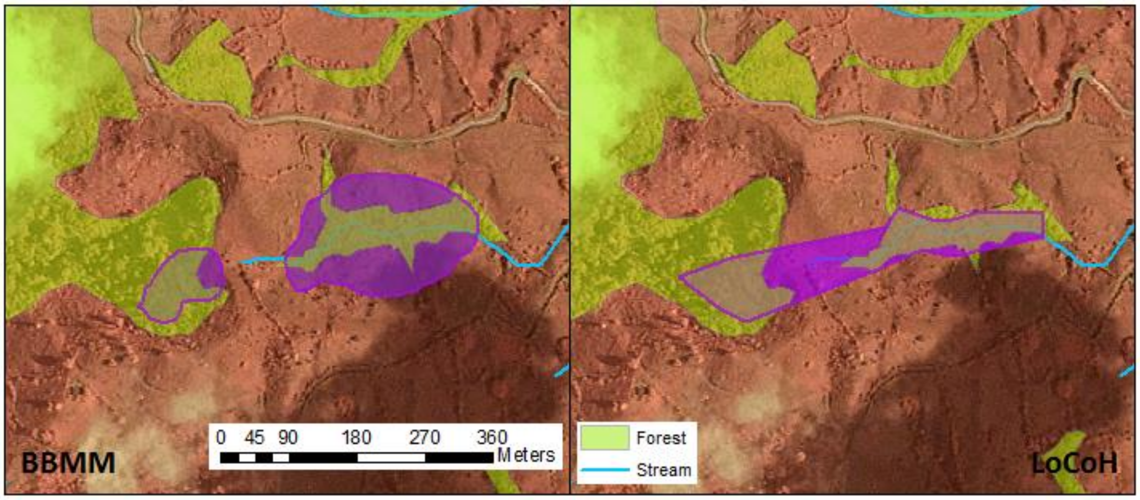

Figure 2.3. Example of home range polygons generated using BBMM and LoCoH estimators.

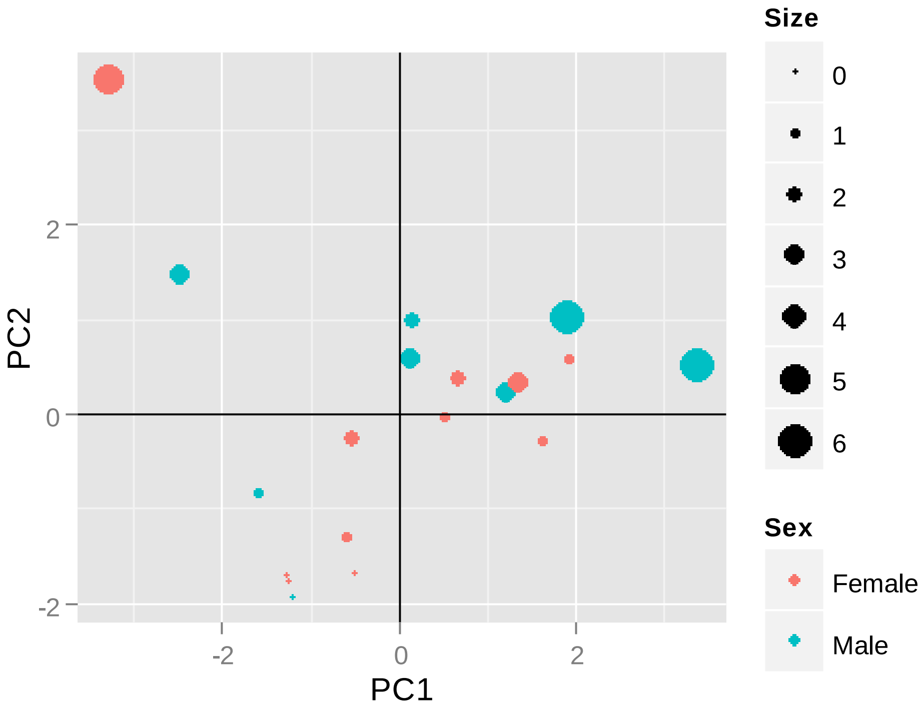

Figure 2.4. Relationship between home range size and landscape structure at the home range scale. An increase in PC1 values correspond to a decrease in forest amount within the home range. An increase in PC2 corresponds to an increase in mean patch size and patch spread. The size of the dots reflects home range size (in hectares).

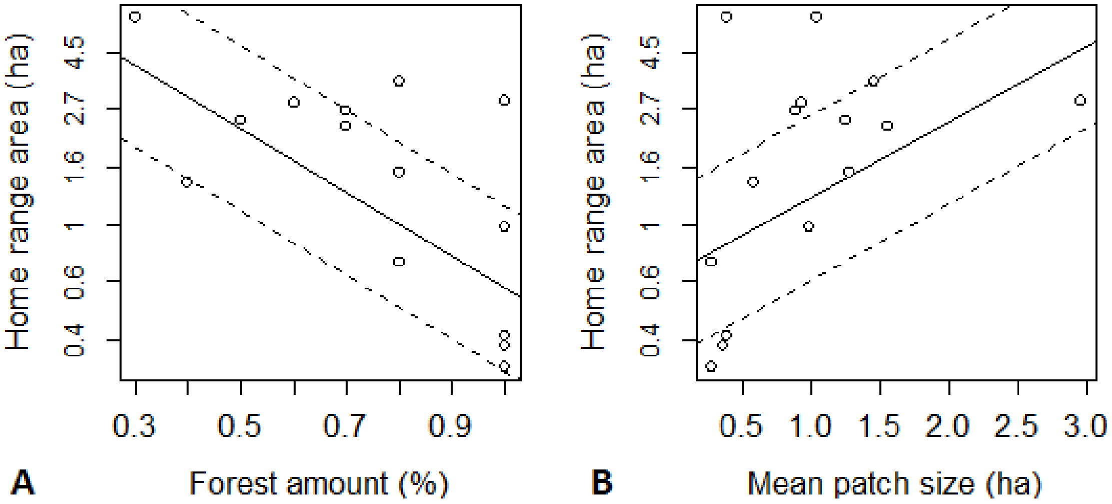

Figure 2.5. Relationship between home range area and forest amount (A) and mean patch size (B) within the home range. Home range area was log-transformed to run the model, but is shown her in normal units (ha) for easier interpretation.

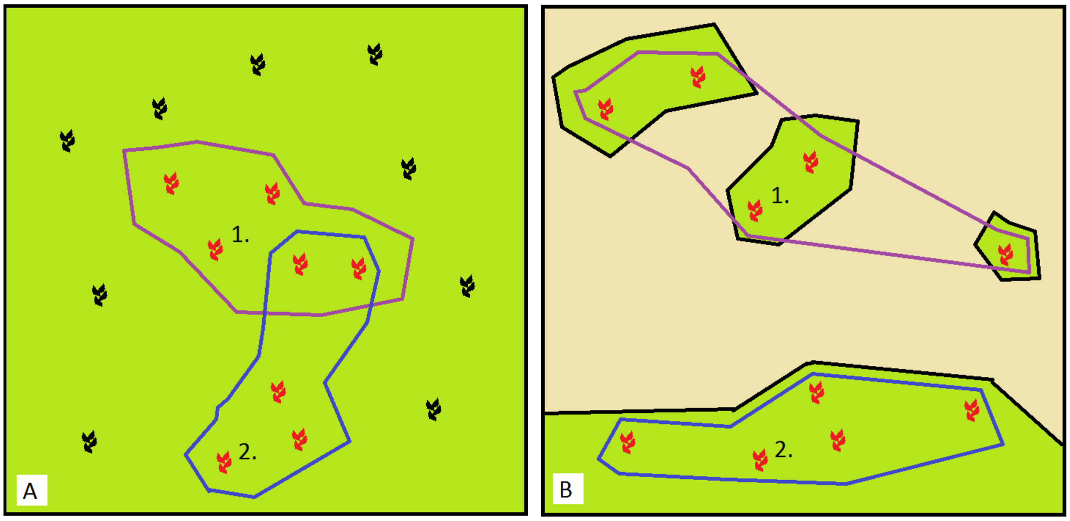

Figure 2.6. Expected effect of isolation on pollen flow. Even when a reduction in landscape-level forest amount and an increase in the separation of patches leads to an increase in the area covered by an individual as found in this study (purple line), this does not necessarily mean an increased pollen flow. The overlap in contiguous forest (A) means that pollen from flower 1 can eventually be transported to flower 2. Alternatively in (B), the large gap between the areas of influence of both individual pollinators means that both populations will not exchange genes.

CHAPTER 3: FUNCTIONAL CONNECTIVITY EXPERIMENTS REFLECT ROUTINE MOVEMENT BEHAVIOR OF A TROPICAL HUMMINGBIRD SPECIES

Abstract

Translocation experiments, in which researchers displace animals 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 standardizing ‘motivation’ to move across individuals. Yet, we lack tests of whether movement behaviors of translocated birds reflect natural behavior of unmanipulated birds. I compared the routine movement behavior of a tropical hummingbird (*Phaethornis guy*) to that of experimentally translocated individuals. I tested for differences in habitat selection patterns at two spatial scales (point and path levels). I 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.

I report the first evidence showing that movement behavior of birds during translocation experiments is similar to natural movement behavior of birds. Therefore, translocation experiments may be reliable tools to address effects of landscape structure on animal movement. I 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. My observations that hummingbirds avoid non-forest matrix and select riparian corridors also provides a potential mechanism for pollen limitation in fragmented tropical forest.

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 (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 the matrix (i.e., the non-habitat surrounding the native patches; -Ricketts, 2001-) is avoided. 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, McCollin, & Ollerton 2012). The degree to which landscapes facilitate or impede animal movements between resource patches is known as a landscape's "functional connectivity" (Taylor *et al.* 1993), a concept that goes beyond the classical structural definition of connectivity (i.e., degree to which landscape elements are physically linked to each other). 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). Functional connectivity varies among species, as it is influenced by factors such as vagility, tolerance to stress, perception of risk and susceptibility to competition and predation.

Translocation experiments have been used extensively to improve our understanding of how behavioral processes influence movements of animals (Stanley 1998; Bélisle, Desrochers, & Fortin 2001; Gobeil & Villard 2002; Bowman & Fahrig 2002; Mazerolle & Desrochers 2005; Bakker 2006; Gillies & St Clair 2008; Kennedy & Marra 2010; Ibarra-Macias, Robinson, & Gaines 2011; Smith *et al.* 2011; Lawes *et al.* 2013; Vergara *et al.* 2013). These experiments involve capturing individuals and releasing them, across gradients in habitat loss and/or fragmentation. Parameters such as homing (return) time and probability of successful return (Gillies & St Clair 2008; Kennedy & Marra 2010; Smith *et al.* 2011; Lawes *et al.* 2013) or total distance travelled (Hadley & 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 non-experimental 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 as they allow researchers to 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, Desrochers, & Fortin 2001; Gobeil & Villard 2002). Translocation experiments have revealed evidence for the importance of matrix type in facilitating movement (Castellón & Sieving 2006; Kennedy & 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 travelling (Hadley & Betts 2009; Gillies, Beyer, & St Clair 2011; Ibarra-Macias, Robinson, & Gaines 2011).

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. However, 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 & Betts 2012). These concerns are relevant to studies using translocation as a proxy for understanding functional connectivity during dispersal (Bélisle & Desrochers 2002), as well as those examining the daily movements (Wilson, Marsh, & Winter 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 it could be in two possible directions: A) the novel environmental context could result in greater wariness of the new surroundings ('neophobia' Greenberg & Mettke-hofmann 2001); or B) high motivation to return to capture locations would override cautious behavior that would usually result in avoidance of particular areas. Here, I compare the movement behavior of green hermit hummingbirds (*Phaethornis guy*) within their normal home range boundaries to that of experimentally translocated individuals. For simplicity, I refer to movements of non-translocated, radio-tracked birds as '*routine movements'* (Van Dyck & Baguette 2005). I refer to movements of birds displaced from their home territories and radio-tracked as they returned home as '*translocation movements'*.

I tested for habitat selection differences between translocation treatments and routine daily movement at two spatial scales: 1) individual point locations and 2) movement paths. I also compared movement rates between translocation and routine movements. I expected that if behavior during translocations is affected by neophobia, translocated birds should show (a) stronger preference for forested areas, (b) greater avoidance of open areas when moving and (c) slower movement rates. If the motivation to return overrides cautious behavior, I expected to see that during translocations (a) a reduced affinity for forested areas, (b) increased likelihood of using open areas when moving, (c) faster movement rates. If translocations experiments did not affect behavior**,** I expected to detect no difference between translocation and routine movements.

Materials and methods

Study site

The study was conducted in a 20,600 ha area surrounding the Las Cruces Biological Station, Costa Rica (8º 47’ N, 82º57’ 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 & Betts 2009).

Focal species

The green hermit is a forest interior species which inhabits tropical forests from Costa Rica to western Colombia and southeastern Peru (Stiles & Skutch 1989). Green hermits do not maintain defended territories but instead exhibit ‘traplining’ behavior in which they move over relatively long distances to feed from isolated nectar-rich flowers (particularly *Heliconia sp.*) (Stiles 1975). This propensity for long-distance daily movements, 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).

I captured green hermits with mist-nets set near food sources (mainly *Heliconia* sp.) and with traps containing a hummingbird feeder. Each bird was fitted with radio-telemetry units (<0.25 g, Blackburn Transmitters), 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 (Hadley & Betts unpublished data); I 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

Green hermits were radio-tracked by Adam Hadley during January – March, 2008 and by me during March – May, 2012. In both years location points were obtained by following the birds as closely as possible on foot using radio receivers and handheld Yagi antennae. Based on trials with known transmitter distances, I 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 when I could detect the signal using the attenuator.

In 2008, Hadley 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 & Betts 2009). Translocation experiments consisted of transporting and releasing individuals at distances ranging from 340-1500 m from their capture point and then tracking them on their return to capture locations. Bird locations were recorded 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 (mean = 7 locations/ individual +/- 2.3). Routine movement data were recorded by following individual birds (n = 13) continuously for tracking periods that lasted up to 1 hour and 40 minutes per day (mean = 5 days / individual), gathering a total of 152 individual location points (mean = 11.7 locations/ individual +/- 5.2).

