University of Alberta

CORRIDOR USE, HABITAT SELECTION, AND ROUTE CHOICE BY FOREST BIRDS IN THE FRAGMENTED TROPICAL DRY FORESTS OF COSTA RICA

by

Cameron Scott Gillies ©

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Abstract

Tropical forests hold the majority of the world's biodiversity, but face tremendous threats from agricultural expansion. Among these forests, dry forests have already undergone extensive clearing and only 2% of the original tropical dry forest remains in Mesoamerica. In such fragmented landscapes, the movement of individuals among subpopulations is fundamental to long term population persistence. Despite the importance of movement, little is known about how forest-dependent birds move through fragmented areas and use connecting habitat elements, like corridors. To address this deficiency, I translocated individuals of two species of forest birds with differing forest dependence in three treatments in the fragmented tropical dry forests of northwestern Costa Rica: along a riparian corridor, along a fencerow, or across pasture. I then followed their return trajectories with unprecedented resolution, recording positions approximately every 15 min for up to four days. Detailed route information yielded four main conclusions. First, riparian corridors facilitated the movement of the forest specialist barred antshrike (*Thamnophilus doliatus*). In riparian corridor treatments, returns to their original territories were faster and more likely, they selected forest habitat more strongly, and they traveled further from the forest edge. Second, fencerows were not sufficient corridors for the specialist, which generally chose longer routes in forest rather than more direct routes via fencerows. Third, individuals adjusted their behaviours based on habitat context. In addition to changes by the specialist in riparian corridor treatments (above), the generalist rufous-naped wren (*Campylorhynchus rufinucha*) selected forest more strongly in riparian corridor treatments and selected edge habitat more strongly with decreases in forest cover. Finally, the specialist chose more forested steps when they were far from their territories and when in forest habitat. They preferred steps ending in stepping stones (isolated trees) when available routes had low forest cover, but avoided them when forest cover was higher. I conclude that forested habitat and corridors benefit the movement of forest specialist birds and the conservation of these habitats will be important in this landscape and likely others. Furthermore, stepping stones may be an important element for the movement of birds through the most inhospitable matrix where forested alternatives do not exist.

Dedication

To my parents, Barry and Luana, my wife, Renee, for their love and support and to Brodie and Maren for the endless joy they bring to life.

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Chapter 1

General Introduction

Tropical forests hold the majority of the world's biodiversity, but they have already undergone extensive clearing and face tremendous threats in the decades ahead (Laurance 1999, Achard 2002). Land use change is expected to drive the loss of biodiversity over the next century primarily because of the expanding human enterprise in the tropics (Sala *et al.* 2000, Tilman *et al.* 2001). Within the tropics, some areas face greater threats than others even while they hold greater biodiversity (Myers *et al.* 2000). Such a 'hotspot' occurs in Mesoamerica, encompassing Central America and Mexico, which has been recognized for the large number of endemic species combined with high human pressure (Myers *et al.* 2000, Cincotta *et al.* 2000). Within Mesoamerica, the first areas to be cleared were generally those most suitable for agriculture. These were primarily tropical dry forests because they were easier to clear, they were more suitable for cattle, and their soils were more fertile than in wetter environments (Murphy and Lugo 1986). Following that initial wave of clearing, less than 2% of Mesoamerica's tropical dry forests remained (Janzen 1986) and probably less than 1% of the total area is protected (Sánchez-Azofeifa *et al.* 2005a). Despite a long history of human use and occupation in dry forests, research there has been relatively rare (Sánchez-Azofeifa *et al.* 2005b). Instead, most research has been conducted in the tropical moist or rain forest where much more forest remains (Sánchez-Azofeifa *et al.* 2005b).

Animals that depend on forest for breeding are threatened by both habitat loss and fragmentation (Turner 1996). These processes lead to increasing isolation of habitats and their associated populations. For isolated subpopulations to persist in the long term, there must be movement of individuals among them (Hanski 1998). Successful movement through fragmented landscapes requires that dispersing individuals are able to reach isolated subpopulations where they can 'rescue' them from chance extinctions (Brown and Kodric Brown 1977). Unfortunately, many forest-dwelling species appear to be unwilling or unable to cross open areas of inhospitable habitat, referred to as the matrix. Research estimating the willingness of animals to cross gaps in forest cover has covered a wide range of taxa, including mammals (e.g. Bowman and Fahrig 2002, Bakker and van Vuren 2004), amphibians (e.g. Rosenberg *et al.* 1997), and insects (e.g. Baum *et al.* 2004). However, the bulk of information about gap-crossing behaviour has come from birds moving under an artificial stimulus (e.g. Sieving *et al.* 1996, Desrochers and Hannon 1997, St. Clair *et al.* 1998, Develey and Stouffer 2001, St. Clair 2003, Creegan and Osborne 2005). Surprisingly, little is known about the longer routes of free-moving individuals through fragmented landscapes (Harris and Reed 2002, Bélisle 2005).

How animals move through fragmented landscapes has been the focus of research in two main disciplines: behavioural ecology and landscape ecology. Over a decade ago, Lima and Zollner (1996) argued that landscape ecology and the ecological modelling therein rest on a weak understanding of two key behavioral phenomena, animal movement and habitat selection, both of which have received a great deal of attention by behavioral ecologists. They suggested that the fields of landscape and behavioural ecology were poised for a synergy as practitioners in the two fields converged on an understanding of ecological processes at similar spatial scales. Since this time, researchers have rapidly developed methods to collect increasingly detailed information about animal movement at scales that are relevant to both conservation and ecological modelling (e.g. Haddad 1999, Schultz and Crone 2001, Whittington *et al.* 2004, Fortin *et al.* 2005, Levey *et al.* 2005, Selonen and Hanski 2006). Complementary information on habitat selection and movement has been collected at scales as large as whole oceans (e.g. Block *et al.* 2005, Croxall *et al.* 2005, Shaffer *et al.* 2006).

One area where animal movement information is particularly lacking is in the study of corridor efficacy. While structural connections of forested corridors may exist in a landscape, movement information is needed to assess their functional connectivity; the degree to which a landscape facilitates or impedes movement among resource patches (*sensu* Taylor *et al.* 1993, Bélisle 2005). Corridors have been widely advocated as a means of maintaining the movement of individuals among subpopulations (Saunders *et* *al.* 1991, Rosenberg *et al.* 1997, Fischer *et al.* 2006), but whether the evidence supports their application has been controversial (Simberloff and Cox 1987, Noss 1987, Simberloff *et al.* 1992, Beier and Noss 1998). While there is now good evidence that animals use corridors for movement (e.g. Beier 1995, Tewksbury *et al.* 2002, Haddad *et al.* 2003, Levey *et al.* 2005), this information has been difficult to collect for many species (Chetkiewicz *et al.* 2006).

Within fragmented landscapes, both riparian corridors and fencerows have been proposed as structural habitat elements that function as corridors (e.g. Rosenberg *et al.* 1997, Şekercioğlu *et al.* 2002), but their efficacy has not been directly compared. A third habitat element that may facilitate animal movement is stepping stones (*sensu* Diamond 1975). These are individual trees or a small group of trees that are typically remnants of the original forest cover surrounded by the matrix. These may be used by animals living in the agricultural matrix (Fischer and Lindenmayer 2002a, Şekercioğlu *et al.* 2007) and also by animals traveling through the matrix (Schultz 1998, Fischer and Lindenmayer 2002b, Baum *et al.* 2004).

All three habitat elements are important in binary depictions (i.e., habitat and matrix) of fragmented landscapes which are typically described by a combination of habitat composition and configuration (Villard *et al.* 1999). For these elements, habitat composition describes the amount of riparian corridors, fencerows, stepping stones and other elements of the landscape. Habitat configuration is the spatial arrangement of these elements in the landscape. Both landscape composition and configuration may affect the persistence and movement of species in fragmented landscapes (Fahrig 1998). A number of studies have examined the relative influence of composition and configuration on patch occupancy and abundance (e.g. Andrén 1994, Villard *et al.* 1999, Betts *et al.* 2006) or habitat selection (e.g. Potvin *et al.* 2000, Stubblefield *et al.* 2006, Radford and Bennett 2007). There is a theoretical expectation that habitat configuration matters to population persistence only when forest cover is low (Fahrig 1998), but it remains unclear how composition and configuration influence the movement of animals.

The effect of configuration on the movement of animals appears to be closely related to the use of edge habitat. Edges seem to direct the movement of butterflies (Haddad 1999, Schultz and Crone 2001, Schtickzelle *et al.* 2007) and voles (e.g. Andreassen *et al.* 1996). In some cases, the apparent benefit of a corridor for facilitating movement may actually be due to the edge created by the corridor (Haddad 1999, Levey *et al.* 2005). However, the apparent attraction to edge has some important conservation implications. For forest animals, edge habitat is climatically different from forest interior (Laurance *et al.* 2002) and in some situations increases the risk of predation (McCollin 1998). These types of edge effects are particularly prevalent in birds (Ries *et al.* 2004). Although there have been several studies showing how birds respond to edge while on their territories (e.g. Desrochers and Fortin 2000, Mazerolle and Hobson 2003, Laurance 2004), there is only one study at a small spatial scale that addresses the responses of birds to edges in the context of movement (Levey *et al.* 2005).

Another process that affects how animals move through corridors and other landscape elements is habitat selection (Lima and Zollner 1996). Habitat selection is typically analyzed using resource selection functions (RSFs; Boyce and McDonald 1999, Manly *et al.* 2002). While this is a powerful and flexible tool for such analyses, it has been difficult to accommodate situations where an individual's preferences vary with the amount or spatial arrangement of the available habitat. Mysterud and Ims (1998) developed a method to examine whether individuals exhibit such a functional response in the simple situation of two categorical habitat types. With the recent application of random effects to RSF models (Gillies *et al.* 2006), it is now possible to explore whether functional responses are present in habitat selection using a broader array of covariates.

Another recent development in the broad field of habitat selection studies is the development of step selection functions (SSFs; Fortin *et al.* 2005). They examine the choice of habitat between locations rather than at the point locations of occurrence. The emphasis is on understanding route choice by a moving animal. The characteristics of the used step from a given location are compared to a number of plausible steps from the same location (Whittington *et al.* 2004, Fortin *et al.* 2005). While this has been done for wolves (*Canis lupus*; Whittington *et al.* 2004) and elk (*Cervus elaphus*; Fortin *et al.* 2005), it has not been applied to other organisms.

Complementary developments in the broad foci of habitat selection and movement behaviour could be profitably combined to understand, and hence predict, how animals choose movement trajectories in fragmented habitats. This union is most tractable for well-studied taxa like birds. Birds are a group that has received abundant attention in the contexts of both habitat selection and movement. However, habitat selection studies of birds have focused primarily on breeding, wintering, or stopover habitat use (e.g. McGarigal and McComb 1995, Buler *et al.* 2007), and there is virtually no information about the habitat preferences of moving birds, particularly at a landscape scale. Several studies have tracked the movement of birds at the scale of a single gap or single patch (e.g. Desrochers and Hannon 1997, St. Clair *et al.* 1998, Sieving *et al.* 2000, Develey and Stouffer 2001, Sieving *et al.* 2004, Creegan and Osborne 2005). In studies where birds were moving at a landscape scale, tracking was infrequent (e.g. Laurance and Gomez 2005, Castellón and Sieving 2006) or only covered a short distance (e.g. 150 m, Levey *et al.* 2005). A notable exception was provided by Norris and Stutchbury (2001), who were able to track the extraterritorial movements of a forest bird species and report gross measures of their gap crossing and corridor use. The paucity of data on the routes of forest birds at landscape scales comes primarily from the difficulty of following their movement (Desrochers *et al.* 1999).

In the context of habitat fragmentation, birds are a taxon of conservation concern in the tropics for several reasons. First, agriculture is rapidly expanding there (Tilman *et al.* 2001) and this is one of the reasons it is recognized as the greatest threat to birds worldwide (Green *et al.* 2005). Second, tropical forest birds are generally considered to be more vulnerable to the effects of fragmentation than their temperate counterparts (Harris and Reed 2002, Stratford and Robinson 2005). This may be because they are more sensitive to edge habitat (Lindell *et al.* 2007) and the most sensitive species avoid crossing even small gaps in forest cover (e.g. Laurance *et al.* 2004, Castellón and Sieving 2006). Within tropical birds, understory and terrestrial insectivores are consistently the most impacted by habitat fragmentation, disappearing from fragments first (Renjifo 1999, Stouffer *et al.* 2006) and showing the greatest edge avoidance (Laurance 2004).

To address deficiencies in the knowledge of how forest dependent birds move through fragmented landscapes, I conducted a translocation experiment in the highly fragmented tropical dry forests of northwestern Costa Rica. The majority of clearing in this area began in the 1960's (Arroyo-Mora *et al.* 2005) and agriculturally productive areas are dominated by cattle pasture with much of the remaining forest confined to riparian corridors. The forest areas within and outside riparian corridors hold a variety of species, many of which are deciduous, loosing their leaves during the pronounced dry season. This dry season lasts from mid-December to mid-May during which very little precipitation falls. Agriculture in this area is primarily cattle pasture for beef production. Less common agricultural uses include sugar cane, melon, rice, teak, and cotton production. Within the agricultural areas there are also fencerows at the edges of fields and individual trees or small groups of trees (stepping stones) in the fields. My study area was located near the town of Liberia with fieldwork occurring primarily between Liberia and Guanacaste or Santa Rosa National Parks to the north, and to a lesser extent in areas immediately west and south of Liberia (Fig. 1-1). This landscape is primarily flat except for slopes into rivers and streams.

I translocated two species of forest bird with differing forest dependence along three configurations, or treatments; along a riparian corridor, along a fencerow and across pasture (Figs. 1-2 and 1-3). Both species are insectivores and are territorial year-round, but the forest specialist barred antshrikes (*Thamnophilus doliatus*) are found in the understory of the most intact sections of forest (Stiles and Skutch 1989). In contrast, the forest generalist rufous-naped wrens (*Campylorhynchus rufinucha*) are found at various heights in the forest, in forest of varying ages and in both intact and degraded forest. The antshrikes most often hold territories as pairs, but lone males also hold some territories. The wrens are cooperative breeders and territories usually have two to five individuals present.

To test the efficacy of corridors in facilitating movement, I compared return success, return time, and the return route of these birds among the three treatments (Chapter 2). I, along with several coauthors, developed methods for applying random effects models to RSFs (Chapter 3)I developed an RSF for the selection of their point locations relative to available locations in the broad landscape that the bird was moving through and I did this for both habitat type and distance to the edge of the forest. I then used the random effects from these models to examine whether birds were adjusting their selection for forest habitat in response to habitat composition, configuration, or availability (Chapter 4). Finally, I used a step selection function to examine the movement decisions of these birds, comparing the characteristics of the steps between locations to other possible steps from the same location. I also examined whether their selection changed with composition, configuration, or availability (Chapter 5). These three approaches offered three scales of analysis to examine how forest birds move through fragmented landscapes, from measures of their whole paths to their selection of locations relative to the broader landscape and finally their fine-scale route choices. I explore the overriding themes from these three scales in chapter 6.

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Figure 1-1. Study area location is approximated by the oval near the town of Liberia. The capital, San Jose, is given for reference.

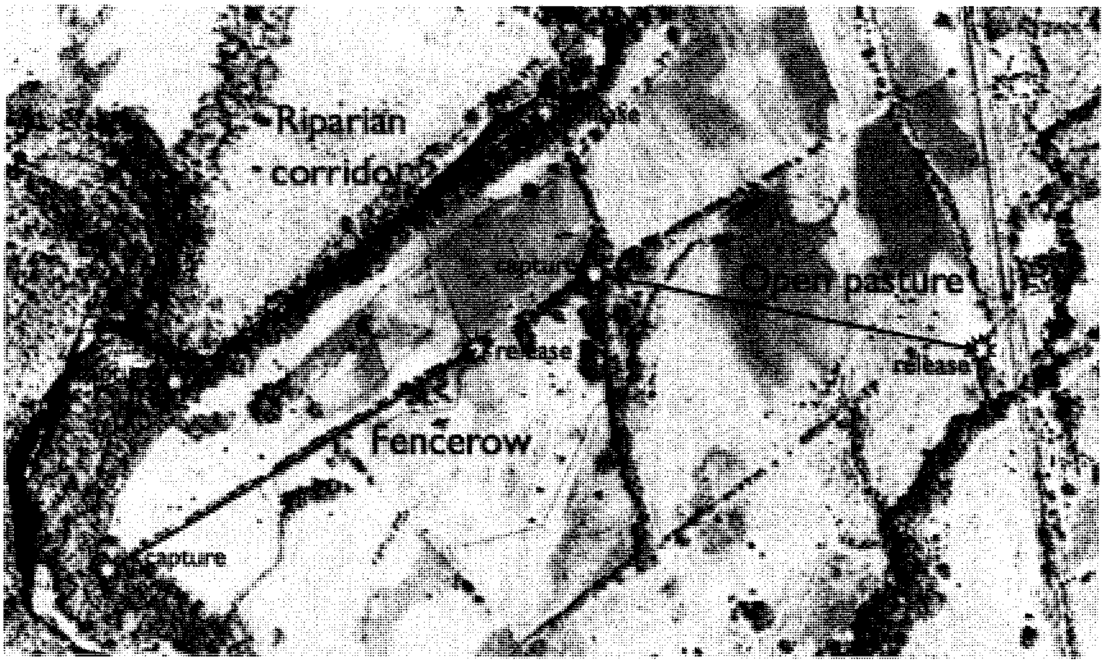

Figure 1-2. Aerial photo of a section of my study area with example translocations for the three treatments.

Barred Antshrike

Rufous-naped Wren

Figure 1-3. The two study species. The forest specialist barred antshrike (*Thamnophilus doliatus*) and Rufous-naped Wren (*Campylorhynchus rufinucha*).

Chapter 2

Riparian corridor use by forest specialist birds in fragmented tropical forest[1]

Abstract

Riparian corridors and fencerows are hypothesized to increase the persistence of forest animals in fragmented landscapes by increasing movement among suitable habitat patches. This function may be critically important for forest birds which have declined dramatically in fragmented habitats and are sensitive to crossing gaps in forest cover. Unfortunately, direct evidence for the use of corridors by moving forest birds has been difficult to collect at landscape scales and this limits the support for their use in conservation planning. Using telemetry and handheld GPS units, I examined the movement of forest birds by translocating territorial individuals with high vs. low forest dependency 0.7 – 1.9 km from their territories in the highly fragmented tropical dry forest of Costa Rica. In each translocation, the directly intervening habitat comprised one of three treatment types: forested riparian corridor, linear living fencerow, or open pasture. For the forest specialist, riparian corridors significantly facilitated movement over pasture treatments. Based on the precise trajectories of these birds, longer forested routes were preferred by forest specialists returning in fencerow and pasture treatments and they did not use fencerows even when they led directly to their home territory. The forest generalist was more likely to use fencerows when returning, and return time and success were equivalent among the three treatments. Both species crossed fewer gaps in riparian corridor treatments than in fencerow or pasture treatments. I conclude that forested corridors can facilitate movement for a forest specialist, that movement within corridors most likely occurs by exploratory rather than directed routes, and that fencerows are not sufficient as movement corridors for some forest-dependent species.