In 2012, I captured an additional 20 individuals 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 (Volpe *et al.* unpublished data). I followed individual birds continuously during tracking periods that lasted from 3 – 8 hours per day (mean = 4 days / individual), gathering a total of 1565 individual location points (mean = 78.25 locations/ individual +/- 38.4). At each point, observers recorded spatial coordinates of the observer (using a Global Positioning System [GPS] device), coordinates of bird (when visually detected), estimated distance from observer to bird (based on the reading of the receiver), azimuth (of the direction in which the signal was strongest), the time, and the type of landscape structure (forest patch or matrix). The UTM coordinates of the birds were calculated *a posteriori* based on the estimated observer-bird distance and the azimuth of the hummingbird location (Appendix B).

Land cover information

I 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. I delineated land cover on this raster image using ArcGIS 10.1 (ESRI 2012) as forest or agricultural matrix. Forest cover in in this region has remained relatively constant (forest cover change between 2005 and 2010 <0.3%) since 2005 (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, I compared observed locations to those I deemed available. I 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, McDonald, &

Thomas 2002). Buffers also account for the fact that animals select mosaics of habitat rather than particular points in space (Rettie & McLoughlin 1999). Available was defined as the proportion of forest within a 500 m buffer around each recorded point. This distance is based on observations that green hermits have the capacity to fly at least 500 m in 40 seconds, presumably without stopping (Volpe *et al.* unpublished data).

I used ArcGIS10.1 to generate the buffers and to calculate forest percentages (Appendix B). To prevent giving excessive weights to location points with multiple records, I did not use records separated by <1 m. The final dataset contained 1799 routine movement points (2012: 1349, 2008: 120, *N* = 33 individuals) and 131 translocation points (*N* = 19 individuals).

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

$$Difference = Total\ Forest * Translocation$$

where 'Difference' corresponds to the difference between observed and available percentage of forest. The use of this variable allowed me to pair observed and available locations and to also test for the effect of translocation experiments on habitat selection in the same model. I included an interaction term in order to assess if the birds responded differently to the translocation treatment depending on the type of landscape they were in. In 2012, sample sites had lower forest amounts at the landscape scale than in 2008. I therefore calculated the percentage of forest (hereafter 'total forest') available inside a single 500 m buffer surrounding all the recorded points for each bird and included this in my statistical models as a covariate to avoid bias (Appendix G). To account for spatial autocorrelation in the residuals, the model included a rational quadratic autocorrelation structure (Zuur *et al.* 2009). I included 'individual' as a random effect to account for potential lack of independence within points selected by each bird (Appendix I).

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, Beyer, & St Clair 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 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, I generated random draws from the frequency distribution of the observed step lengths and turning angles. The random steps associated to 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.ssfsamples" from the program Geospatial Modeling Environment (GME). I wrote a Python script (which incorporated ArcGIS10.1 functions) to obtain the distribution of step lengths and rotation angles, as well as to extract the information associated with each step (Appendix B). Following Gillies *et al.* (2011) I 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 meters) but close enough in time to not be completely unrelated (15 minutes). 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, I only used those that ended in forest habitat, as observed steps ending in open land were rare (~1%).

I 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 chosing a particular movement step instead of an alternative available one. I followed a similar strategy to Gillies *et al.* 2011 to identify the best model. First, I identified four 'exposure variables', i.e., variables that influence the level of exposure of the individuals to unfavorable conditions (increased predation rate, suboptimal 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 (Appendix G) so I built competing candidate models to decide which of them should be kept in the final model. I also included a variable I expected to facilitate movement – distance to the nearest stream – because 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. I had no a priori reason to expect interactions among these two variables, so I did not include interaction terms in the models. I compared models using Akaike's Information Criterion corrected for small sample size (AICc). All 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 choice decisions (Gillies *et al*. 2006, 2011). In order to test for these potential correlates of selection decisions of individual birds, I ran a linear regression of the individual selection coefficients as a function of broad-scale landscape measures (overall forest availability) and individual-specific characteristics (sex). Finally, I 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. I 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). I therefore tested whether the average movement rates during translocations differed from non-experimental individuals by applying the linear mixed effects model:

$$\log Speed = Time\ Interval + Translocation * Step\ Forest$$

“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 ($\beta = -0.82$, CI 95%: -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 which I was not able to detect, leading to an underestimation of distance travelled and associated speed. Regardless, this does not constitute a bias in my study because the same effect occurred for both translocated and non-translocated birds. I 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 versus non-translocated birds differently.

I 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, I could not average all the values per bird but rather had to include all the individual points in the model. I restricted the data points to those that were separated by 20 minutes or less, in order to diminish the effect that long time intervals had on overall speed (Appendix G). This restriction reduced the sample size for this analysis to 1244 points (29 birds) for routine movement 2012, 83 points (18 birds) for translocations. I eliminated 50 points from the 2008 dataset due to lack of information on the time when they were recorded (translocations = 11, routine movement = 39). The final model included 'Date' nested within 'Individual' as a random effect (Appendix I).

Model Selection and Spatial Autocorrelation

In all analyses I performed mixed effect models to account for the lack of independence between points belonging to the same bird. To do the analyses that required working with consecutive points (speed, path selection) I subset the routine movement data so that the time intervals between locations measured for each bird were similar in the 2008 and 2012 data (Appendix H).

To identify top-ranked models in linear regressions, I followed the top-down approach proposed by Zuur *et al.* 2009, which has three stages: 1) identify the optimal error structure (using AICc); 2) identify the optimal fixed effect structure for the given random effect structure (using likelihood ratio tests); 3) check model assumptions (heterogeneity, normality and independence of residuals). I used Restricted Maximum Likelihood Estimation (REML) as the likelihood estimator of the models, as it is considered to be a less biased estimator (Zuur *et al.* 2009). Maximum Likelihood was only used for the comparison of alternative models that had different fixed effects, but the final numerical output was always generated using REML. The linear mixed effects models were run using the R package nlme. I generated correlograms (R package ncf) of the models' residuals to check for spatial autocorrelation. In cases where I detected spatial autocorrelation (Moran's I values >0.1), I accounted for it using model error structures that reflected these dependencies (Appendix I). Before combining the routine movement data from 2008 and 2012, I tested for differences in movement patterns between years. The inter-annual difference (2008 versus 2012) in the amount of forest cover in 'used' locations was small and not statistically significant (-4.07%, CI 95%: -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 (CI 95%: 0.01 to 0.6, P = 0.045). The very minor differences in habitat selection behavior enabled me 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 to either true differences in movement behavior, or to differences attributable to year of sampling.

Results

Point-level habitat selection

Green hermits used areas with higher proportions of mature tropical forest than were available. This habitat selection behavior was consistent between translocation and routine movement studies (Fig. 3.1) after controlling for forest amount at the landscape scale (translocated $\overline{x}$ = 29.08% more forest than available, routine movements $\overline{x}$ = 29.09%, t = 0.09, P = 0.93). Confidence intervals around the difference (0.01%) in mean forest selected were small (+/- 4.4%) and likely to exclude a biologically meaningful effect. There was no evidence of an interaction between translocation treatment and landscape context (β = 0.003, CI95%: -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 drecreasing exposure (i.e., forest amount, proportion of step in forest) had clear positive effects on the likelihood of choosing a given path, while those variables that increased exposure (i.e., number of gaps and total gap length) had negative effects (Table 3.1). 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. 3.2). All candidate models showed variability at the individual bird level in the selection coefficients for all 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).

None of the bird-specific variables (i.e., sex, total forest available and tranlsocation 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 females. I found support for a weak interaction between forest amount and sex; males' avoidance for large gaps was amplified as the overall forest amount increased (Table 3.2). I did not detect a difference between translocated and non-experimental birds in their selection coefficients for either of the top-ranked variables (Table 3.2). The multiplicative effect of the translocation treatment on the selection coefficient for total gap length was 1.00 (CI 95%: 0.99 to 1.01) and for distance to stream was 0.993 (CI 95%: 0.993 to 1.01). 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

I detected significantly faster rates of movement for green hermits when homing during a translocation experiment than during routine movements (Fig. 3.3); the median speed for translocation studies at a given time interval was 4.48 times faster than for routine movements (CI 95%: 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 one percent of forest amount was associated to a decrease in the median speed by a factor of

0.986 (CI 95%: 0.983-0.989, P <0.001). I detected no evidence of interaction between translocation treatment and forest amount (likelihood ratio test, L = 3.5, df = 8, P = 0.06).

Discussion

Translocations versus routine movements

My 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, I demonstrate that i) point-level habitat selection was consistent between translocation and routine treatments, ii) path-level analyses showed avoidance of similar features between treatments (e.g., forest gaps), iii) translocations did not appear to result in neophobia and iv) decreasing movement rates as a function of mature forest occurred to a similar degree between treatments.

Despite the congruencies I 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, the primary objective in translocation studies was to approximate functional connectivity for adult green hermits during their daily movements as pollinators (Hadley & 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 & Villard 2002). Dispersal behavior could differ fundamentally from daily foraging movements in the vagility of individuals, level of motivation to move and the degree of risk-taking behavior. For instance, dispersing individuals might be less motivated to cross inhospitable areas than translocated individuals, as the latter have the incentive to return to an area where they have already invested in reproduction (Gillies & St Clair 2010). However, it is interesting to note that >50% of individuals in Hadley's 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 which approximates the new conditions encountered during natal dispersal. Further, my results show that translocated birds do not use open areas with greater frequency than routinely moving birds; if translocations increase motivation to cross open areas in a substantial way, then I 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, I 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, I 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, and (2) reduced movement rates, reflecting wariness about the new environment or stress from handling. However, I found support for neither of these trends. On the contrary, I observed an increased movement rate in translocated birds that could indicate a reduced wariness of the surroundings due to a strong motivation to return home. So, though I observed no differential use of forest at point or path levels for translocated versus non-translocated birds, higher speeds during homing indicate that for this metric at least, translocations represent a liberal measure of movement capacity.

Hummingbird habitat selection behavior

My 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, while at the path-level they avoided movement steps that required crossing open areas. In addition, hummingbirds exhibited strong selection for steps with large forest amounts. These results are all consistent with previous 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 & Betts 2009). This effect sheds light on an important mechanism for pollen limitation in isolated tropical forest fragments (Hadley *et al.* 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.

I 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 (Betts & 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 (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, Robinson, & Gaines 2011), or directly by analyzing the homing patterns of radio-tracked individuals (Gillies & St Clair 2008).

I 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 raging from cougars (Dickson, Jenness, & Beier 2005) to crickets (Berggren, Birath, & Kindvall 2002).

Limitations and future directions

A large portion of the passive data collection took place in different years (20 out of 33 passive treatments were done in 2012), which might have introduced confounding factors to the analyses. I consider that this strengthens my conclusion of no-difference in the selection patterns of translocated and non-translocated birds, since these results were found despite potential presence of factors that could affect the birds' behavior between years. Movement rates did differ between passive and translocated birds, but I have no reason to think that this is a year-related factor. The observed difference in movement rates of natural movement studies carried during different years was too small (0.01 to 0.6 times slower in 2012) to be able to justify the large observed difference between natural and translocation movement rates (3.39 to 6.04 faster in translocations).

My results regarding selection for forested areas in this species are likely conservative. At the point level, the 30 m radius buffers are likely to be incorporating un-used habitat, making the contrast between what was considered used and what was considered available less marked. On the other hand, it is possible that the birds could move away from the point more than the 500 meters. Given the spatial autocorrelation of vegetation structure, it is more likely that habitat within the "available" buffers will have similar characteristics to the central (recorded) point, making the available habitat seem to be more alike the observed one than it really was. Both factors reduce the likelihood of detecting differences in observed versus available proportions of forest. Despite this, I was able to detect a strong selection for areas with high proportion of forest. The path-level selection results are also conservative; by using straight lines to represent movement steps I likely included in the analysis gap-crossing events that did not really take place, making the birds seem more likely to use open areas than they really were. Despite this potential bias, I still found that the green hermits used movement steps with shorter stretches of open areas than expected.

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 (Hadley & Betts 2009). 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, as potential differences in movement rates and homing success could be more pronounced.

In conclusion, my 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 where dispersal behavior is a central research question.

Tables

Table 3.1. Model coefficients, standard errors, odds ratios (OR) and AICc values for the candidate models used to predict observed hummingbird movement steps 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 AICc model is bold.

Model	Variable	Coefficient		SE	OR	AICc	ΔAICc
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

*P <0.05; **P <0.01; ***P <0.001

Table 3.2. Effect of sex, overall forest availability and translocation treatment on the selection coefficients for total gap length and distance to stream estimated from the 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 * Sex (male)	-0.0004	0.0002	0.046
Stream distance	Intercept	-0.016	0.002	<0.0001
	Translocation	-0.0006	0.003	0.856

Figures

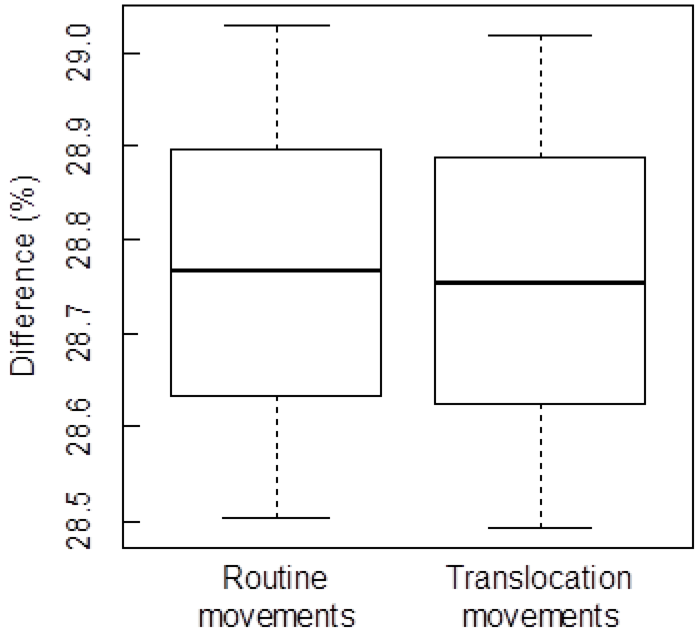

Figure 3.1. Predicted difference in the amount of forest inside observed and available buffers for translocated and non-translocated birds, after accounting for total forest in the area.