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[1] I intend to submit this paper to *Proceedings of the National Academy of Sciences.*

Introduction

Land-use change in tropical forests is expected to be the primary threat to global biodiversity for the remainder of this century (Sala *et al.* 2000). Because movement among remaining patches is important to population persistence (e.g., González *et al.* 1998), corridors have been widely advocated as a means to maintain biodiversity and ecological processes in fragmented landscapes (da Silva and Tabarelli 2000, Lens *et al.* 2002). Several studies have demonstrated that target organisms occur in corridors (Beier and Noss 1998), providing indirect evidence that they facilitate movement. A few studies have measured movement directly to assess the functional connectivity (*sensu* Bélisle 2005) provided by corridors (Beier 1995, Tewksbury *et al.* 2002, Haddad *et al.* 2003, Levey *et al.* 2005), but this has been difficult to achieve for small species, like birds, that move at landscape scales (Bélisle 2005). This information is especially important for forest specialists, particularly understory insectivores, because this group appears to be most sensitive to the isolation effects of fragmentation (Şekercioğlu *et al.* 2002, Lens *et al.* 2002, Stouffer *et al.* 2006). Both forested corridors and fencerows of individual, living trees have been promoted as landscape elements to facilitate the movement of birds and other forest dependent animals (Rosenberg *et al.* 1997, Şekercioğlu *et al.* 2002), but no studies of birds have directly measured and then compared their effects on movement rates.

One tropical region where corridors and other landscape configurations appear to be important is the dry forest of Costa Rica. This area is part of the Mesoamerican biodiversity hotspot (Myers *et al.* 2000), but the contiguous tropical dry forest that once dominated the landscape is now dominated by pasture. Consequently, these dry forests are now highly fragmented and are one of the most endangered forest types in the tropics (Laurance 1999). The relatively low rates of forest cover that remain in the dry forest likely increase the importance of habitat configuration to biodiversity conservation (Fahrig 1998). Indeed, much of the remaining dry forest exists as riparian corridors, which typically has a closed canopy and moderate understory. Another forest element is formed by the linear fencerows of individual living trees that demark pasture edges. There are also individual trees scattered within the pastures, which may function as stepping stones (*sensu* Diamond 1975) for forest-dependent animals. Because agricultural demands are expected to place large pressures on remaining forest over the next 50 years (Tilman *et al.* 2001), demonstrations of the utility to forest animals of riparian corridors and fencerows could provide important information to landowners and land use planners in Mesoamerica and elsewhere.

Here I test the efficacy of forested corridors and fencerows in facilitating the movement of forest birds in a highly fragmented tropical forest. Previously, direct information about corridor use and gap crossing has come from experiments at small scales (Desrochers and Hannon 1997, St. Clair *et al.* 1998, Sieving *et al.* 2000, Bowman and Fahrig 2002). Studies at broader landscape scales have shown that birds make some use of corridors, but have not followed moving individuals closely enough to collect detailed information about their route (e.g., Haas 1995, Castellón and Sieving 2006). I followed moving forest birds in real time at a landscape scale with unprecedented resolution, collecting information about their route, their pattern of movement, and gap crossing propensity. I translocated 30 territorial Barred Antshrikes (*Thamnophilus doliatus*, hereafter antshrikes) and 30 Rufous-naped Wrens (*Campylorhynchus rufinucha*, hereafter wrens) between 0.7 and 1.9 km. Both are common insectivores that hold territories year-round, but antshrikes are forest specialists, being found only the in the understory of the most intact forest in this region (Stiles and Skutch 1989). Birds were moved away from their territory in one of three treatments: along riparian corridors, along fencerows, and through pasture (see *Methods*). Using translocations allowed us to standardize the bird's motivation for moving, anticipate the direction it would predominantly travel, and choose the configuration of the intervening habitat (Bélisle 2005). I predicted that birds would travel more quickly and successfully through the riparian corridors than through pasture, and that fencerows would provide intermediate travel speed and success.

Methods

To collect information about forest bird movement in fragmented landscapes, I captured territorial individuals of two species in an agricultural landscape of northwestern Costa Rica near the town of Liberia. This landscape was once contiguous tropical dry forest, but is now dominated by cattle pasture. Remaining forest covers approximately 25% of the landscape and is often confined to riparian areas. Captured birds were translocated from their home territory to another location after which I followed their return with radio-telemetry.

I conducted translocations from June to August 2000 and January to June 2002. All individuals were caught by 0940 local time (mean capture time = 0659 hours ± 65 min) by attracting them into a mistnet with a playback of a conspecific song. Antshrikes typically hold territories as a pair and the wrens, which breed cooperatively, hold territories as a family group with 2 to 5 individuals (Stiles and Skutch 1989). I moved male antshrikes and both male and female adults of the monomorphic wrens. I attached a radio transmitter using eyelash adhesive to trimmed feathers on the backs of translocated individuals. A plastic colored leg band was also attached to facilitate identification if the transmitter fell off prematurely. Individuals were moved from unique forested territories to unique release locations in one of three treatments: along a riparian corridor, along a fencerow, or across pasture. Birds were released in fencerow or forest habitat. Due to the rarity of fencerows in the study area, the same fencerow was used for two treatments (one of each species) on three occasions. In these cases, I moved an individual of each species differing distances. Most wrens (23 of 30) were sexed by extracting DNA from a whole tail feather (Griffiths *et al.* 1998). The remaining individuals were sexed by comparing their weight, tarsus length, and exposed culmen length to measurements of individuals of known sex using a discriminant function analysis. I translocated 14 female and 16 male wrens.

Following release, I recorded with radio-telemetry and hand-held GPS units the location of each translocated bird approximately every 15 minutes (mean = 14.8 min ± 8.2 min standard deviation) for up to 4 days and daily thereafter for 10 days or until they returned, whichever was earlier. Two observers closely followed individuals by simultaneously triangulating their location from a mean distance of 27 m ± 13 m. These positions provided trajectories of moving birds from which I assessed the habitat used for movement as well as their return time and success. The return of 9 birds that lost their transmitters was checked daily by playing the song of a conspecific at the capture site. Sixty individuals were translocated; one bird from each species was translocated in each treatment at each of ten distances (0.7-1.3 km in 0.1 km intervals, then 1.45, 1.6, and 1.9 km). Even the shortest translocations were well outside the home range of these birds. Although empirical information for the home range size of these species is not available, home range radius was ~ 60 m for a cogener to the antshrike in Brazil (*T. caerulescens*; Duca *et al.* 2006) and ~ 75 m for a cogener to the wren in Venezuela (*C. nuchalis*; Yaber and Rabenold 2002). Riparian corridors were forested and typically between 50 m and 150 m wide. Fencerows were typically 15 m to 30 m wide with little understory.

While following birds, I recorded the distance of all the gaps crossed that were greater than 15 m. I report this information for each bird as the mean gap width and the number of gaps/km of path where the path of he bird was known. Because the birds only traveled during the day, I calculated total monitoring time by summing the total daylight between a bird's release and its return or end of monitoring. I defined day length as the time between the beginning and end of local civil twilight (Nautical Almanac Office 2000, 2002), because observed waking timest of these birds most closely matched the beginning of local civil twilight.

Land cover information for the study area was developed from a series of high-resolution (~1 m pixel size) infrared images taken by the Airborne Sensor Facility at the National Aeronautics and Space Administration (NASA) as part of the CARTA program during March 2003 (http:\\asapdata.arc.nasa.gov). Images were orthorectified using a digital elevation model and the coordinates of known locations in the field with the OrthoBASE package in ERDAS IMAGINE 8 (ERDAS Inc. 2002). Land cover was delineated on these images using ArcGIS (ESRI 2005). The calculation of total tree cover for each individual was measured inside an ellipse with foci on the release and capture points and an eccentricity of 1.4. This ellipse approximated the region in which these birds typically moved while returning.

Unless otherwise noted, candidate variables for inclusion in my statistical models were treatment, distance, proportion of tree cover in the ellipse, whether the bird returned, and sex (wrens only). Because $n = 30$ for most of the analyses, I felt it was inappropriate to include all the covariates in a single model. Statistical models were built using forward step-wise entry of variables ($p < 0.1$ for the coefficient for addition, Tables 2-1 to 2-3). I used $p < 0.1$ as the threshold for addition to models and considered variables in combined models to be statistically significant at $p < 0.05$. Analyses were performed using Stata 8.2 (Statacorp 2003). Return success and return time analyses used logistic and Cox regression, respectively. Analysis of the mean gap size and gaps/km used gamma regression with a log link function. Post-hoc tests for group membership used the *test* procedure in Stata (Statacorp 2003).

Results

Return success

Of the 30 translocated individuals of each species, 18 antshrikes and 20 wrens returned (Fig. 2-1). Non-returning birds did not die, but typically settled in a new territory after attempting to return home. The return of both species was less likely, measured using logistic regression, as translocation distance increased (Table 2-1; overall models; antshrikes $\chi^2 = 14.79$, df = 3, $P = 0.002$, pseudo $r^2 = 0.37$; wrens $\chi^2 = 5.04$, df = 1, $P = 0.025$, pseudo $r^2 = 0.13$). Treatment was an important predictor of return success only for the antshrikes where success was significantly lower in pasture translocations relative to riparian corridor translocations (Fig. 2-1). Fencerow returns were intermediate for antshrikes, but not statistically different from either riparian corridor or pasture translocations. The proportion of tree cover (total area of forest, fencerow and stepping stone habitat) within an ellipse around the capture and release points (see *Methods*) was not a significant predictor of return success for either species.