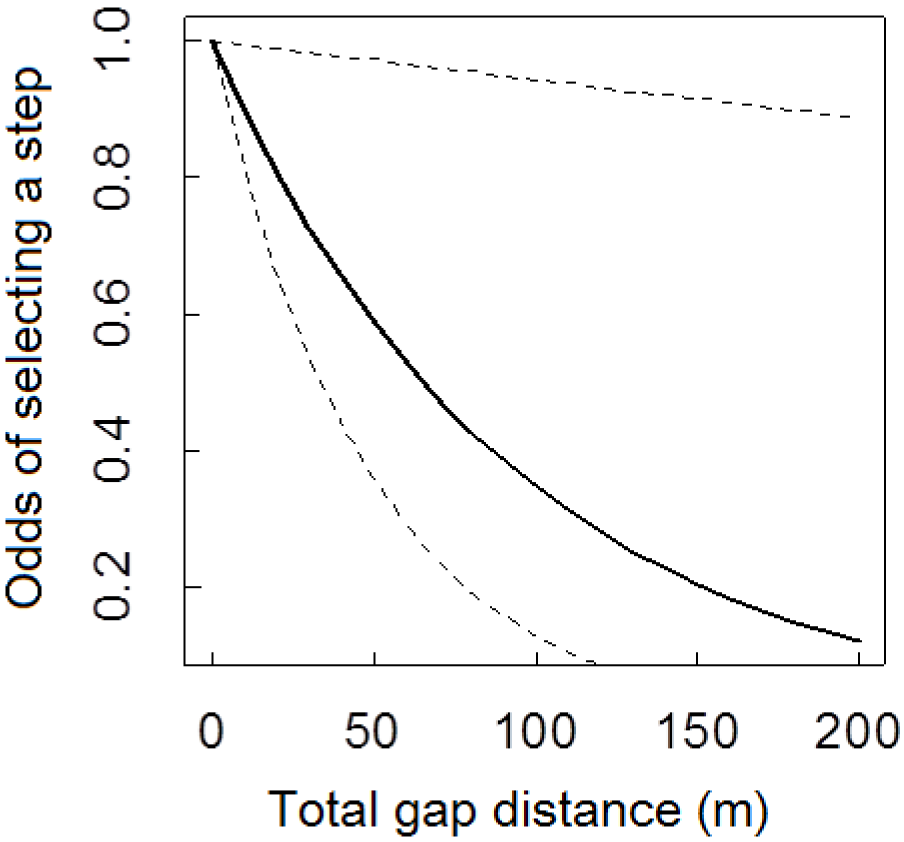

Figure 3.2. Effect of total gap distance on the odds of the green hermit hummingbird choosing a given step, as calculated from the top step selection function model provided in Table 3.1.

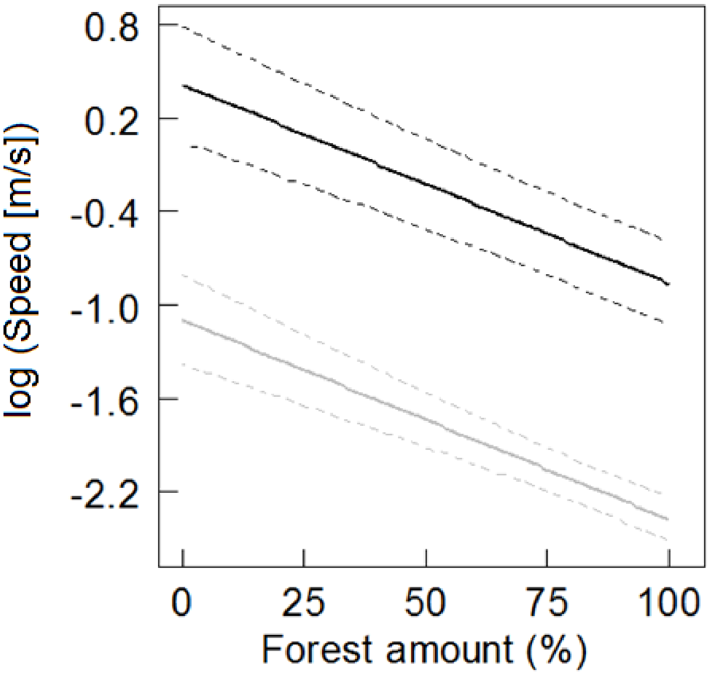

Figure 3.3. Predicted effect of forest amount on log speed after accounting for the time interval between consecutive points. The gray line represents the regression line for the routine movement data (β_0 = -1.1. CI 95%: -1.38 to -0.8 dashed lines-) and the black line represents the regression line for the translocation data (β_2 = 0.41, CI 95%: 0.045 to 0.78 -in dashed lines-). Fitted values were calculated using the mean time interval (4.89 min).

CHAPTER 4: CONCLUSIONS

I researched the relationships between landscape structure and space use by green hermits (*Phaethornis guy*) to understand the potential effects of habitat loss and fragmentation on pollination systems. Given that gene flow in flowering plants is mediated by the ability of pollinators to transport pollen between them, the role of changes in movement patterns by animals are likely to affect pollinator networks (Kremen *et al.* 2007; Hadley & Betts 2012).

I found that green hermits show a marked preference for locations with high forest amount and density of *Heliconia* plants. Green hermits are generalist pollinators, which visit up to 13 different plants species (Borgella *et al.* 2001). Yet, field observations and pollen data (Betts & Hadley, unpublished data) reveal that *Heliconia* plants are visited more often than other species. My analyses showed that only the abundance of *Heliconia*, but not of other flowering plants, could predict the presence of green hermits at a point. *Heliconia* plants, in particular *H. tortuosa*, could be thus acting as a 'magnet species'(Thomson 1978), i.e. a high rewarding species that increases local visitation by pollinators to the benefit of other low-rewarding plants species (Laverty 1992; Molina-Montenegro *et al.* 2008). If this is the case, a reduction of *Heliconia* density could have a broader effect in the ornithophilous plant community, as the diminished visitation rates would affect a broad suite of species (the network collapse hypothesis of Kaiser-Bunbury *et al.* 2010). In fragmented landscapes, such a reduction in *Heliconia* density might be caused by lower reproductive output in small forest patches. Hadley *et al.* (In Press) found evidence of a negative relationship between the seed set of *Heliconia tortuosa* plants and the size of the patches where they were growing. These observations are consistent with my findings of a negative association between fragmentation and how far a green hermit travels, with landscapes that have small mean patch size supporting smaller home ranges. In addition, the birds showed a tendency to avoid crossing open areas. Such restricted movements could increase the likelihood of transporting pollen from closely related plants (i.e., low quality pollen), which could be explaining the observed reduction in seed set (Aizen & Harder 2007).

My results point toward the importance of maintaining connectivity between patches to facilitate pollen flow (Haddad 2000; Townsend & Levey 2005). In particular, riparian corridors may be especially important as green hermits have shown a preference to move along streams. green hermits are generalist pollinators and are affected by landscape structure despite their high vagility and capability to enter open areas. That green hermits indicate some responses to fragmentation suggests that pollinators with higher forest affinity and reduced mobility may exhibit even stronger responses for forest fragmentation. If this is the case, the effect of forest fragmentation on the pollinator network might be larger than expected.

I also assessed, for the first time, the effectiveness of translocation experiments, a tool increasingly used to study effects of habitat fragmentation on animal movement. I found that behaviors documented during translocation experiments were similar to those observed during routine movements: both translocated and non-translocated birds showed similar levels of preference for mature tropical forest and avoided moving across non-forested matrix while selecting streams as movement corridors. Movement rates were generally higher during translocation experiments and were probably associated with a high motivation to return to the capture site. Yet, both studies yield the same results regarding the effect of forest cover on movement speed: birds moved faster across areas with low forest amount.

My results show that movement behavior of birds during translocation experiments is similar to natural movement behavior of birds. Therefore, translocation experiments may be reliable tools to address effects of landscape structure on animal movement. Similar comparative studies should be done on different taxa and with species expected to be more sensitive to landscape fragmentation. In particular, working with juveniles during the dispersal stage of their life cycle would be particularly useful, as predicting dispersal patterns through fragmented landscapes is one of the main uses of translocation experiments (Gobeil & Villard 2002; Castellón & Sieving 2006; Desrochers *et al.* 2011; Gillies *et al.* 2011).

Future research

Future research should expand on other members of the pollination network. Regarding the plant community, the hypothesis that *H. tortuosa* is acting as a ‘magnet species’ should be tested by 1) contrasting its nectar productivity with the other ornithophilous plants and 2) conducting manipulation experiments to reduce *H. tortuosa* density and measure changes in visitation rate to other flowers. Regarding the pollinator community, similar studies on the effect of landscape structure on movement patterns should be done on other hummingbird species, in particular with less vagile ones, to have a better understanding of how deforestation will affect pollen flow. In addition, incorporating more detailed information on matrix characteristics and resource availability in models would help identify characteristics that might improve connectivity across open areas. For such study, I recommend implementing translocation experiments, given they seem to produce accurate information on behavior and are less time and resource consuming than routine-movement studies. Finally, it would be interesting to see how fruit dispersers are being affected by landscape disturbance as well, in order to evaluate how fruit and pollen dispersal interact in the maintenance of genetic variability in *Heliconia*.

BIBLIOGRAPHY

Aben, J. & Adriaensen, F. (2012). Effects of matrix composition and configuration on forest bird movements in a fragmented Afromontane biodiversity hotspot. *Animal Conservation*, **15**, 658–668.

Aizen, M.A. & Harder, L.D. (2007). Expanding the Limits of the Pollen-Limitation Concept: Effects of Pollen Quantity and Quality. *Ecology*, **88**, 271–281.

Arnold, G.W., Steven, D.E., Weeldenburg, J.R. & Smith, E.A. (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.

Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mazer, S.J., Mitchell, R.J., Morgan, M.T. & Wilson, W.G. (2004). Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology*, **85**, 2408–2421.

Bakker, V.J. (2006). Microhabitat features influence the movements of red squirrels (Tamiasciurus hudsonicus) on unfamiliar ground. *Journal of Mammalogy*, **87**, 124–130.

Bascompte, J., Jordano, P. & Olesen, J.M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, **312**, 431–433.

Bélisle, M. (2005). Measuring Landscape Connectivity: The Challenge of Behavioral Landscape Ecology. *Ecology*, **86**, 1988–1995.

Bélisle, M. & Desrochers, A. (2002). Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology*, **17**, 219–231.

Bélisle, M., Desrochers, A. & Fortin, M.J. (2001). Influence of forest cover on the movements of forest birds: A homing experiment. *Ecology*, **82**, 1893–1904.

Bell, J.M., Karron, J.D. & Mitchell, R.J. (2005). Interspecific competition for pollination lowers seed production and outcrossing in Mimulus ringens. *Ecology*, **86**, 762–771.

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., Birath, B. & Kindvall, O. (2002). Efecto de los Corredores y los Bordes del Hábitat Sobre la Conducta de Dispersión, las Tasas de Movimiento y los Ángulos de Movimiento del Grillo de Arbusto de Roesel (Metrioptera roeseli). *Conservation Biology*, **16**, 1562–1569.

Betts, M.G., Forbes, G.J., Diamond, A.W. & Taylor, P.D. (2006). Independent Effects Of Fragmentation On Forest Songbirds: An Organism-Based Approach. *Ecological Applications*, **16**, 1076–1089.

Beyer, H.L. (2012). *Geospatial Modelling Environment*. Retrieved from http://www.spatialecology.com/gme.

Borgella, R., Snow, A.A. & Gavin, T.A. (2001). Species richness and pollen loads of hummingbirds using forest fragments in southern Costa Rica. *Biotropica*, **33**, 90–109.

Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. & Coulson, T. (2006). Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75**, 1393–1405.

Boscolo, D., Candia-Gallardo, C., Awade, M. & Metzger, J.P. (2008). Importance of Interhabitat Gaps and Stepping-Stones for Lesser Woodcreepers (Xiphorhynchus fuscus) in the Atlantic Forest, Brazil. *Biotropica*, **40**, 273–276.

Bosschieter, L., Goedhart, P.W., Foppen, R.P.B. & Vos, C.C. (2010). Modelling small-scale dispersal of the Great Reed Warbler Acrocephalus arundinaceus in a fragmented landscape. *Ardea*, **98**, 383–394.

Bowman, J. & Fahrig, L. (2002). Gap crossing by chipmunks: an experimental test of landscape connectivity. *Canadian Journal of Zoology*, **80**, 1556–1561.

Brosi, B.J. & Briggs, H.M. (2013). Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 13044–13048.

Brown, B.J. & Mitchell, R.J. (2001). Competition for pollination: effects of pollen of an invasive plant on seed set of a native congener. *Oecologia*, **129**, 43–49.

Castellón, T.D. & Sieving, K.E. (2006). An Experimental Test of Matrix Permeability and Corridor Use by an Endemic Understory Bird. *Conservation Biology*, **20**, 135–145.

Collinge, S.K. (1996). Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. *Landscape and Urban Planning*, **36**, 59–77.

Collinge, S.K. (2009). *Ecology of Fragmented Landscapes*. Johns Hopkins University Press.

Côrtes, M.C., Uriarte, M., Lemes, M.R., Gribel, R., John Kress, W., Smouse, P.E. & Bruna, E.M. (2013). Low plant density enhances gene dispersal in the Amazonian understory herb Heliconia acuminata. *Molecular Ecology*, **22**, 5716–5729.

Cranmer, L., McCollin, D. & Ollerton, J. (2012). Landscape structure influences pollinator movements and directly affects plant reproductive success. *Oikos*, **121**, 562–568.

Desrochers, A., Bélisle, M., Morand-Ferron, J. & Bourque, J. (2011). Integrating GIS and homing experiments to study avian movement costs. *Landscape Ecology*, **26**, 47–58.

Desrochers, A., Renaud, C., Hochachka, W.M. & Cadman, M. (2010). Area-sensitivity by forest songbirds: theoretical and practical implications of scale-dependency. *Ecography*, **33**, 921–931.

Dickson, B.G., Jenness, J.S. & Beier, P. (2005). Influence of Vegetation, Topography, and Roads on Cougar Movement in Southern California. *The Journal of Wildlife Management*, **69**, 264–276.

Diekoetter, T., Haynes, K.J., Mazeffa, D. & Crist, T.O. (2007). Direct and indirect effects of habitat area and matrix composition on species interactions among flower-visiting insects. *Oikos*, **116**, 1588–1598.

Duchesne, T., Fortin, D. & Courbin, N. (2010). Mixed conditional logistic regression for habitat selection studies. *The Journal of animal ecology*, **79**, 548–555.

Van Dyck, H. & Baguette, M. (2005). Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology*, **6**, 535–545.

Environmental Systems Research Institute, Inc. (ESRI). (2012). *ArcGIS Desktop: Release 10.1*. Redlands, California.

Everaars, J., Strohbach, M.W., Gruber, B. & Dormann, C.F. (2011). Microsite conditions dominate habitat selection of the red mason bee (Osmia bicornis, Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany. *Landscape and Urban Planning*, **103**, 15–23.

Fahrig, L. (2003). Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.

Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, **40**, 1649–1663.

Farwig, N., Bailey, D., Bochud, E., Herrmann, J.D., Kindler, E., Reusser, N., Schueepp, C. & Schmidt-Entling, M.H. (2009). Isolation from forest reduces pollination, seed predation and insect scavenging in Swiss farmland. *Landscape Ecology*, **24**, 919–927.

Fieberg, J. & Börger, L. (2012). Could you please phrase ‘home range’ as a question? *Journal of Mammalogy*, **93**, 890–902.

Fischer, J.W., Walter, W.D. & Avery, M.L. (2013). Brownian Bridge Movement Models to Characterize Birds’ Home Ranges. *The Condor*, **115**, 298–305.

Fondo Nacional de Financiamiento Forestal (FONAFIFO). (2012). *Estudio de cobertura forestal de Costa Rica 2009 - 2010*. Ministerio de Ambiente, Energía y Telecomunicaciones, San José, Costa Rica.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**, 1320–1330.

Van Geert, A., Van Rossum, F. & Triest, L. (2010). Do linear landscape elements in farmland act as biological corridors for pollen dispersal? *Journal of Ecology*, **98**, 178–187.

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C.C. (2007). LoCoH: Nonparameteric Kernel Methods for Constructing Home Ranges and Utilization Distributions. *PLoS ONE*, **2**, e207.

Ghazoul, J. (2005). *Implications of plant spatial distribution for pollination and seed production.* Cambridge University Press.

Gilbert-Norton, L., Wilson, R., Stevens, J.R. & Beard, K.H. (2010). A Meta-Analytic Review of Corridor Effectiveness. *Conservation Biology*, **24**, 660–668.

Gillies, C.S., Beyer, H.L. & St Clair, C.C. (2011). Fine-scale movement decisions of tropical forest birds in a fragmented landscape. *Ecological Applications*, **21**, 944–954.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E. & Jerde, C.L. (2006). Application of Random Effects to the Study of Resource Selection by Animals. *Journal of Animal Ecology*, **75**, 887–898.

Gillies, C.S. & St Clair, C.C. (2010). Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology*, **47**, 182–190.

Gillies, C.S. & St Clair, C.C. (2008). Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences*, **105**, 19774–19779.

Gobeil, J.-F. & Villard, M.-A. (2002). Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos*, **98**, 447.

Graham, C.H. (2001). Factors Influencing Movement Patterns of Keel-Billed Toucans in a Fragmented Tropical Landscape in Southern Mexico. *Conservation Biology*, **15**, 1789–1798.

Greenberg, R. & Mettke-hofmann, C. (2001). Ecological Aspects of Neophobia and Neophilia in Birds. *Current Ornithology* (eds V.N. Jr & C.F. Thompson), pp. 119–178. Current Ornithology. Springer US.

Haddad, N. (2000). Corridor Length and Patch Colonization by a Butterfly, Junonia coenia. *Conservation Biology*, **14**, 738–745.

Haddad, N.M. (2008). Finding the corridor more traveled. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 19569–19570.

Hadley, A.S. & Betts, M.G. (2012). The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews*, **87**, 526–544.

Hadley, A.S. & Betts, M.G. (2009). Tropical deforestation alters hummingbird movement patterns. *Biology Letters*, **5**, 207–210.

Hadley, A.S., Frey Hadley, S., Robinson, W.D., Kress, W.J. & Betts, M.G. (In Press). Tropical forest fragmentation limits pollination of a keystone understory herb. *Ecology*.

Hansteen, T.L., Andreassen, H.P. & Ims, R.A. (1997). Effects of spatiotemporal scale on autocorrelation and home range estimators. *Journal of Wildlife Management*, **61**, 280–290.

Heinrich, B. & Raven, P. (1972). Energetics and Pollination Ecology. *Science*, **176**, 597–&.

Herrera, C.M. (1995). Microclimate and Individual Variation in Pollinators: Flowering Plants are More than Their Flowers. *Ecology*, **76**, 1516–1524.

Hole, A.R. (2007). Fitting mixed logit models by using maximum simulated likelihood. *Stata Journal*, **7**, 388–401.

Horne, J.S., Garton, E.O., Krone, S.M. & Lewis, J.S. (2007). Analyzing Animal Movements Using Brownian Bridges. *Ecology*, **88**, 2354–2363.

Huck, M., Davison, J. & Roper, T.J. (2008). Comparison of two sampling protocols and four home-range estimators using radio-tracking data from urban badgers Meles meles. *Wildlife Biology*, **14**, 467–477.

Husband, B.C. & Schemske, D.W. (1996). Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution*, **50**, 54+.

Ibarra-Macias, A., Robinson, W.D. & Gaines, M.S. (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.

Jennings, S.B., Brown, N.D. & Sheil, D. (1999). Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. *Forestry*, **72**, 59–74.

Johnson, D.H. (1980). The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. *Ecology*, **61**, 65–71.

Johnson, S. & Bond, W. (1992). Habitat Dependent Pollination Success in a Cape Orchid. *Oecologia*, **91**, 455–456.

Jones, J. (2001). Habitat selection studies in avian ecology: A critical review. *Auk*, **118**, 557–562.

Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters*, **13**, 442–452.

Kennedy, C.M. & Marra, P.P. (2010). Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations. *Biological Conservation*, **143**, 2136–2145.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mitchell, R.J. & Ashman, T.-L. (2005). Pollen Limitation of Plant Reproduction: Pattern and Process. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 467–497.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J. & Ricketts, T.H. (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology letters*, **10**, 299–314.

Kucharcik, S. & Collins, S. (2001). Effects of Vegetative Factors on the Winter Distribution of Color Phases of the Eastern Screech Owl, Otus Asio, in Central Pennsylvania. *Journal of Eological Research*, **3**, 27–31.

Lander, T.A., Boshier, D.H. & Harris, S.A. (2010). Fragmented but not isolated: Contribution of single trees, small patches and long-distance pollen flow to genetic connectivity for Gomortega keule, an endangered Chilean tree. *Biological Conservation*, **143**, 2583–2590.

Laver, P.N. & Kelly, M.J. (2008). A critical review of home range studies. *Journal of Wildlife Management*, **72**, 290–298.

Laverty, T. (1992). Plant Interactions for Pollinator Visits - a Test of the Magnet Species Effect. *Oecologia*, **89**, 502–508.

Law, B.S. & Lean, M. (1999). Common blossom bats (Syconycteris australis) as pollinators in fragmented Australian tropical rainforest. *Biological Conservation*, **91**, 201–212. Retrieved December 4, 2013,

Lawes, T.J., Anthony, R.G., Robinson, W.D., Forbes, J.T. & Lorton, G.A. (2013). Movements and settlement site selection of pygmy rabbits after experimental translocation. *The Journal of Wildlife Management*, **77**, 1170–1181.

Lichti, N.I. & Swihart, R.K. (2011). Estimating utilization distributions with kernel versus local convex hull methods. *The Journal of Wildlife Management*, **75**, 413–422.

Lima, S.L. & Zollner, P.A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution*, **11**, 131–135.

Lindenmayer, D.B. & Fischer, J. (2006). *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis*. Island Press.

Lloyd, H. & Marsden, S.J. (2011). Between-Patch Bird Movements within a High-Andean *Polylepis* Woodland/Matrix Landscape: Implications for Habitat Restoration. *Restoration Ecology*, **19**, 74–82.

Manly, B.F.J., McDonald, L. & Thomas, D.L. (2002). *Resource selection by animals statistical design and analysis for field studies*. Kluwer Academic, Dordrecht; Boston.

Mazerolle, M.J. & Desrochers, A. (2005). Landscape resistance to frog movements. *Canadian Journal of Zoology*, **83**, 455–464.

Memmott, J., Waser, N.M. & Price, M.V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 2605–2611.

Molina-Montenegro, M.A., Badano, E.I. & Cavieres, L.A. (2008). Positive interactions among plant species for pollinator service: assessing the ‘magnet species’ concept with invasive species. *Oikos*, **117**, 1833–1839.

Moore, R.P., Robinson, W.D., Lovette, I.J. & Robinson, T.R. (2008). Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters*, **11**, 960–968.

Powell, R.A. & Mitchell, M.S. (2012). What is a home range? *Journal of Mammalogy*, **93**, 948–958.

Rettie, W.J. & McLoughlin, P.D. (1999). Overcoming radiotelemetry bias in habitat-selection studies. *Canadian Journal of Zoology*, **77**, 1175–1184.

Richards, C.M., Church, S. & McCauley, D.E. (1999). The Influence of Population Size and Isolation on Gene Flow by Pollen in Silene alba. *Evolution*, **53**, 63–73. Retrieved March 2, 2014,

Ricketts, T. (2001). The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, **158**, 87–99.

Van Rossum, F. & Triest, L. (2010). Pollen dispersal in an insect-pollinated wet meadow herb along an urban river. *Landscape and Urban Planning*, **95**, 201–208.

Smith, M.J., Betts, M.G., Forbes, G.J., Kehler, D.G., Bourgeois, M.C. & Flemming, S.P. (2011). Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landscape Ecology*, **26**, 709–721.

Smith, J.N.M. & Hellmann, J.J. (2002). Population persistence in fragmented landscapes. *Trends in Ecology & Evolution*, **17**, 397–399.

Snow, B. (1977). Comparison of Leks of Guys Hermit Hummingbird Phaethornis-Guy in Costa-Rica and Trinidad. *Ibis*, **119**, 211–214.

Snow, B. (1974). Lek Behavior and Breeding of Guys Hermit Hummingbird Phaethornis-Guy. *Ibis*, **116**, 278–297.

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.* StataCorp, College Station, TX, USA.

Stiles, F.G. (1975). Ecology, Flowering Phenology, and Hummingbird Pollination of Some Costa Rican Heliconia Species. *Ecology*, **56**, 285–301.

Stiles, F.G. & Skutch, A. (1989). *A Guide to the Birds of Costa Rica*. Cornell University Press, Ithaca, NY.

Stouffer, P.C. & Bierregaard, R.O. (1995). Effects of Forest Fragmentation on Understory Hummingbirds in Amazonian Brazil. *Conservation Biology*, **9**, 1085–1094.

Taki, H., Okabe, K., Yamaura, Y., Matsuura, T., Sueyoshi, M., Makino, S. & Maeto, K. (2010). Effects of landscape metrics on Apis and non-Apis pollinators and seed set in common buckwheat. *Basic and Applied Ecology*, **11**, 594–602.

Taylor, P., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity Is a Vital Element of Landscape Structure. *Oikos*, **68**, 571–573.

Taylor, P.D. & Merriam, G. (1995). Wing Morphology of a Forest Damselfly Is Related to Landscape Structure. *Oikos*, **73**, 43–48.

Tewksbury, J.J., Levey, D.J., Haddad, N.M., Sargent, S., Orrock, J.L., Weldon, A., Danielson, B.J., Brinkerhoff, J., Damschen, E.I. & Townsend, P. (2002). Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences*, **99**, 12923–12926.

Thompson, J.N. (2005). *The Geographic Mosaic of Coevolution*. University of Chicago Press.

Thomson, J.D. (1978). Effects of Stand Composition on Insect Visitation in Two-Species Mixtures of Hieracium. *American Midland Naturalist*, **100**, 431.

Townsend, P.A. & Levey, D.J. (2005). An Experimental Test of Whether Habitat Corridors Affect Pollen Transfer. *Ecology*, **86**, 466–475.

Trzcinski, M.K., Fahrig, L. & Merriam, G. (1999). Independent Effects of Forest Cover and Fragmentation on the Distribution of Forest Breeding Birds. *Ecological Applications*, **9**, 586–593.

Turner, M.G. (1989). Landscape Ecology: The Effect of Pattern on Process. *Annual Review of Ecology and Systematics*, **20**, 171–197.

Vergara, P.M., Pérez-Hernández, C.G., Hahn, I.J. & Jiménez, J.E. (2013). Matrix composition and corridor function for austral thrushes in a fragmented temperate forest. *Landscape Ecology*, **28**, 121–133.

Wikelski, M., Moxley, J., Eaton-Mordas, A., López-Uribe, M.M., Holland, R., Moskowitz, D., Roubik, D.W. & Kays, R. (2010). Large-Range Movements of Neotropical Orchid Bees Observed via Radio Telemetry. *PLoS ONE*, **5**, e10738.

Wilson, R.F., Marsh, H. & Winter, J. (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., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY, USA.

APPENDICES

Appendix A: Tools used to process data

Table A.1. List of tools used to obtain the data needed for the analyses.

Task	Tools	Platform
Obtain location points based on recorded observer-bird distance and azimuth	Bearing Distance to Line, Feature Vertices to Points	ArcGIS 10.1
Point Selection		
Generate 30 m diameter buffers around the points	Buffer	ArcGIS 10.1
Estimate percentage of forest inside buffers	Tabulate intersection	ArcGIS 10.1
Path Selection		
For each bird, generate frequency distribution of length and turning angles of the remaining birds	Pyhton script*	Wing IDE Pro 4.1
Generate random steps based on the length and turning angle distributions	movement.ssfsamples	GME**
Generate 30 m diameter buffers around the lines	Buffer	ArcGIS 10.1
Estimate percentage of forest inside buffers	addarea	GME
Divide each line into segments according to the type of habitat they are running through	intersect (analysis), multipart to single part, dissolve (data management)	ArcGIS 10.1

Estimate lengths of segments	addlength	GME
Use the segments to calculate the proportion of the step composed of open area or forest and number and length of gaps	Pyhton script	Wing IDE Pro 4.1
Estimate distance of end point to closest stream	Feature vertices to points, Near (analysis)	ArcGIS 10.1
Movement rate		
Calculate speed based on distance and time interval between points	Pyhton script	Wing IDE Pro 4.1

***** Python script = script written by N. Volpe

**GME = Geospatial Modeling Environment

Appendix B: Protocols for canopy cover measurements

The observer walked along two perpendicular 10-meter transects which crossed at the center of the plot. The direction of the first transect line was randomly selected. The direction of the second line was set at a right angle to the first. The observer stopped at 1m-intervals to look up through an ocular tube (20 observations per plot) and recorded a positive if the crosshairs of the ocular tube intersected with a vegetation structure (leaf, branch) and a negative otherwise. The percent of canopy cover is calculated as the number of positive hits over the total observations (per plot) multiplied by 100.

Appendix C: Selection of flowering plants to use in point-scale selection analysis

Table C1. Groups used to assess the importance of plants with different levels of affinity for the green hermit to predict the presence of birds at a given location.