Return time

Returns of both species were slower, measured using Cox proportional hazards regression, as translocation distance increased (Table 2-2; overall models; antshrikes $\chi^2 = 15.80$, df = 3, $P = 0.001$; wrens $\chi^2 = 8.96$, df = 1, $P = 0.003$). The returns of antshrikes were significantly faster in riparian corridor than pasture treatments. Fencerow treatments were intermediate and not significantly different from riparian corridor or pasture treatments. As for return success, the return time of wrens was not affected by treatment and the return time of neither species was significantly affected by the amount of tree cover.

Gap crossing

The reluctance of forest-dwelling species to cross gaps in forest cover is often used to infer the importance of contiguous habitat configuration (Desrochers and Hannon 1997, St. Clair *et al.* 1998, Sieving *et al.* 2000, Bowman and Fahrig 2002). The mean width of gaps crossed was similar between species (54.6 m for wrens, 57.2 m for antshrikes, n = 45, gamma regression $P = 0.787$), but wrens crossed a greater number of gaps / km of known path (2.77 vs. 1.37 gaps / km, n = 60, gamma regression $P = 0.026$). For antshrikes, the proportion of tree cover was negatively correlated with mean gap size and returning individuals crossed larger gaps than non-returning ones (Table 2-3; gamma regression, overall model $\chi^2 = 14.4$, df = 2, $P < 0.001$). Antshrikes crossed fewer gaps / km in riparian corridor treatments than in fencerow or pasture treatments (Table 2-3; gamma regression, overall model $\chi^2 = 14.6$, df = 2, $P < 0.001$). In contrast, wrens crossed fewer gaps / km in fencerow and riparian corridor treatments than in pasture treatments (Table 2-3; gamma regression, overall model $\chi^2 = 54.0$, df = 4, $P < 0.001$).

Returning wrens crossed more gaps / km than non-returning birds and female wrens crossed more gaps / km than males (Table 2-3). These results, based on the number of gaps / km were qualitatively unchanged when I based analyses (not presented here) on the total distance of gaps crossed / km in return trajectories.

Habitat used to return

Although individuals from both species returned in fencerow and pasture treatments, there were strong differences between the species in the habitat used to return within those treatments. For the antshrikes returning in fencerow and pasture treatments, eight used an indirect forested route for the majority (>50%) of the distance during their return and two crossed open pasture habitat by moving among stepping stones or small forest patches (Fig. 2-2). None of the antshrikes used fencerows for the majority of their return. In contrast only one of 13 wrens returning in fencerow and pasture treatments used a forested route for the majority of its return. The remainder used fencerows or crossed gaps by moving among stepping stones and small forest patches. Returning antshrikes moved generally directly along the corridor in riparian corridor treatments, but traveled longer routes around the direct fencerow home in fencerow treatments and around the pasture in pasture treatments (Fig. 2-3). Translocated birds typically made forays out from the release point before moving in a more directed way to their territories (Fig. 2-3; Appendix 1).

Discussion

Using translocations that standardized movement, I have provided the first detailed information about movement behavior collected from birds using corridors at a landscape scale. My results revealed substantial differences between two forest bird species and have several implications for the importance of habitat configuration in fragmented landscapes. To recap, riparian corridors facilitated the movement of the forest specialist antshrikes. Their returns were more likely and faster in riparian corridor treatments over pasture treatments. They preferred forest habitat for their return in fencerow and pasture treatments and avoided fencerows even when the provided a direct route to their capture location. They also crossed fewer gaps / km in riparian corridor treatments than in the other two treatments. By contrast, forest generalist wrens exhibited no differences in return time or success as a function of treatment and made extensive use of fencerows in their returns. They also crossed more gaps / km in their return trajectories although the mean gap width crossed was similar.

One reason that antshrikes generally avoided fencerows may be because fencerows in this landscape were composed of large trees with little or no understory. Antshrikes and other birds that breed in areas with dense understory may not feel secure traveling through this relatively open habitat (Sieving *et al.* 2000). This result is consistent with other work on gap crossing behavior which has reported that specialist species are generally less likely to cross gaps than generalists (Desrochers and Hannon 1997, Harris and Reed 2002, St. Clair 2003). Ultimately, this intolerance may contribute to the greater susceptibility of specialist species to extinction (Şekercioğlu *et al.* 2004). There are many species in other tropical forests that are more reclusive than barred antshrikes. In the Neotropics, terrestrial insectivores are one of the guilds most sensitive to fragmentation (Renjifo 1999, Stouffer *et al.* 2006) and species in these guilds are unwilling to cross forest gaps (Sieving *et al.* 1996, Laurance *et al.* 2004, Stouffer *et al.* 2006). Further work on landscape-level movement for the benefit of conservation planning may benefit from targeting species that are terrestrial or require dense understories.

A second cause of the more conservative movement behavior of the antshrikes relative to the wrens may have to do with their willingness to cross the pasture matrix. My results suggest that this matrix offered high resistance to the movement of the forest specialist species and more moderate resistance for the forest generalist. This resistance seemed to generate a high dependency on corridors for the specialist. Interestingly, corridors and stepping stones were more important in a low-resistance matrix for a meadow-dependent arthropod (Baum *et al.* 2004). For forest understory birds, a more hospitable matrix facilitated greater movement (Castellón and Sieving 2006, Stouffer *et al.* 2006).

A third potential contributor to the more conservative movement behavior of the forest specialist stems from differences in gap crossing behavior. Gaps in forest cover are likely to be perceived as inhospitable and risky by forest birds (Harris and Reed 2002), but no previous corridor study has provided enough spatial resolution to assess gap crossing behavior at a landscape scale. The ability to cross gaps may be critical to travel in fragmented landscapes as suggested by the fact that returning antshrikes crossed larger gaps than antshrikes that did not return. Moreover, the size of gaps they crossed declined in areas with higher forest cover and they crossed fewer gaps / km in riparian corridor treatments, suggesting a preference to detour in forested routes when they are available. On average, wrens crossed twice as many gaps / km on their return paths as antshrikes did, but even they appear to be limited by gap-crossing ability: successfully returning wrens crossed more gaps / km of path than non-returning birds.

In addition to the differences between species, my results revealed some aspects of movement behavior that might be more generalizable among species or differ for reasons other than forest dependency. First, some information about the mechanisms of homing is provided by the general pattern of movement of these birds upon release. Birds of both species typically spent time exploring by moving out from the release point and returning before making a foray in another direction. These forays increased in length until birds appeared to determine the correct direction of travel and found a suitable route to their territory. Non-returning birds made the same forays but eventually abandoned their search and settled in a new territory or wandered to a new area. The period of searching generally lasted longer as translocation distance increased. These forays suggest that these birds were released in unfamiliar areas and that they do not posses a 'bird's eye view' of the landscape. Homing pigeons (*Columba livia*) exhibit a similar pattern with their movement becoming more directed as they recognize landmarks closer to their home loft (Guilford *et al.* 2004). This pattern of movement appears to be similar to the way other animals explore with increasing forays prior to dispersal [red squirrels (*Tamiasciurus hudsonicus*) Haughland and Larsen 2004; butterflies (*Maniola jurtina* and *Pyronia tithonus*), Conradt and Roper 2006, flying squirrels (*Pteromys volans*), Selonen and Hanski 2006].

A second similarity between species with the potential to generalize to other species is the negative effect of translocation distance on return time and success. The implication is that birds are more likely to be able to navigate when they are closer to home where they may encounter familiar aspects of the landscape. In this context, the effect of distance may be greater for tropical species that are year-round residents on their territories and which are unlikely to have familiarity with much of the surrounding landscape. By contrast, migrants in temperate or tropical regions may generally have much greater familiarity with the area surrounding their territories and this may be why translocation distances of comparable magnitudes were not a significant predictor of return time or success for three similar homing studies in temperate regions (Bélisle *et al.* 2001, Bélisle and St. Clair 2001, Gobeil and Villard 2002). It would be interesting to know if migratory behavior provides information to birds about the landscape around their territory and a comparison between tropical year-round residents and tropical breeding migrants may be a profitable line of further study.

A third general implication of my results is to address the ongoing debate about the relative importance of habitat configuration and composition for conservation (Fahrig 1998). Although much of this literature has focused on predicting occurrence or population size (Andrén 1994, Villard *et al.* 1999, Betts *et al.* 2006), movement is the domain most pertinent to configuration. My measure of configuration (treatment) was included in models much more often than my composition variable (proportion tree cover). Configuration of the habitat influenced all of my measures of movement behavior for the antshrikes as well as the gap crossing of the wrens. By contrast, the amount of forest cover affected only the size of gaps crossed by antshrikes. This result contrasts with other studies which have found that percent forest cover predicts return time and success in translocated birds (Bélisle *et al.* 2001, Gobeil and Villard 2002), but they did not have an analogous measure of configuration. These results suggest that configuration is an important component influencing movement, perhaps predictably so in this region of generally low habitat amount (Fahrig 1998).

In sum, my study, which provides the first detailed assessment of how birds use corridors at a landscape scale, suggests that forested riparian corridors are critical to the landscape-scale movement of at least one forest specialist, barred antshrikes, in the highly fragmented dry forests of Costa Rica. Interestingly, my conclusions would have been quite different if I had tested only the forest generalist wren or without the detailed route information: both would have suggested that living fencerows are adequate to facilitate movement, whereas the detailed results from antshrikes revealed fencerows to be almost useless for them as movement corridors. This difference amplifies the caution provided 10 years ago by Beier and Noss (1998) that corridor assessment requires detailed knowledge of movement behavior. While my information was collected from birds moving under the artificial stimulus of capture and translocation, these results are likely to be conservative relative to the context of dispersal that is more pertinent to conservation planning. A dispersing bird would presumably have less motivation to reach a particular destination than would birds returning to a territory and mate and, therefore, are likely to take fewer risks while dispersing. Consequently, I expect dispersing forest specialists to be even more reliant on riparian forested corridors than my results demonstrated. Corridors of natural forest containing intact understory may be important to the movement, and hence persistence, of many other forest-dependent species (Stratford and Robinson 2005).