Affinity	**Description**
High	Species from the family Heliconiaceae*
Medium	Species from other families used as food resources **
No	Species not observed to be used as food resources***

* *Heliconia danielsiana, H. latispatha, H. rostrata, H. tortuousa, H. wilsonii;*** Fam. Bromeliaceae: *Pitcairnia brittoniana*; Fam. Campanulaceae: *Burmeistera cyclostigmata, Centropogon granulosus*; Fam. Fabaceae: *Mucuna holtonii*, *Erynthrina costaricensis* (or *E. lanceolata), E. poeppigiana*; Fam. Gesneriaceae: *Columnea polyantha*, *Drymonia macrantha*, *D turrialvae*, *Glossoloma tetragonus*; Fam. Malvaceae: *Hibiscus* sp.; Fam. Musaceae: *Musa* sp.; Fam. Zingiberaceae: *Costus barbatus* (or *C. scaber)*, *Etlingera elatior*, *Zingiber spectabile*; Fam. Marantaceae: *Calathea guzmanioides* (an unidentified species from Fam. Acanthaceae was also included); ***These plants were included in order to account for the fact that some of the species might have been used by the green hermit even when we did not observe it.

Table C2. Effect of canopy cover and number of plants from the three affinity groups (high -H- , medium -M- or no -N-) on the likelihood of a green hermit using a given 20 m radius plot.

	Coefficient		SE
Intercept	-1.611	***	0.236
H	0.049	**	0.017
M	0.052		0.033
N	0.018		0.021
Canopy	0.021	***	0.003

*P <0.05; **P <0.01; ***P <0.001

Table C3. Effect of canopy cover and number of plants from two affinity groups (high -H- or medium -M-) on the likelihood of a green hermit using a given 20 m radius plot.

	Coefficient		SE
Intercept	-1.590	***	0.233
H	0.052	**	0.017
M	0.053		0.033
Canopy	0.021	***	0.003

*P <0.05; **P <0.01; ***P <0.001

Appendix D: Variability in flower detection

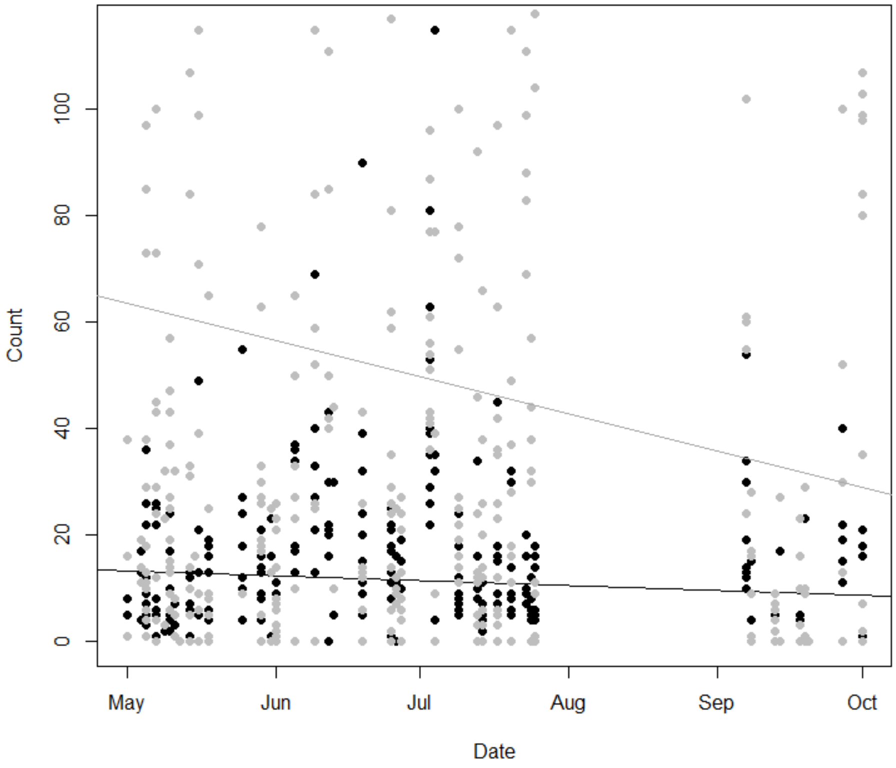

Figure D1. Relationship between number of detected plants (black) and inflorescences (gray) as a function of time.

Appendix E: Home range sensitivity analysis

Regularity of points

In order to asses if the observed shaped were being driven by multiple points taken in a short time period, I generated BBMM and LoCoH home range polygons using points that were separated by time intervals between 10-20 minutes. To generate the regular dataset, I was forced to reduce the total sample size from 1606 to 505 records, with a minimum of

9 and a maximum of 47 locations per bird. Thus, in order to assess the effect of regular data independently from sample size, I randomly subsampled my "irregular" dataset to reach the sample size of the regular data for each bird.

For LoCoH home ranges, the effect was small, being the average home range area for the regular dataset 1.50 ha (range 0.06- 6.00 ha) and for the irregular dataset 1.82 ha (range 0.12-7.07 ha). For BBMM home ranges, the effect was larger, with the mean home range area for the irregular dataset being almost three times larger than the mean for the regular dataset (15.64 ha vs 5.92 ha). Conclusions regarding forest use were identical for LoCoH polygons created using regular and irregular datasets (78%) and very similar for BBMM (69% regular, 63% irregular).

Yet, the differences in area might be an artifact of the randomly selected subset of records, as due to time constrains only one resampling of the irregular dataset could be made. This is supported by the fact that the size and shape of the reduced regular dataset closely resembled the values obtained using the complete irregular dataset, even when the sample size was much smaller. This consistency makes me confident that the home range estimates here presented are not being greatly affected by temporal sampling patterns.

Effect of missing data

I ran this analysis in order to assess how including location points where the birds were present but not detected would affect home range estimations. I used the low-certainty points taken from more than 30 m, not included in my main analysis, as proxies for missing data. In the BBMM calculations, I assigned location errors of 50 m to points recorded from a distance between 30 - 100 m, and 100 m to those recorded from a distance larger than 100 m.

The effect of incorporating the points with low level of certainty greatly affected home range estimations, leading to a two-fold increase in the mean home range size for both LoCoH and BMM estimators (LoCoH 2.18 ha vs 4.97 ha and BBMM 5.95 ha vs 10.80 ha). The mean percentage of forest inside the home range remained relatively stable for LoCoH estimators, with a reduction of 5% when using the complete dataset (77% vs 72%). In the case of BBMM polygons, the mean percentage of forest was much more affected, being reduced from 70% to 58%. This reduction was probably product of the fact that the low level of accuracy of the new points lead to broader estimates that incorporated un-used open areas. The results of this comparison reinforce the idea that the home range areas here presented are conservative estimates, and that real home ranges are most likely larger than reported.

Appendix F: Relationship between home range size and landscape structure

500 meters buffer

Two principal components had high explanatory power for describing home ranges according to the Kaiser criterion, accounting for 84% of the variation of the dataset (Table F1). The first principal component (PC1) was an indicator of forest availability in the landscape, being negatively associated to landscapes with large forest amount concentrated in spread large patches. The second principal component (PC2) was associated to landscapes with low variability in patch size. A correlation analysis showed that none of the components influenced home range size (PC1 $\beta_1 = 0.012$, $P = 0.94$; PC2 $\beta_2 = -0.011$, $P = 0.63$; Sex $\beta_3 = 0.84$, $P = 0.18$).

1500 meters buffer

Two principal components had high explanatory power for describing home ranges according to the Kaiser criterion, accounting for 86% of the variation of the dataset (Table F1). The first principal component (PC1) was an indicator of forest availability in the landscape, being negatively associated to landscapes with large forest amount concentrated in spread large patches. The second principal component (PC2) was an indicator of fragmentation, being associated to an increase in edge density and decrease in mean patch size. A correlation analysis showed that none of the components influenced home range size (PC1 $\beta_1 = 0.01$, $P = 0.90$; PC2 $\beta_2 = -0.074$, $P = 0.74$; Sex $\beta_3 = 0.75$, $P = 0.17$).

Table F1. Output of principal components analysis at three different scales. Only the significant (eigenvalues >1) components are shown. Component loadings >± 0.40 are in boldface type.

Scale	Home range		500		1500	
Principal component	PC1	PC2	PC1	PC2	PC1	PC2
Eigenvalue	2.81	1.83	3.83	1.34	3.89	1.29
% variance	46.9	30.56	63.87	22.38	64.86	21.56
Cum. % variance	46.9	77.47	63.87	86.25	64.86	86.42
Component loadings						
PLAND	**-0.52**	-0.25	**-0.49**	-0.22	**-0.49**	0.04
LPI	**-0.53**	-0.25	**-0.50**	-0.18	**-0.50**	-0.08
ED	0.42	0.05	0.31	-0.16	-0.13	**0.68**
AREA_MN	-0.33	**0.61**	-0.43	0.39	-0.33	**-0.61**
AREA_CV	0.37	0.10	0.09	**-0.84**	-0.35	0.40
GYRATE_AM	-0.18	**0.70**	**-0.48**	-0.19	**-0.50**	-0.03

Appendix G: Exploratory analysis for chapter 3

Point-level habitat selection

Boxplots of the difference between observed and available percentage of forest (Fig. G1) showed an apparent preference for forest in all of the studies, though the contrast between observed and available was more marked in 2012 than in 2008.

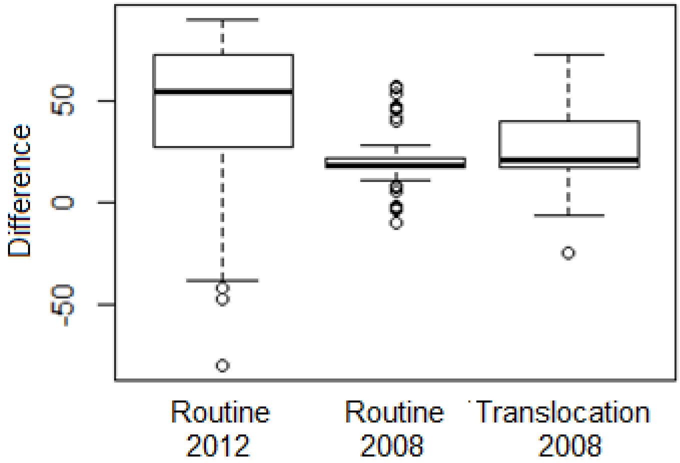

Figure G1. Difference in the percentage of forest inside observed and available buffers for each type of study.

I suspected that the difference could be related to the fact that in the 2012 field season many of the captures took place in highly fragmented areas, making it more likely for the available buffers to include non-forested land. 2008 studies were based in Las Cruces, so the forest availability was often large (Fig. G2.A). A plot of the mean observed difference per bird versus the total forest available for each of them confirmed a negative relationship between the two variables (Fig. G2.B).

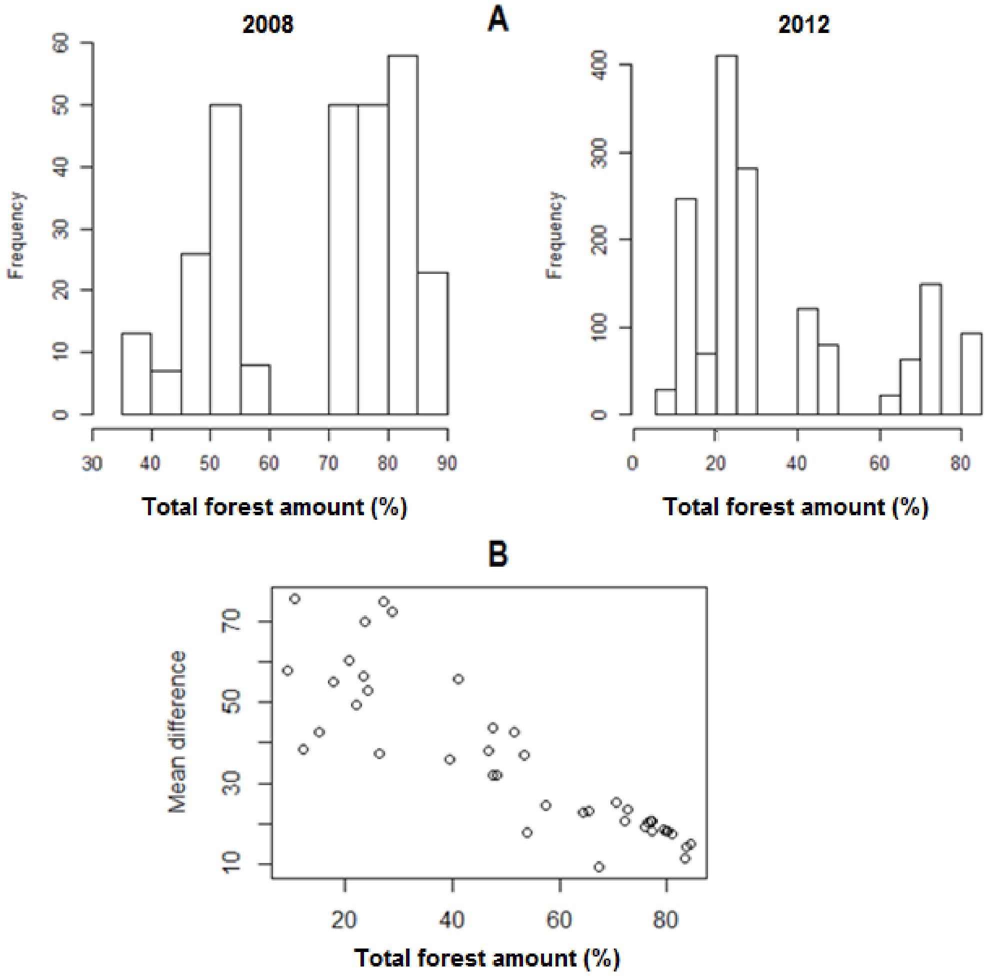

Figure G2. A) Distribution of total forest amount associated to each observed record in 2008 and 2012 studies; **B)** Effect of total forest amount on mean difference between observed and available forest within sampled buffers.

In order to account for these year-differences in overall forest availability, I included in the model the variable “total forest”, consisting of the percentage of forest available inside a single 500 m-buffered surrounding all the recorded points for each bird.

Path-level habitat selection

Table G1. Correlation matrix of variables used for the Step Selection Function analysis.

	Stream	**NumGap**	**PropInFor**	**ForAm**	**TotGap**
Stream	1				
NumGap	0.09	1			
PropInFor	-0.12	-0.77	1		
ForAm	-0.08	-0.78	0.90	1	
TotGap	0.16	0.58	-0.71	-0.66	1

Movement rate

To assess if speed values were influenced by the sampling process, I made a visual assessment of the relationship between speed and distance to observer (only for the 2012 routine movement study) and speed and time interval (routine movement and translocation studies). There did not seem to be an influence of estimated distance to observer on the recorded speed for the 2012 study (Fig. G3). This analysis could not be done on the data of 2008 because there was no information available on the distance from which each point was recorded.