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Table 2-1. Variables influencing the return success of translocated birds. The reference category for Treatment is pasture. Superscripts on the treatment variables indicate group membership based on post-hoc comparisons ($P \geq 0.05$ for membership).

Species	Variable	Coefficient	SE	*P*
Antshrikes	Distance (km)	-4.88	1.89	0.010
	Treatment-riparian corridor	2.78^{A}	1.42	0.051
	Treatment-fencerow	1.26^{A}	1.17	0.282
	Constant	5.14	2.19	0.019
Wrens	Distance (km)	-2.55	1.24	0.040
	Constant	3.86	1.63	0.018

Table 2-2. Variables influencing the return time of translocated birds. The reference category for Treatment is pasture. Superscripts on the treatment variables indicate group membership based on post-hoc comparisons ($P \geq 0.05$ for membership).

Species	**Variable**	**Hazard ratio**	**SE**	***P***
Antshrikes	Distance (km)	0.046	0.044	0.001
	Treatment-riparian corridor	3.726^A	2.423	0.043
	Treatment-fencerow	2.422^A	1.628	0.188
Wrens	Distance (km)	0.121	0.092	0.005

Table 2-3. Variables influencing the mean gap size crossed and number of gaps crossed / km for translocated antshrikes and wrens. Pasture treatments are the reference category. Superscripts on the treatment variables indicate group membership based on post-hoc comparisons ($P \geq 0.05$ for membership).

Species	Measure	Variable	Coefficient	SE	*P*
Antshrikes	Mean gap	Returned	0.91	0.22	<0.001
	Size	Proportion tree cover	-2.11	0.99	0.032
		Constant	4.13	0.33	<0.001
	Gaps/km	Treatment-riparian corridor	-2.92^{A}	0.69	<0.001
		Treatment-fencerow	-0.02^{B}	0.69	0.976
		Constant	0.70	0.48	0.148
Wrens	Gap size	Constant	4.00	0.12	<0.001
	Gaps/km	Treatment-riparian corridor	-1.92^{A}	0.45	<0.001
		Treatment-fencerow	-0.89^{B}	0.45	0.048
		Constant	1.67	0.32	<0.001

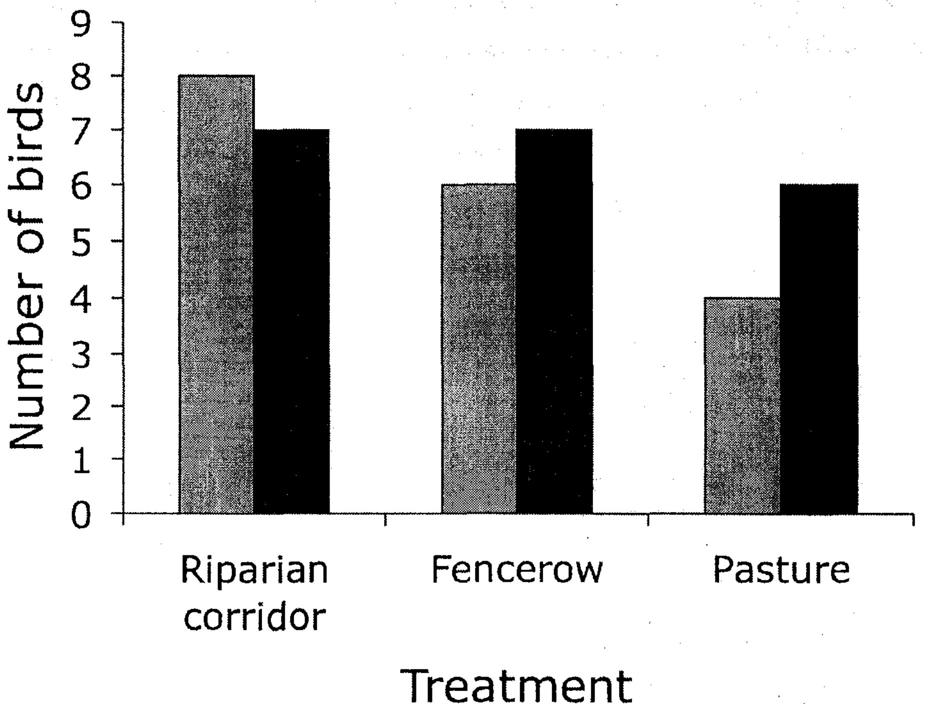

Figure 2-1. Return success by antshrikes (grey bars) and wrens (black bars) in the three treatments following translocation. Ten individuals of each species were translocated in each treatment.

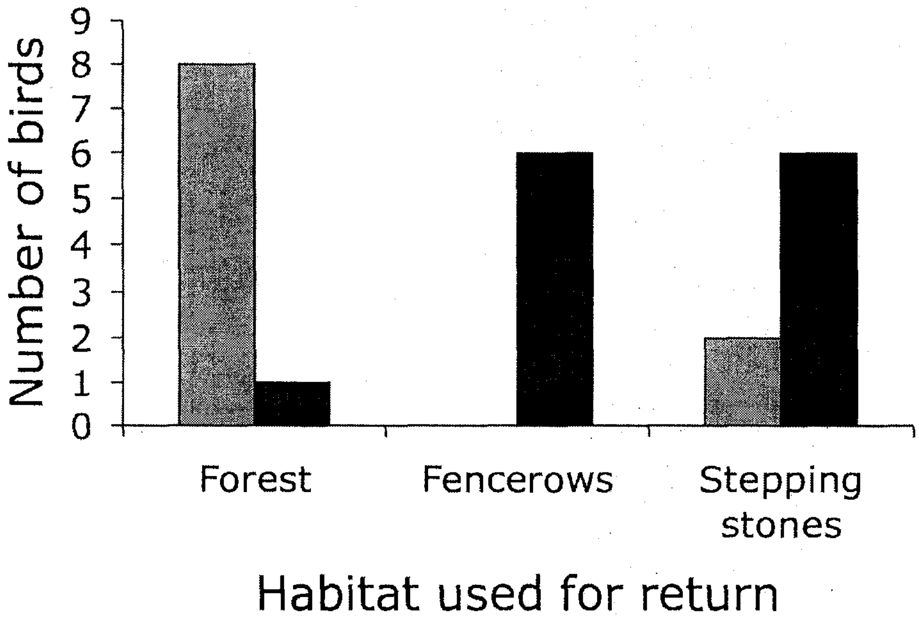

Figure 2-2. Habitat used by antshrikes (grey bars) and wrens (black bars) that returned after translocation in fencerow or pasture treatments.

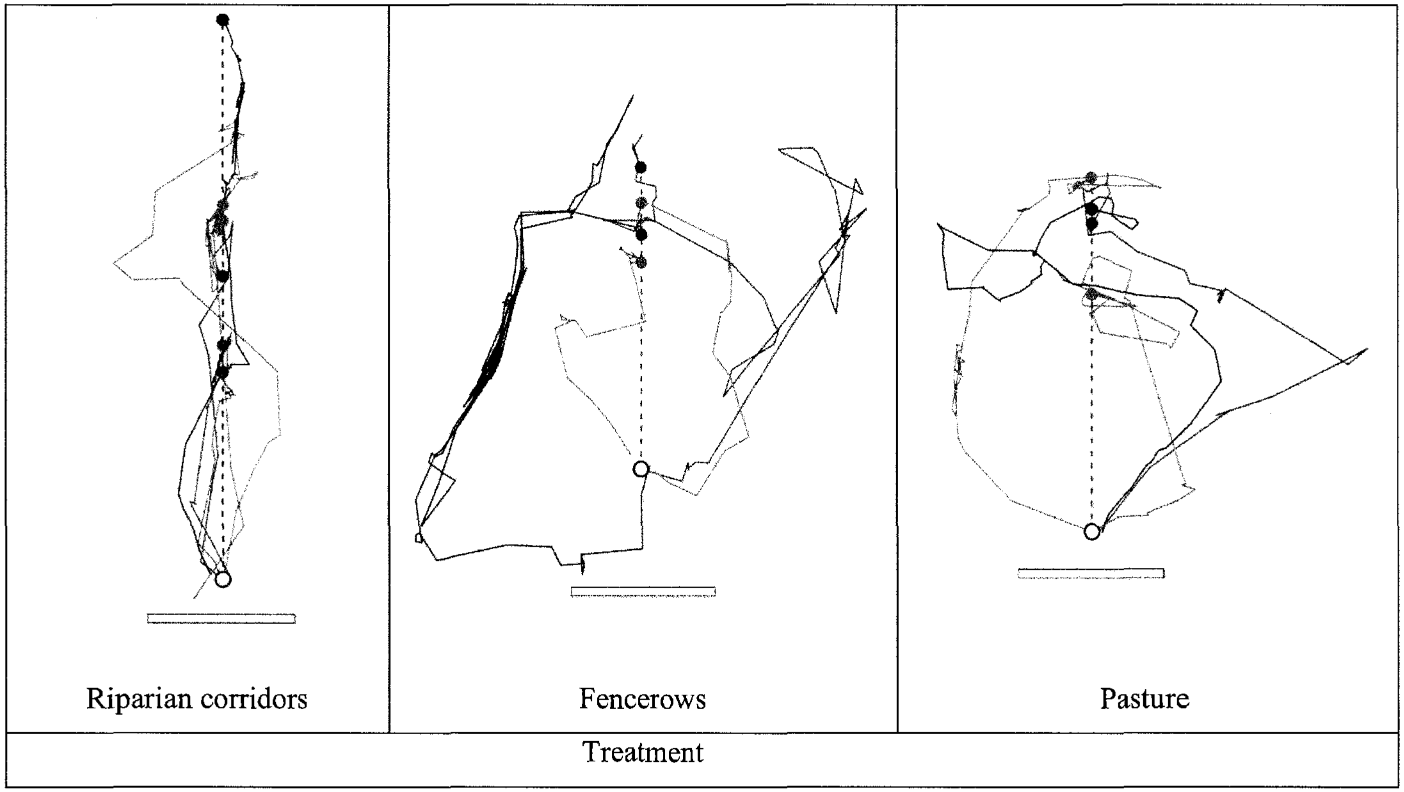

Figure 2-3. Complete paths of returning antshrikes shifted to a common release (open circle) point in riparian corridor (n = 6), fencerow (n = 4), and pasture (n = 4) treatments. Each line represents one individual. The dashed line represents the direct route between the release and capture locations. For scale, the bar at the bottom of each panel is 500 m long. Antshrikes demonstrated consistently direct paths in riparian corridor treatments, but traveled longer routes around fencerows and open pasture in the other two treatments.