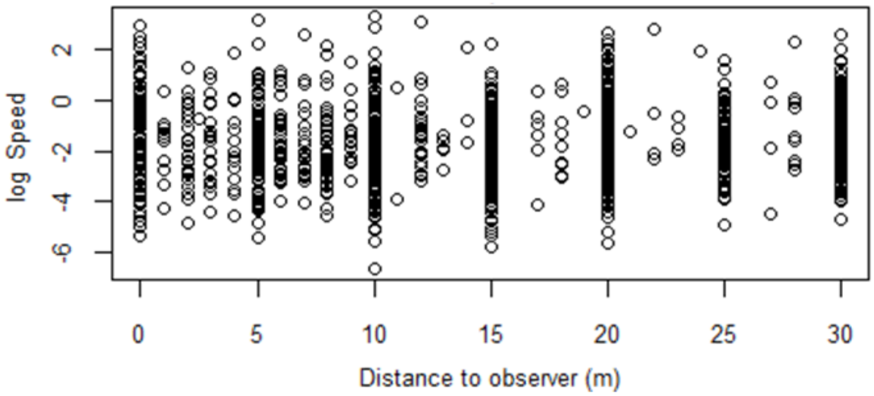

Figure G3. Relationship between estimated distance of bird to observer and log-Speed.

On the other hand, there was a significant effect of time interval between consecutive points on speed: the largest the time interval, the slowest the detected speed (Fig. G4). This relationship was the same for routine movement and translocation studies. Given the correlation between speed and time interval, I decided to include the latter as an independent variable in the model. In addition, I restricted my dataset to records separated by intervals equal or shorter than 20 minutes.

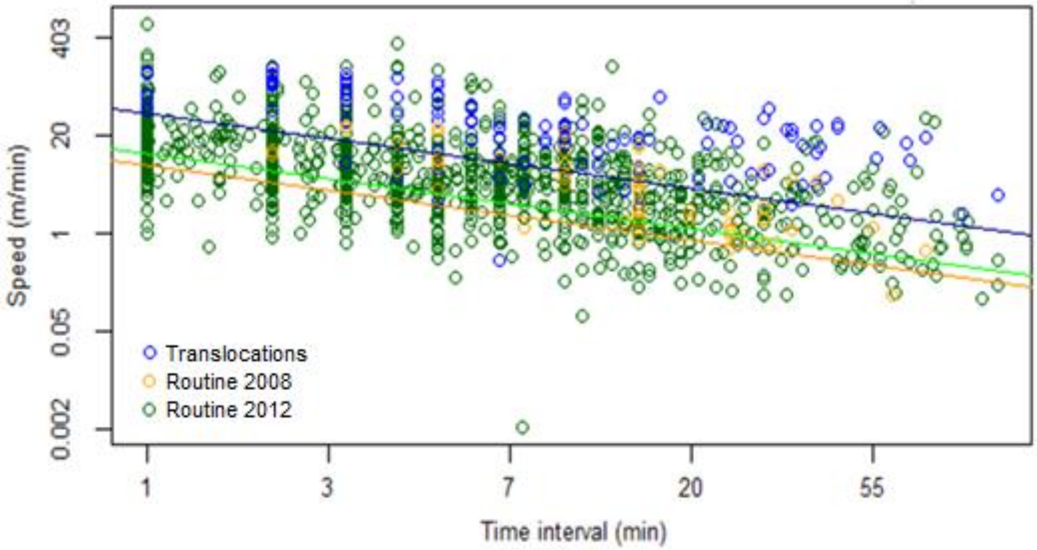

Figure G4. Relationship between log-transformed time interval and log-transformed speed. The values in the axis were back-transformed for easier interpretation. The regression lines were generated from the output of the top regression model.

In order to meet the linear relationship assumption of the model, I log-transformed both speed and time interval (Fig. G5).

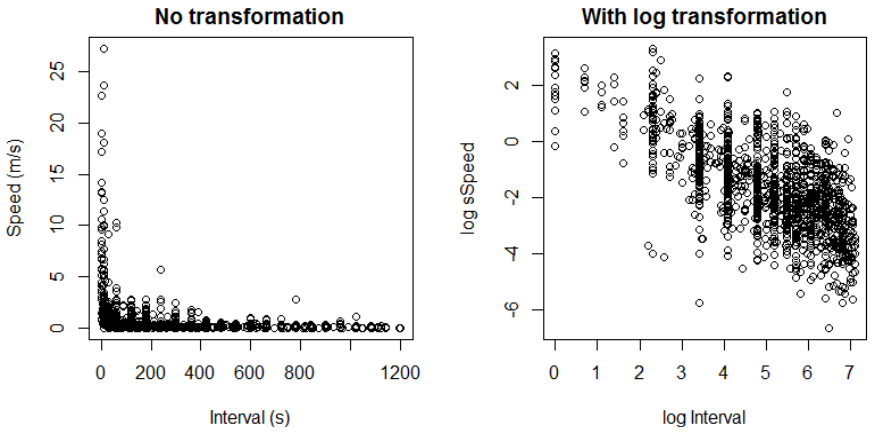

Figure G5. Relationship between speed and time interval with and without log-transformation.

Appendix H: Subsetting data for movement rate and path selection analyses

In order to make the time intervals between consecutive locations similar in the 2008 and 2012 data I used records that were: a) obtained within the same observation period and b) separated by similar time intervals. I defined “observation period” as an extent of time when a bird was followed continuously. “Continuous” was defined as taking place between two “lost events”, where a lost event refers to periods of time longer than 20 minutes during which there was either no signal or the bird was detected at distances greater than 200 m. I only used observation periods greater than 10 minutes (the minimum value in the 2008 dataset) to select the tracks used for the comparison. Both datasets show a similar pattern of time intervals between points, having mostly records separated by short time intervals and fewer records separated by long time intervals (Fig. H1). Depending on the analysis, my criteria to use different time intervals varied (explained in each section).

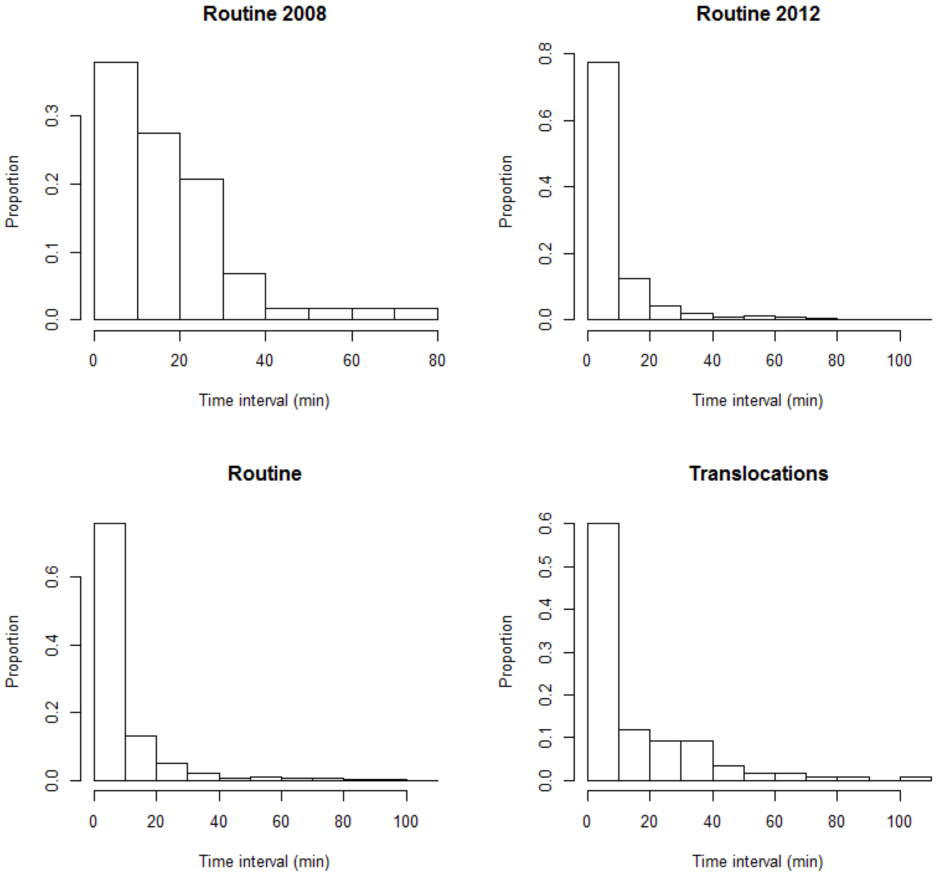

Figure H1. Distribution of the percentages in which each time interval was observed for each study.

Appendix I: Model selection

Point-level habitat selection

After comparing the results using standardized and non-standardized overall percent forest I decided to use the latter in the model, as the slope of the resulting models were almost identical but using non-standardized measurements allowed for an easier interpretation of the regression coefficients.

Model I.1: effect of year on habitat selection done during routine movement studies

$$Difference_{OBS-AVAIL} = Forest * Year|Bird$$

1) Identification of optimal error structure

Starting with a full model with both Forest and Year and their interactions as fixed terms, I tested different error structures which included: a) the use of individual bird or date nested inside individual bird as a random effect, b) allowing for differing variances each year and c) four types of spatial autocorrelation structures (spherical, gaussian, rational quadratic and exponential). The inclusion of the random effects aimed to account for the potential lack of independence between records corresponding to each individual and, within each bird, those that were taken on the same day. The decision to test if a variable variance improved the model intended to account for the differences in spread and sample size between the two categorical variables. The incorporation of a correlation structure aimed to eliminate spatial autocorrelation pattern observed in the first models I ran.

A comparison of the models' AICc showed that the best model was one that only included individual as a random effect, variable variances per year and a rational quadratic autocorrelation structure (Table I1).

Table I1. Comparison of different optimal error structures for the Year-effect model. In all the cases the fixed effects portion of the equation included an interaction term. REML was used as the maximum likelihood estimator.

Random effect		Variance*		Autocorrelation structure**					AICc	K	ΔAICc	W
Bird	Bird/Date	F	V	None	E	S	G	R				
x			x					x	6332	9	0	1
x		x						x	6382	8	49	0
x			x				x		6922	9	590	0
x		x					x		6989	8	657	0
	x		x					x	8232	10	1899	0
	x	x						x	8303	9	1971	0
	x		x				x		8588	10	2255	0
	x	x					x		8664	9	2331	0
x			x			x			8989	9	2656	0
x		x				x			8995	8	2662	0
x			x		x				9040	9	2708	0
x		x			x				9047	8	2714	0
	x		x			x			10058	10	3725	0
	x	x				x			10100	9	3768	0
	x		x		x				10132	10	3799	0
	x	x			x				10180	9	3848	0
	x		x	x					12806	8	6474	0
	x	x		x					12868	7	6536	0
x			x	x					12960	7	6627	0
x		x		x					13035	6	6703	0

*Variance was fixed (F) or variable (V); ** Autocorrelation structures used were Exponential (E), Spherical (S), Gaussian (G) and Rational quadratic (R).

Identifying the optimal fixed effect structure for the given random effect structure I used a likelihood ratio test to determine the significance of dropping the interaction term as well as the variable Year from the model (Table I2).

Table I2. Comparison of models with different fixed effects structures. ML was used as the maximum likelihood estimator.

Model	Explanatory variables	DF	Test	L.Ratio	P
1	**Forest**	7			
2	**Forest+Year**	8	1vs2	0.96	0.32
3	**Forest*Year**	9	2vs3	5.94	0.015

The comparison shows that both terms can be dropped from the model as their addition is non-significant. Thus, the optimal model was one that only included total forest as the dependent variable. These results indicate there are no significant differences in the detected habitat selection patterns in 2008 and 2012 (Fig. I1). Based on this, I fused both datasets in order to compare the routine movement data with the translocation data.

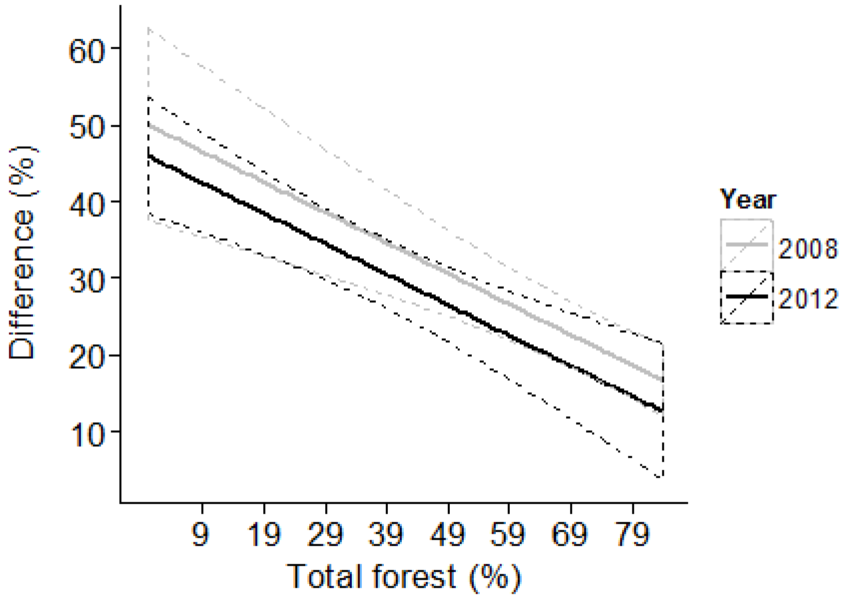

Figure I1. Predicted effect of total forest on difference of forest amount within observed and available buffers: regression lines for 2008 (gray lines, $\beta_0 = 50.09$, CI 95%: 37.77 to 62.4) and 2012 routine movement data (black lines, $\beta_2 = 0.41$, CI 95%: 0.045 to 0.78).

2) Validation

An analysis of the residuals of the model shows no clear violation of heterogeneity, normality or independence (Fig. I2). The spatial autocorrelation of the residuals seen in the initial models I ran was corrected by adding a rational quadratic autocorrelation structure to the model (Fig. I3).

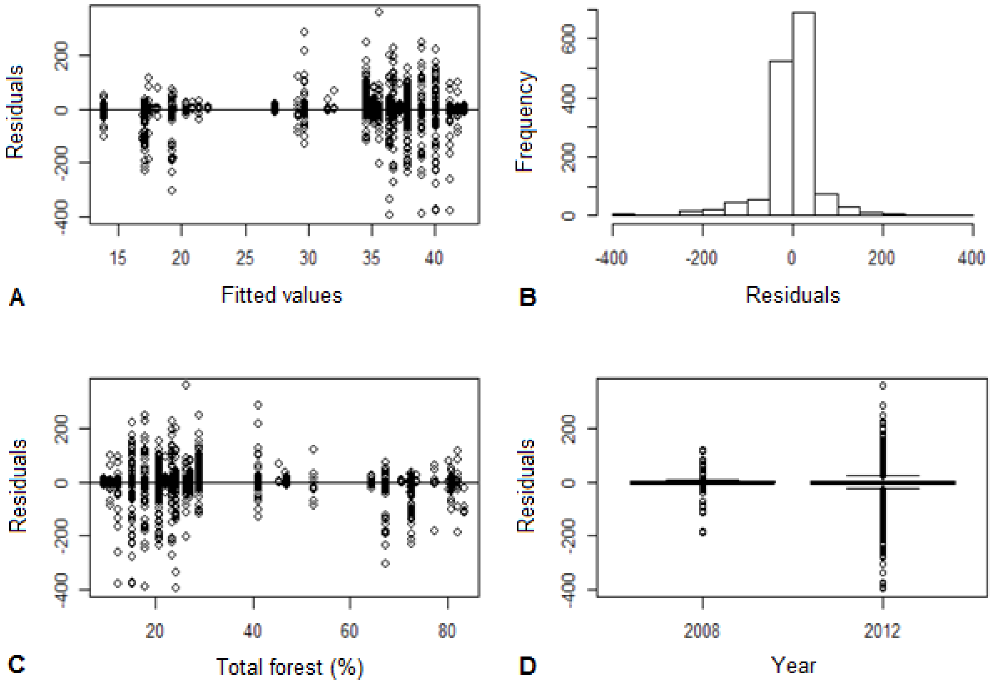

Figure I2. Model validation graphs for the optimal model for the difference between observed and available percentage of forest in relationship to the year when the data was recorded. **A:** Residuals vs fitted values; **B:** Frequency distribution of residuals; **C:** Residuals vs percentage of total forest; **D**: Residuals vs year of the study.

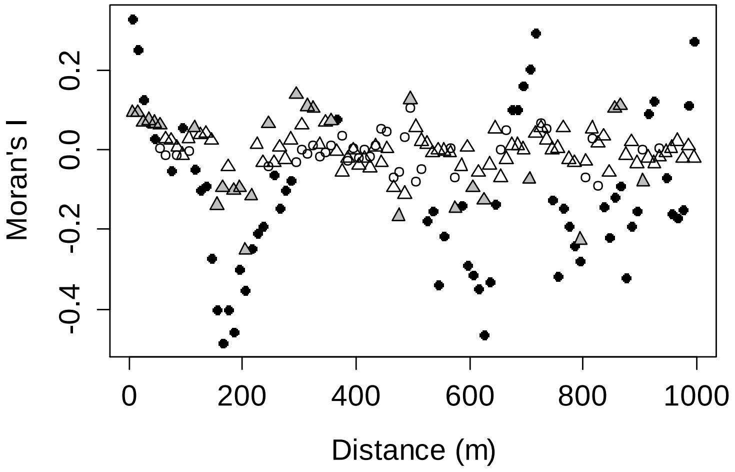

Figure I3. Correlogram of the residuals of the model Difference~Forest+Year|Bird. Including the rational quadratic autocorrelation structure in the model (triangles) greatly reduced the Moran's I values when compared to a model that does not include it (circles). The filled points (gray and black) correspond to statistically significant correlation values. Note that almost all of the significant Moran's I values for the corrected model (gray triangles) have absolute values smaller than 0.2.

<u>Model I.2: effect of translocation treatment on habitat selection</u>

$$Difference_{OBS-AVAIL} = Forest * Translocation|Bird$$

In order to find the optimal model to describe the relationship between selection and 'translocation treatment' (i.e. data obtained from translocated or non-translocated individuals) I followed similar steps as the ones used for the previous model.

1) Identification of optimal error structure

As before, the best model included only the individual birds as a random effect and a rational quadratic correlation structure. Unlikely the previous one, allowing variable variance did not improve the model (Table I3).

Table I3. Comparison of different optimal error structures for the translocation treatment effect model. In all the cases the fixed effects portion of the equation included an interaction term. REML was used as the maximum likelihood estimator.

Random effect		Variance*		Autocorrelation structure**					AICc	K	ΔAICc	W
Bird	Bird/Date	F	V	None	E	S	G	R				
x		x						x	7446	8	0	0.73
x			x					x	7448	9	2	0.27
x		x					x		8065	8	620	2E-135
x		x					x		8067	9	621	1E-135
	x		x					x	9414	10	1969	0
	x	x						x	9429	9	1983	0
	x		x				x		9772	10	2327	0
	x	x					x		9786	9	2341	0
x		x				x			10059	8	2614	0
x			x			x			10061	9	2616	0
x		x			x				10118	8	2673	0
x			x		x				10120	9	2674	0
	x	x				x			11199	9	3754	0
	x		x		x				11286	10	3841	0
	x	x			x				11287	9	3841	0
	x	x		x					13986	7	6541	0
	x		x	x					13986	8	6541	0
x			x	x					14149	7	6703	0
x		x		x					14154	6	6708	0

*Variance was fixed (F) or variable (V); ** Autocorrelation structures used were Exponential (E), Spherical (S), Gaussian (G) and Rational quadratic (R)

2) Identifying the optimal fixed effect structure for the given random effect structure

I used a likelihood ratio test to determine the significance of dropping the interaction term as well as the variable Translocation from the model (Table I4). The comparison shows that both can be dropped from the model as their addition is non-significant.

Table I4. Comparison of models with different fixed effects structures. ML was used as the maximum likelihood estimator.

Model	Explanatory variables	DF	Test	L.Ratio	P
1	**Forest**	6			
2	**Forest+Translocation**	7	1vs2	2.63	0.105
3	**Forest*Translocation**	8	2vs3	2	0.121

3) Validation

An analysis of the residuals of the model showed no clear violation of heterogeneity, normality or independence (Fig. I4). The spatial autocorrelation of the residuals seen in the initial models I ran was corrected by adding a rational quadratic autocorrelation structure to the model (Fig. I5).

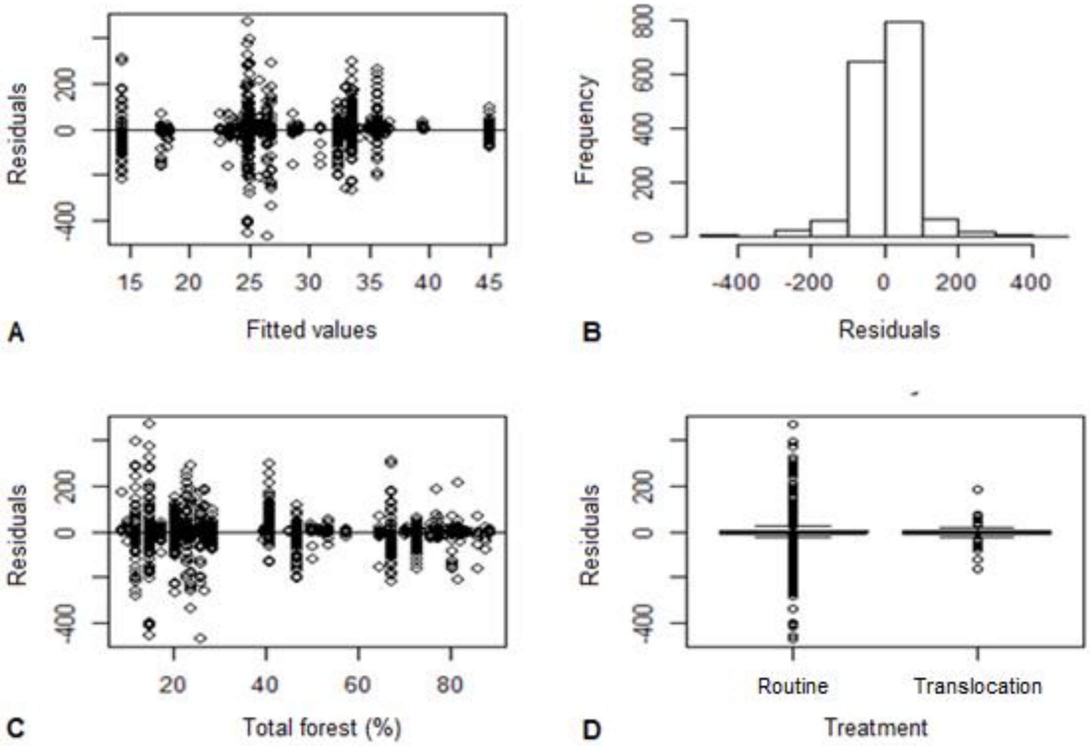

Figure I4. Model validation graphs for the optimal model for the difference between observed and available percentage of forest during routine and translocation movements. **A:** Residuals vs fitted values; **B:** frequency distribution of residuals; **C:** Residuals vs percentage of total forest; **D**: Residuals vs translocation treatment.

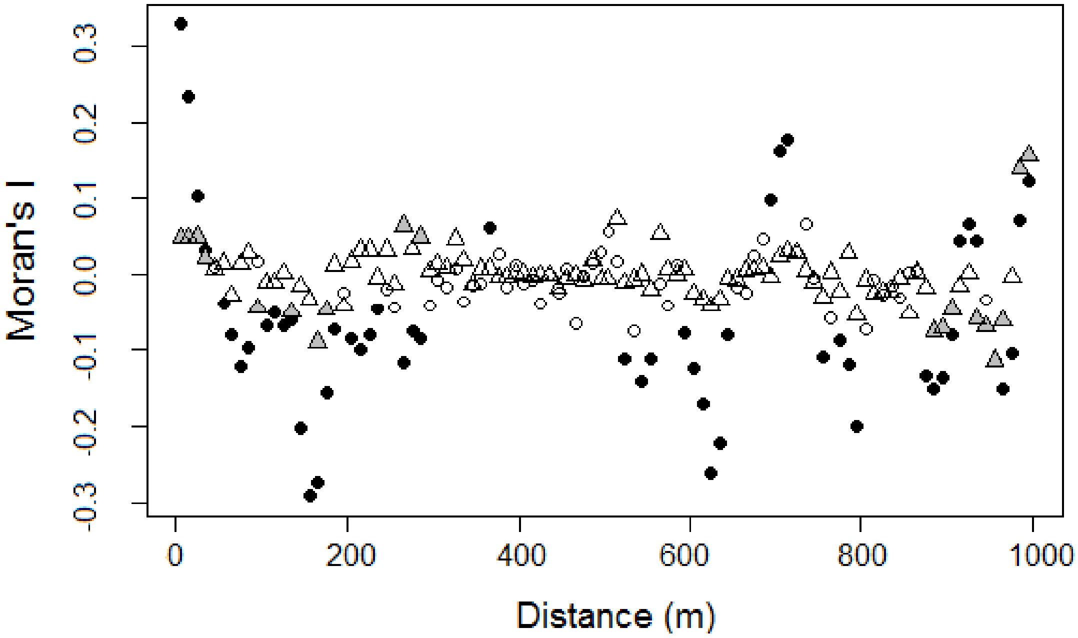

Figure I5. Correlogram of the residuals of the model Difference ~ Forest + Translocation | Bird. Including the rational quadratic autocorrelation structure in the model (triangles) greatly reduced the Moran's I values when compared to a model that does not include it (circles). The filled points (gray and black) correspond to statistically significant correlation values. Note that almost all of the significant Moran's I values for the corrected model (gray triangles) have absolute values smaller than 0.1.

Movement rate

Model II.1: effect of year on movement rate

$$logSpeed = Time\ Interval + Step\ Forest + \ Year|Bird/Date$$

1) Identification of optimal error structure

Starting with a full model with both log Interval, Year and Step Forest amount, as well as their interactions as fixed terms, I tested different error structures which included: the use of individual bird or date nested inside individual bird as a random effect, allowing for differing variances each year and including a spatial autocorrelation structure.

A comparison of the models' AICc (Table I5) showed there were four competing models, all of them including date nested inside individual as a random effect and an autocorrelation structure (either exponential or rational quadratic). I decided to use a fixed variances structure in order to keep the model simple. The final model thus, included date nested inside individual as a random effect, a rational quadratic autocorrelation structure and fixed variances.

Table I5. Comparison of different optimal error structures for the Year-effect model. In all the cases the fixed effects portion of the equation included all possible interaction terms. REML was used as the maximum likelihood estimator.

Random effect		Variance*		Autocorrelation structure**					AICc	K	ΔAICc	W
Bird	Bird/Date	F	V	None	E	S	G	R				
	x		x					x	3421	14	0	0.350
	x		x		x				3422	14	1	0.271
	x	x						x	3422	13	1	0.209
	x	x			x				3423	13	2	0.161
	x		x	x					3431	12	9	0.004
	x	x		x					3432	11	10	0.002
	x		x				x		3433	14	12	0.001
	x		x			x			3434	14	12	0.001
	x	x				x			3434	13	13	<0.001
	x	x					x		3435	13	13	<0.001
x			x					x	3442	13	21	<0.001
x			x		x				3443	13	21	<0.001
x		x						x	3443	12	22	<0.001
x		x			x				3444	12	22	<0.001
x			x	x					3457	11	35	<0.001
x		x		x					3458	10	37	<0.001
x			x				x		3460	13	38	<0.001
x			x			x			3460	13	38	<0.001
x		x					x		3461	12	40	<0.001
x		**x**				x			3461	12	40	<0.001

*Variance was fixed (F) or variable (V); ** Autocorrelation structures used were Exponential (E), Spherical (S), Gaussian (G) and Rational quadratic (R).

2) Identifying the optimal fixed effect structure for the given random effect structure

I used a likelihood ratio test to determine the significance of dropping the interaction term as well as the variable Year and Step Forest from the model (Table I6).

Table I6. Output of the likelihood ratio test for models with different fixed-effect structures. ML was used as the maximum likelihood estimator.

Model	Explanatory variables	DF	Test	L.Ratio	P
1	Interval	5			
2	Interval + Step Forest	6	1 vs 2	80.9	<.0001
3	Interval + Step Forest + Year	7	2 vs 3	4.4	0.04
4	Interval + Step Forest * Year	8	3 vs 4	0.2	0.62

The comparison shows that only the interaction should be dropped from the model. Thus, the optimal model was one that includes time interval, forest around the step and year as the dependent variables. There was some evidence of the existence of differences in the movement rates between years for the routine movement dataset, being the speed in 2012 0.37 times slower than in 2008 (CI 95%: 0.01 to 0.6, P = 0.045).