Chapter 3

Application of random effects to the study of resources selection by animals[1]

Summary

1) Resource selection estimated by logistic regression is increasingly used in studies to identify critical resources for animal populations and to predict species occurrence.

2) Most frequently, individual animals are monitored and pooled to estimate population-level effects without regard to group or individual-level variation. Pooling assumes both observations and their errors are independent and, resource selection is constant given individual variation in resource availability.

3) Although researchers have identified ways to minimize autocorrelation, variation between individuals caused by differences in selection or available resources, including functional responses in resource selection, have not been well addressed.

4) Here we review random effects models and their application to resource selection modelling to overcome these common limitations. We present a simple case study of an analysis of resource selection by grizzly bears in the foothills of the Canadian Rocky Mountains with and without random effects.

5) Both categorical and continuous variables in the grizzly bear model differed in interpretation, both in statistical significance, and coefficient sign, depending on how a random effect was included. We used a simulation approach to clarify the application of random effects under three common situations for telemetry studies: a) discrepancies in sample sizes among individuals, b) differences among individuals in selection where availability is constant, and c) differences in availability with and without a functional response in resource selection.

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[1] This chapter has been published. Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L, Saher, D. J., Stevens, C. E., and Jerde, C. L. 2006. Journal of Animal Ecology. 75: 887-898.

6) We found random-intercepts accounted for unbalanced sample designs, and models with random intercepts and coefficients improved model fit given variation in selection among individuals and functional responses in selection. Our empirical example and simulations demonstrate how including random effects in resource selection models can aid interpretation and address difficult assumptions limiting their generality. This approach will allow researchers to appropriately estimate marginal (population) and conditional (individual) responses, and account for complex grouping, unbalanced sample designs, and autocorrelation.

Introduction

Resource selection by animals is an important determinant of fitness and is a focus of many ecological studies (Franklin *et al.*, 2000). A common approach for examining species occurrence and habitat selection in the ecological literature are Resource Selection Functions (RSF, (2002). RSF models are attractive to ecologists because they provide quantitative, spatially-explicit, predictive models for animal occurrence (Mladenoff *et al.*, 1995; 2002). RSF models are commonly developed by comparing habitat characteristics at sites that were used by animals to those that were potentially available (RSF; Manly *et al.* 2002). Model coefficients are estimated using logistic regression, which assumes independence among observations (1989). While independence is feasible in some RSF designs, recent reviews emphasize most studies fail to satisfy this assumption (Lennon, 1999; Garshelis, 2000; Morrison, 2001). Autocorrelation among observations produces incorrect variance estimates (Otis & White, 1999; Buckland & Elston, 1993) and an increased Type I error rate (Leban *et al.* 2001). To avoid pseudoreplication (Hurlbert, 1984), researchers often rarify data to achieve independence (Swihart & Slade, 1985) resulting in an unfortunate loss of information (Mcnay & Bunnell, 1994).

There have been two general solutions for non-independence among observations in resource selection studies. The first is compositional analysis (Aebischer *et al.*, 1993) in which individual animals are identified as the unit of replication. Unfortunately, compositional analysis is limited by increased Type I error rates from rare habitats (Bingham & Brennan, 2004). In addition, it cannot accommodate continuous covariates or interaction terms when comparing among individuals, nor Poisson, binomial, or other dependent variable structures. A second solution is the Huber-White sandwich variance estimator, which can be used to calculate robust standard errors without affecting coefficient estimates (Newey & West, 1987; Pendergast *et al.*, 1996). However, because unbalanced numbers of locations among individuals are common in telemetry studies, coefficients will be biased toward the most sampled individuals (Follmann & Lambert, 1989). Therefore, in the presence of an unbalanced design, variance inflators only provide a partial solution to non-independence.

Mysterud and Ims (1998) discuss an additional difficulty in studies of resource selection that has yet to be comprehensively addressed. They demonstrated how use of a resource might differ contingent upon the availability of that resource, which they define as a functional response in resource selection. If animals require a particular amount of a given resource, they may show strong selection for it when scarce but avoid it when it is abundant. Although Mysterud and Ims (1998) criticized the assumption that selection is independent of availability, a flexible treatment of functional responses has not been attempted.

The dual problems of non-independence and functional responses in resource selection can be addressed through application of random effects to RSF models. Random effects are widely applied in cohort, survival, and other hierarchical designs where individuals or groups are sampled repeatedly (Begg & Parides, 2003; Burnham & White, 2002; Franklin *et al.*, 2002; Natarajan & Mcculloch, 1999; Krawchuk & Taylor, 2003). Random effects can accommodate non-independence within groups, such as samples within individuals, or individuals within populations (Breslow & Clayton, 1993)). Although Aebischer *et al.* (1993) first suggested using random effects in resource selection studies, few have incorporated random effects into resource selection or species distribution models in general (see reviews in Rushton, Ormerod, & Kerby 2004, Guisan and Thuiller 2005).

Recent developments of generalized linear mixed models extend random effect designs to binomial responses (Breslow & Clayton, 1993; 2004) and, thus, to modeling resource selection.

In this paper, we first provide a brief overview of random effects models and introduce their application to resource selection modelling. We then illustrate the application of random effects models to a case study of Grizzly bear (*Ursus arctos* L.) resource selection in the Canadian Rocky Mountain Foothills (Nielsen *et al.* 2002). We consider Grizzly bear resource selection for simple categorical and continuous covariates, and compare fixed-effects (without random effects) RSF models to those with random effects for the intercept, categorical, and continuous variables. To aid in our interpretation of random effects in this empirical example, we simulated data for three common scenarios where random effects are included in RSF models: 1) balanced versus unbalanced samples, 2) differences in selection among individuals for a continuous or categorical covariate where availability is constant, and 3) availability varying among individuals and selection is either constant or follows a functional response. We conclude with a discussion of how the inclusion of random effects can control for common limitations in resource selection studies and yield more robust ecological insights.

A brief overview of random effects

Following from their first exposition in ANOVA-type models (e.g., Bennington & Thayne 1994), a variable is considered random when the investigator has not explicitly controlled for levels of the variable in the experimental design, but has chosen a random sample of levels from the population (Bennington & Thayne, 1994; 1996). An example would be individual red deer (*Cervus elaphus* L.) within a population where levels of individual variation (e.g. age) were not fixed but assumed to be representative of the population. By including a random effect for individuals, individual variability is explicitly identified and the scope of inference can be extended to the entire population (Neter *et al.* 1996).

In addition to providing valid population-level inferences, random effects are often invoked to control for correlations among samples. For example, a particular response variable (e.g. telemetry locations) may be correlated within particular strata, for example, within a group (individual deer) or hierarchical association (deer within herds). This unobserved heterogeneity within levels could produce pseudoreplicated samples (Hurlbert 1984) that lack independence, even after controlling for the fixed effects of covariates (Skrondal & Rabe-Hesketh 2004). Parameter estimates from such fixed-effects models will often be biased (Skrondal & Rabe-Hesketh 2004). An added benefit of random effect models is to allow group-level specific estimates for a response, known as the conditional estimate. In comparison, the overall model estimate is known as the marginal, or population-level estimator for a particular response variable (Breslow & Clayton 1993; Begg & Parides 2003; Skrondal & Rabe-Hesketh 2003).

In addition to accounting for within-strata variation, random effects can be used to control for unbalanced designs in the number of observations among individuals or groups (Bennington & Thayne, 1994). Without a random intercept for individual with unbalanced data, sample size differences may influence model coefficients. By accounting for these relationships among samples, including correlation or sampling design-related issues, random effects provide more robust ecological inferences (Pendergast *et al.*, 1996).

Random effects can be added to fixed-effects regression models, including RSF models, in two ways. Random-intercepts allow the intercept or *magnitude of the response* to vary among groups (Fig. 3-1a) whereas the inclusion of random coefficients allows the *effect of covariates* to vary among groups (Fig. 3-1b) (Begg & Parides, 2003; Skrondal & Rabe-Hesketh 2004). In RSF models, random intercepts influence overall prevalence, which, as we illustrate below, often arises because of unbalanced samples (Fig. 3-1a). Random coefficients can be included when there is variation in individual animal, group, etc., responses to a particular covariate (Fig. 3-1b). Random effects models can easily accommodate two or more levels, e.g. samples from individual deer within herds within populations, or wolves (*Canis lupus* L.) within packs. When a model contains both random and fixed-effects, it is termed a mixed-effect model. Functional responses in selection might be accommodated through the combination of a random intercept and random coefficient (Fig. 3-1c).

Assumptions of random effects models include 1) correlations within groups are constant over time unless explicitly modeled, 2) the random effects are normally distributed with a zero mean and unknown variance components, and 3) the variance-covariance structure is specified correctly (Breslow 1993; Skrondal & Rabe-Hestketh 2004). The most common structure is compound symmetric, which considers covariance among all responses of an individual to be constant (Skrondal & Rabe-Hesketh 2004). For time series data, an autoregressive structure could be useful (Pinheiro & Bates 2000). More complex structures could include average, lagged, factor, unrestricted, and hybrid correlation structures that are beyond our purview (see Pinheiro & Bates 2000 for more detailed information).

Materials and methods

Including random effects in RSF models

Following Manly *et al.* (2002: p100), we use a typical fixed-effects exponential RSF,

$$\hat{w}(x) = \exp(\hat{\beta}_0 + \hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \ldots + \hat{\beta}_n x_n)\,, \qquad \text{Eq. 1}$$

with covariates x_n, and $\hat{\beta}_n$ are the coefficients (parameters) estimated from logistic regression (Manly *et al.* 2002). Commonly, the intercept $\hat{\beta}_0$ is dropped from the RSF formulation as discussed and justified by Manly *et al.* (2002), however, because we will be using random intercepts, we include $\hat{\beta}_0$ in the expression for $\hat{w}(x)$.

Coefficients for the random intercept and random effect RSF model are estimated using logistic regression by a generalized linear mixed-effects logit model (Skrondal & Rabe-Hesketh 2004). The conditional mean of Y given x, $\pi(x)$, follows the standard logistic regression notation presented, discussed, and reviewed by Hosmer and Lemeshow (2000). In our example, we consider a two-level random effect model, where observations i=1...n are clustered within strata j=1...m, for example, locations within individuals. For a random intercept model, the logit model, $g(x)$, is estimated for location i for grizzly bear j,

$$g(x) = \ln\left[\frac{\pi(x)}{1-\pi(x)}\right] = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \ldots + \beta_n x_{nij} + \gamma_{0j}\ , \qquad \text{Eq. 2}$$

where x_n are covariates with fixed regression coefficients β_n , β_0 is the mean intercept, and γ_{0j} is the random intercept, which is the difference between the mean intercept β_0 for all groups and the intercept for group j (Skrondal & Rabe-Hesketh 2004, pp 51-54). Note that γ_{0j} is the random effect in Eq. 2 and all preceding terms represent the normal fixed effects as in Eq. 1. Here and throughout, we assume random effects are normally distributed as is common in mixed-effects modelling (Hosmer & Lemeshow 2000, Skrondal & Rabe-Hesketh 2004). However, this assumption should be investigated using exploratory data analysis and plots of the residuals.

For the model with a random intercept and a random coefficient, the RSF coefficients are estimated following:

$$g(x) = \beta_0 + \beta_1 x_{1ij} + .. + \beta_n x_{nij} + \gamma_{nj} x_{nj} + \gamma_{0j} \qquad \text{Eq. 3}$$

where notation follows from Eq. 2 with the addition of $\gamma_{nj} x_{nj}$ where γ_{nj} is the random coefficient of covariate x_n for group j. Models with a random coefficient include a random intercept because a random coefficient forces variation in the intercept (Skrondal and Rabe-Hesketh 2004).

Recent advances in maximum likelihood theory have made implementing random effects in generalized linear models easier in many statistical packages. For STATA, the standard function is GLLAMM, reviewed by Skrondal & Rabe-Hesketh (2004), available at http://www.gllamm.org. For SAS, the standard procedure is GLIMMIX from http://support.sas.com/rnd/app/papers/glimmix.pdf. For S-Plus and R, standard functions include glme and glmmPQL, and glmmML, glmm, respectively (Pinheiro & Bates 2000).

Application of random effects to grizzly bear resource selection

Grizzly (brown) bears are a species of conservation concern across the circumpolar north, and as a result, their resource selection patterns have frequently been the subject of applied research (e.g. McLellan & Hovey 2001, Nielsen *et al.* 2002). To explore how random effects can influence RSF models, we re-analyzed a grizzly bear GPS radiotelemetry dataset from Nielsen *et al.* (2002) in the Eastern slopes of Alberta's Canadian Rocky Mountain Foothills. To minimize complications in seasonal variation in habitat use we focus on only the late summer and fall period (1 August to denning). In total, 2,471 use locations from 3 adult male and 6 adult female bears during 1999 were used from a 5,332 km^2 study area. Samples were unbalanced, varying from 89 to 494 observations per individual (Table 3-1). Availability was defined for each animal by drawing 1000 random locations from 100% minimum convex polygon (MCP) home ranges (ranging in size from 383 – 1588 km^2) thus the measure of availability was unique to each animal. As such, our analysis corresponded to analyzing resource selection at the 3rd-order scale of selection (Johnson 1980). For each used and available location, two environmental variables were queried from a geographic information system (GIS): open habitats (a categorical landcover variable from Franklin *et al.* (2001) identifying the location as either open = 1 or forested = 0) and elevation (in 100m units). A more detailed description of the study design, data, and study area can be found in Nielsen *et al.* (2002).

We estimated grizzly bear RSF models using four approaches. We first used fixed-effects logistic regression to estimate the coefficients of the RSF in Eq. 1, which we refer to as the naïve RSF model. Second, we evaluated a common method used to account for autocorrelation within individuals, namely, by employing the Huber-White sandwich variance estimator (*sensu* Nielsen *et al.* 2002) within a fixed-effects logit model. Finally, we compare these 2 models to the RSF models derived from a random intercept model (Eq. 2), and models with a random intercept and random coefficient (Eq. 3) for either open habitat or elevation.

Random effect models were estimated using the GLLAMM procedure with adaptive quadrature (2001; 2004) in STATA 8.2 (StataCorp 2003) and a compound symmetric covariance structure, which assumes that all samples within a group are, on average, equally correlated (Skrondal & Rabe-Hesketh 2004). Conditional coefficient estimates for each individual were produced using the GLLAPRED procedure (Rabe-Hesketh *et al.* 2001). Model selection for models with random effects is complicated because the intended scope of inference, conditional or marginal, influences the derivation of information theoretic metrics such as the consistent AIC (cAIC) developed specifically for application to such models (Burnham & Anderson 2002; Burnham & White 2002). See Vaida & Blanchard (2005) for details of model selection with random effects; herein, we do not consider model selection for random effects further. We focus instead on evaluating changes to model fit based on Log-Likelihoods, *log(£)*, marginal coefficient estimates, their standard errors (SE), and the variance of the random effects.

Understanding Random Effects in Resource Selection Studies: simulated examples

To provide insight into interpreting RSF models with random effects, we simulated data under three common sampling designs. We designed our simulation following the grizzly bear data, generating used and available points, and estimated the coefficients for RSF models following Eq. 1-3 above. Due to the computational time required to solve mixed models using conventional software, our study was a demonstration using a single simulation for each of the scenarios considered, not a statistical simulation study with 1000's of iterations to reveal inferential bounds of random effects in RSF models (*sensu* Burnham & White 2002).

Simulating Use-Availability Data

Using STATA 8.2 (2003), we simulated data with a logit function of the form $\pi(x)= e^{g(x)} / (1 + e^{g(x)})$, because it allowed us to generate used (1) and unused (0) points, based on the simulation selection function $g(x)$. We retained only simulated use (1) points and generated an independent random sample of available points. The linear function, $g(x)$, of the parameters is provided for each example discussed below. Our set of covariates (fixed effects) included one standardized continuous variable, elevation, (x_1) and one categorical variable, open habitat (x_2). Unless otherwise noted, all elevations were standardized to be uniformly available over a range of 0 to 2 for x_1, and the two categories of x_2, open and closed canopy, were equally prevalent. For each analysis, we randomly selected 500 available points for each individual from its range of available elevations and from the available habitat types. We simulated population-level resource selection producing a distribution of used points that selected higher elevations (higher values of x_1) and selected open habitat, with 61% of used points being in open habitat. A copy of our simulation and analysis code for STATA 8.2 is available from the senior author, and our simulations were independently verified (M. Taper, pers.comm., Montana State University).

Example 1: Fixed effects for balanced and unbalanced designs

Model 1: $g(x) = \beta_0 + \beta_1(x_{1,i,j}) + \beta_2(x_{2,i,j})$

β_0 is the intercept, β_1 and β_2 are the coefficients on the variables x_1 and x_2, respectively (i designates the observation while j designates the group). In all three examples $\beta_0 = -0.5$, $\beta_1 = 1$, and $\beta_2 = 1$. In this example, selection was invariant across individuals for both elevation and open habitat, and animals had the same availability. For our balanced design we observed 20 individuals ($j = 1 \ldots 20$) with 100 observations each ($i = 1 \ldots 2000$). For the unbalanced design, the number of observations per individual was drawn from a normal distribution ($\mu = 100$, $\sigma = 40$). No random effect was used in the generation of these example data.

Example 2: Differences in selection among individuals using a random effect

Model 2a: $g(x) = \beta_0 + \beta_1(x_{1,i,j}) + \beta_2(x_{2,i,j}) + \gamma_1(x_{1,i,j}) + \gamma_{0j}$

Model 2b: $g(x) = \beta_0 + \beta_1(x_{1,i,j}) + \beta_2(x_{2,i,j}) + \gamma_2(x_{2,i,j}) + \gamma_{0j}$

For model 2a, γ_1 was drawn from a Normal distribution ($\mu = 0$, $\sigma = 2$) for each individual *j*, while γ_2 for model 2b was drawn from a Normal distribution ($\mu = 0$, $\sigma = 1$) for each individual *j*. The gamma (γ) terms are random effects that add differences in selection among individual animals (as in Eq. 2, 3). We considered differences in selection among animals for either elevation or open habitat across the same range of availability, with balanced samples among individuals (Fig. 3-1b).