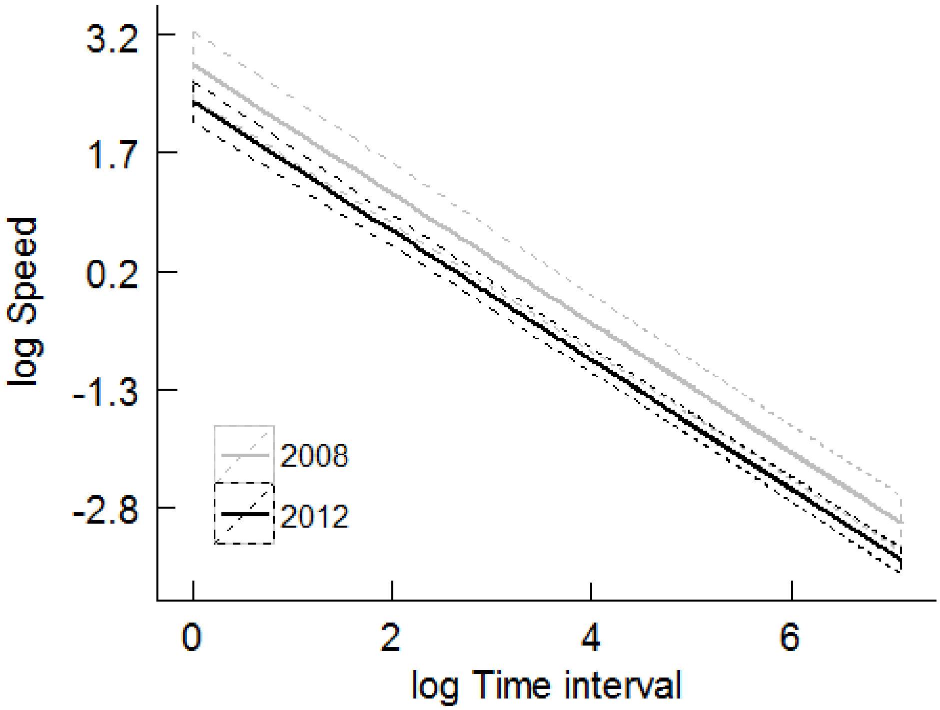

Figure I7. Predicted effect of time interval on log speed after accounting for percentage of forest around the movement steps: regression lines for 2008 (gray lines, $\beta_0 = 4.08$, CI 95%: 3.58 to 4.59) and 2012 routine movement (black lines, $\beta_2 = -0.47$, CI 95%: -0.84 to -0.089). Fitted values were calculated using the mean forest amount (90.2%).

3) Validation

An analysis of the residuals of the model shows no clear violation of heterogeneity, normality or independence (Fig. I8). A correlogram of the residuals showed very weak signs of autocorrelation (max Moran's I value = -0.19) (Fig. I9).

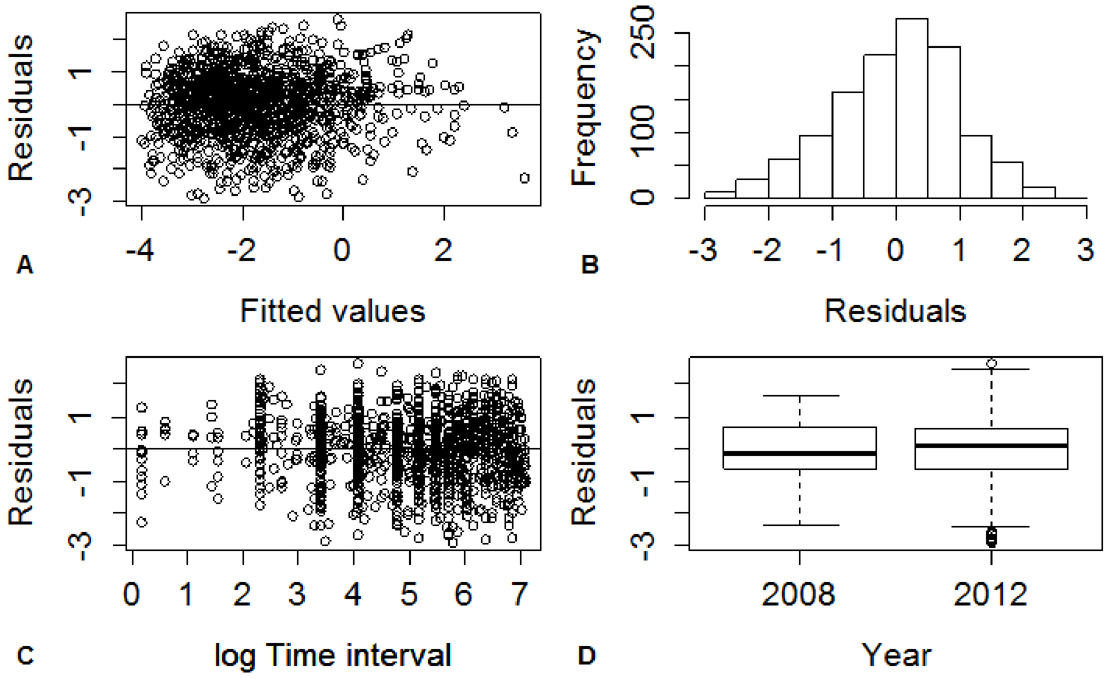

Figure I8. Model validation graphs for the optimal model for speed during 2008 and 2012 routine movement studies. **A:** Residuals vs fitted values; **B:** Frequency distribution of residuals; **C:** Residuals vs log-interval. **D.** Residuals vs year of data collection.

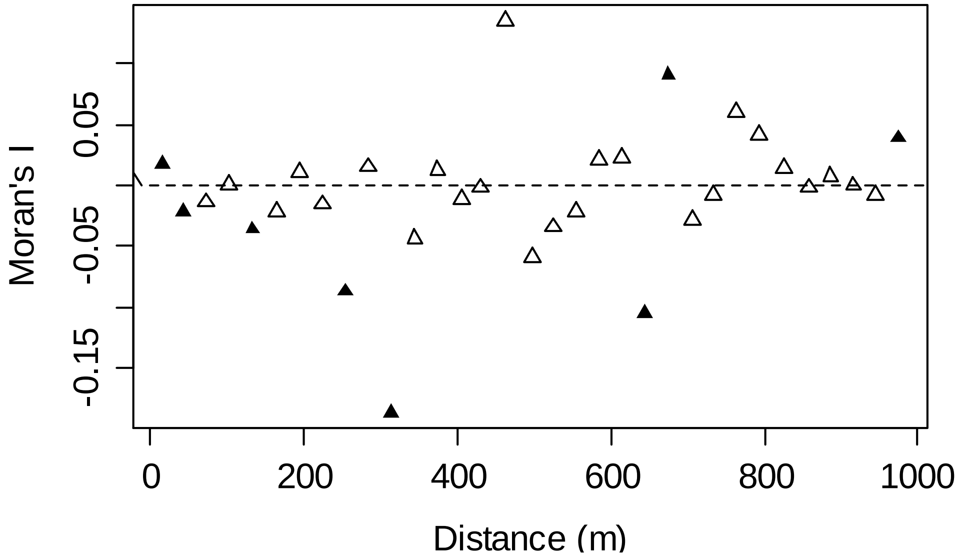

Figure I9. Correlogram of the residuals of the model logSpeed~logInterval + Year + Step Forest | Bird. The model included a rational quadratic autocorrelation structure. The filled points correspond to statistically significant correlation values.

Model II.2: effect of translocation treatment on movement rate

1) Identification of optimal error structure

The comparison of the models' AICc showed that the best model was one that included date nested inside individual as a random effect (Table I7). There was no need to include an autocorrelation structure as the residuals of the model did not show signs of autocorrelation (Fig. I11)

Table I7. Comparison of different optimal error structures for the translocation treatment effect model. In all the cases the fixed effects portion of the equation included all possible interaction terms. REML was used as the maximum likelihood estimator.

Random effect		Variance*		Autocorrelation structure**					AICc	K	ΔAICc	W
Bird	Bird/Date	F	V	None	E	S	G	R				
	x	x		x					3666	11	0	0.40
	x		x	x					3668	12	2	0.16
	x	x					x		3669	13	3	0.09
	x	x				x			3670	13	3	0.08
	x	x						x	3670	13	3	0.08
	x	x			x				3670	13	3	0.07
	x		x				x		3671	14	5	0.03
	x		x			x			3672	14	5	0.03
	x		x					x	3672	14	5	0.03
	x		x		x				3672	14	5	0.03
		x		x					3691	10	25	2E-06
			x	x					3693	11	26	8E-07
		x					x		3694	12	27	5E-07
		x						x	3694	12	28	4E-07
		x				x			3694	12	28	4E-07
		x			x				3694	12	28	4E-07
			x				x		3695	13	29	2E-07
			x					x	3696	13	29	2E-07
			x			x			3696	13	29	2E-07
			x		x				3696	13	29	2E-07

*Variance was fixed (F) or variable (V)

** Autocorrelation structures used were Exponential (E), Spherical (S), Gaussian (G) and Rational quadratic (R).

2) Identifying the optimal fixed effect structure for the given random effect structure

I used a likelihood ratio test to determine the significance of dropping the interaction term as well as the variable Translocation and Step Forest from the model (Table I8).

Table I8. Output of the likelihood ratio test for models with three different fixed-effect structures. ML was used as the maximum likelihood estimator.

Model	Explanatory variables	DF	Test	L.Ratio	P
1	**Interval**	5			
2	**Interval + Step Forest**	6	1 vs 2	77.1	<.0001
3	**Interval + Step Forest + Translocation**	7	2 vs 3	78.1	<.0001
4	**Interval + Step Forest * Translocation**	8	3 vs 4	3.5	0.06

The comparisons showed that that adding both Translocation and Step Forest significantly improved the model, while adding the interaction did not. Thus, the best model is one that includes time interval and translocation treatment:

$$logSpeed = Time\ Interval + Step\ Forest + \ Translocation|Bird/Date$$

3) Validation

An analysis of the residuals of the model shows no clear violation of heterogeneity, normality or independence (Fig. I10). A correlogram of the residuals (Fig. I11) showed no signs of spatial autocorrelation.

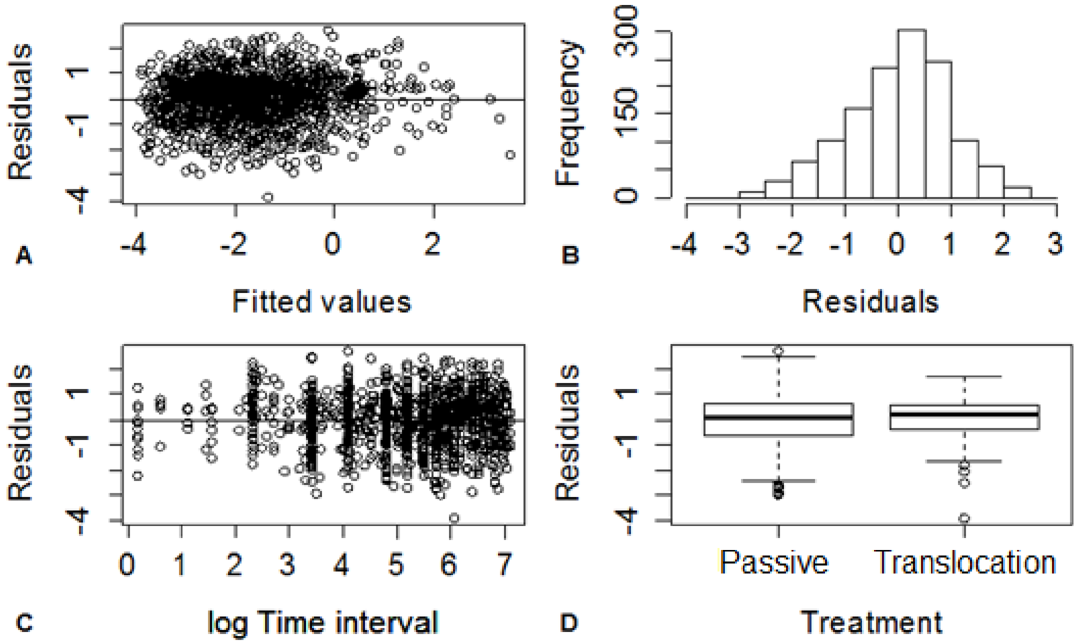

Figure I10. Model validation graphs for the optimal model for speed during routine and translocation movements. **A:** Residuals vs fitted values; **B:** Frequency distribution of residuals; **C:** Residuals vs log-interval. **D.** Residuals vs translocation treatment.

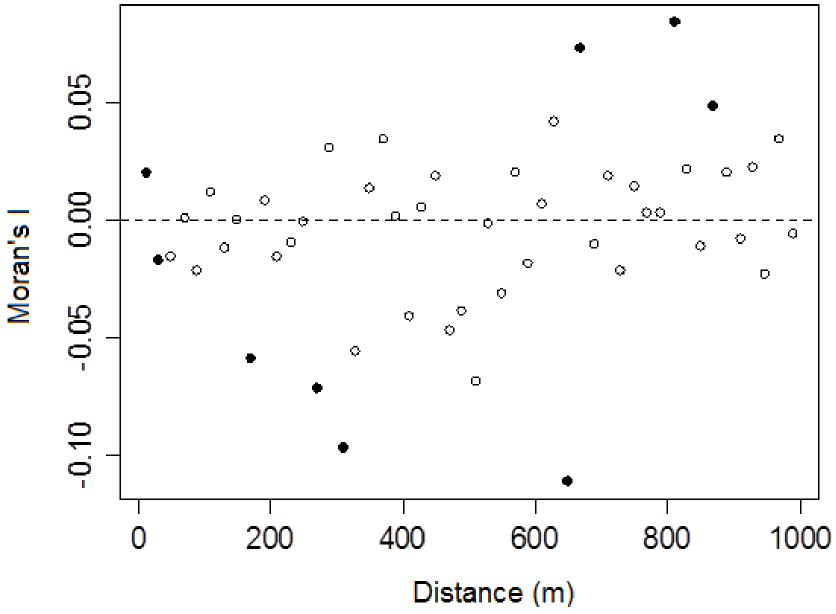

Figure I11. Correlogram of the residuals of the model logSpeed ~ logInterval + Translocation | Bird/Date. The filled points correspond to statistically significant correlation values. Note that only one of them has Moran's I value larger than 0.1.