Example 3: Differences in availability and functional responses among individuals

Model 3a: $g(x) = \beta_0 + \beta_1(x_{1,i,j}) + \beta_2(x_{2,i,j})$

Model 3b: $g(x) = \beta_0 + \beta_1(x_{1,i,j}) + \beta_2(x_{2,i,j}) + \gamma_1(x_{1,i,j}) + \gamma_{0j}$

Model 3c: $g(x) = \beta_0 + \beta_1(x_{1,i,j}) + \beta_2(x_{2,i,j})$

Model 3d: $g(x) = \beta_0 + \beta_1(x_{1,i,j}) + \beta_2(x_{2,i,j}) + \gamma_2(x_{2,i,j}) + \gamma_{0j}$

We hypothesized that availability and the corresponding selection function could differ among individuals in two ways. Individuals with differences in availability could exhibit the same selection despite differences in availability (Fig. 3-1a). Alternately, selection could change with availability for each individual, with the population exhibiting a functional response (see Fig. 3-1c). Model 3a uses a fixed effects model but the range of available elevations ($x_{1,i,j}$) for each *j* individual was different. All individuals had the same selection. Model 3b uses the same shifts in the range of available as in Model 3a but the strength of selection (represented as $\gamma_{1,j}$) for higher elevations by an individual (*j*) was inversely related to the shift in $x_{1,i,j}$. This produced stronger selection for higher elevations when the mean elevation available to that individual was low and weaker selection when the mean elevation available was high. This reflects a situation where bears living at lower elevations show strong selection for higher elevations within their home range, whereas bears living in high mountain areas do not exhibit selection for high elevations areas because these areas may be unproductive high alpine areas. Models 3c and 3d mirrored those above but for the categorical open habitat covariate. In both scenarios, the availability of the two resource categories differed among individuals. The prevalence of open habitat ranged from 7% to 84% and in 3d, selection for open habitat was related to its prevalence such that selection increased as open habitat declined in prevalence and selection decreased when open habitat was more prevalent. This type of functional response to open habitat could occur if grizzly bears were getting most of their forage in this open habitat so they would exhibit strong selection for this habitat when it is rare, but much weaker selection for this habitat when it, and the forage it contains, is abundant.

Statistical Analyses

The statistical analyses of our simulated data were the same as for the grizzly bear data, but we used XTLOGIT in STATA 8.2 (StataCorp 2003) to solve models with only a random intercept.

Results

Grizzly bear RSF

Model coefficients, their standard errors and random effect variances are presented in Table 3-2. The 'naïve' RSF model indicated that relative probability of use was higher in open habitats and declined at higher elevations (Table 3-2). Instead of reducing variance by clustering on individual bears, the Huber/White variance estimator (cluster) increased the standard error on the coefficients for both open habitat and elevation (Table 3-2). The addition of a random intercept improved model fit substantially and changed the magnitude of the coefficients with the coefficient for elevation becoming marginally significant and, notably, changing sign (Table 3-2). In the model with a random coefficient for open habitat, model fit improved again, and the coefficient for elevation changed markedly from being negative and non-significant to being positive and highly significant (Table 3-2). The model with a random coefficient for elevation exhibited similar results to the model with only a random intercept with relatively large variance in the random intercept (Table 3-2). Conditional estimates for selection for elevation for individual grizzly bears (Fig. 3-2) confirms the absence of functional responses or more complex patterns in selection, yet reveals clearly how much individual variation in selection for elevation occurs. Clearly, the variability in coefficients and their significance yields differing conclusions depending on the model used. In most of the models, managers would conclude that elevation is not an important variable, but its effect becomes very strong once a random coefficient for open habitat is added to the model. The model with the random coefficient for elevation is, however, a much better fit to the data, measured by the log(L).

In these data, individual bears had differing sample sizes of used points, differing home ranges and hence differing availability, and they appear to have differing selection for both elevation and the open habitat variable. It is not clear, however, which of these individual differences are exerting the greatest influence in the random effects models.

Simulations

Balanced versus Unbalanced Designs

When simulated data contained no variation in resource selection among individuals and the design was balanced across individuals, as expected, the inclusion of a random effect did not improve model fit (Table 3-3a). Log-Likelihoods (*log(L)*) and coefficient estimates were stable across all modelling approaches. As expected, there was very little variation in the intercept and coefficient estimates for models that included respective random variables. In contrast, when the design was unbalanced across individuals (a range of 31 to 181 use points per individual) model fit was improved with the inclusion of a random intercept (Table 3-3b, Fig. 3-3a). All three mixed effect models resulted in a similar decrease in *log(L)*compared to the fixed effect logistic model. Coefficients and standard errors were fairly robust across all models with coefficients in mixed effect models only deviating slightly from the fixed effect logistic model. In the unbalanced design, where the model included both a random intercept and coefficient, the variance in the random intercept was much larger than the variance in the random coefficient, when compared relative to the coefficient estimate, suggesting that individuals vary primarily in their intercept. In both balanced and unbalanced designs, clustering on individuals using the Huber-White sandwich estimator resulted in decreased standard errors for both the continuous and categorical coefficients (Table 3-3).

Differences in Selection

Simulations introduced variation among individuals in selection for either elevation or open habitat when availability was constant (Table 3-4). Adding a random intercept did not affect model fit or coefficient estimates. The Huber-White sandwich estimator (clustering) inflated standard errors for simulated random individual coefficients (Table 3-4a,b). However, clustering deflated the standard error associated with open habitat where individuals varied only in their response to elevation (Table 3-4a, Fig. 3-3b) and for elevation where individuals varied only in their selection for open habitat (Table 3-4b). Models including a random intercept and coefficient (Table 3-4a,b) resulted in different parameter estimates and standard errors relative to the fixed effect logistic models as would be expected based on the substantial variance estimated in the random effect (Table 3-4). Changes in standard errors and coefficients were seen predominantly in the covariate for which we simulated individual variation.

Differences in Availability and Functional Responses

Adding random effects for data with a differing range of available elevations (Table 3-5a), improved model fit (*log(£)*) and altered β_1 and its standard error compared to the fixed effect logistic model. Adding random effects had no influence on the model fit or parameters when there was differing availability of the two habitat types among individuals (Table 3-5c). In contrast, with a functional response in resource selection for either elevation or open habitat (Table 3-5b, d, Fig. 3-3c), incorporation of a random intercept and random coefficient improved model fit. Parameter estimates changed significantly for the variables that were simulated to have functional responses. Again, clustering inflated standard errors for variables that included random variation and deflated standard errors for variables simulated without individual variation.

Discussion

Our empirical and simulated examples demonstrate the utility and need for the application of random effects for estimating population-level responses in studies of resource selection. The analysis of the grizzly bear telemetry data demonstrated that inferences from resource selection models can change with the addition of random effects, suggesting important group level correlation that would otherwise be overlooked. For example, the strength of grizzly bear selection for elevation varied greatly depending on whether a random coefficient for open habitat was included in the model (Table 3-2). Model fit was greatly improved with the addition of random effects suggesting that random effects have merit in grizzly bears RSF models, and conditional estimates of selection (Fig. 3-2) for elevation illustrates wide individual variation in this trait. The greatest improvement in model fit came from the addition of a random intercept (Table 3-2), which our simulations revealed could compensate for the widely unbalanced samples among bears (Tables 3-1, 3-3). Further improvements in model fit to the grizzly bear data with the addition of random coefficients combined with the results from the simulations illustrates that there appears to be differences among individual bears in their selection for these two variables. While a functional response could be conceivable for elevation, conditional estimates from Fig. 3-2 clearly illustrated the pattern was a result of variation in selection, not a functional response.

Where sample sizes are balanced among individuals and animals respond to resources in a similar way, we found, as expected, random effects to be unnecessary for estimating coefficients for an RSF model. However, for unbalanced designs, including a random intercept provides an alternative to compositional analyses (Aebischer *et al.* 1993) or rarefaction of data (Swihart & Slade 1985). The individual animal is accounted for as the sample unit, and the predicted probability of use for the population is independent of the sampling intensity for individuals (Table 3-1). In the grizzly bear data, three bears had roughly five times as many locations as three other bears, which would normally result in those bears having five times the influence on model coefficients (Table 3-1). Using a random intercept alone to account for this imbalance changed the direction of the response to elevation and the coefficient changed from being non-significant to being marginally significant, and dramatically improved model fit. Use of the Huber/White variance estimator to generate "robust" standard errors would have concluded that the selection for open habitat was only marginally significant, a conclusion quite different from the one drawn from the model with a random intercept.

Our results suggest using the Huber-White variance estimator (White, 1982; Pendergast *et al.*, 1996) may help identify correlation structure among individuals. In our simulated balanced design case with no correlation structure among individuals (Table 3-1a), standard errors estimated with the Huber-White estimator (clustering) decreased relative to the fixed effect logistic model. In the simulation, where variation was induced among individuals in their selection, and in the grizzly bear example (Table 3-2), clustering inflated standard errors. Thus, clustering may have utility as a diagnostic, directing researchers to where random effects may be necessary. Further work is needed to verify these preliminary suggestions.

We only considered one level of nesting in our simulated examples. In the presence of multiple hierarchies, random effects become even more important (Berlin *et al.*, 1999; Ten Have *et al.*, 1999; Begg & Parides, 2003). For example, individuals can be nested within herds, which are nested themselves in river basins, or subpopulations. Studies of resource selection of social animals in such settings have suffered from an inability to accommodate multiple level of nesting (Morrison, 2001; Garshelis, 2000). The most important consideration, however, is that including a random effect in studies with inherent hierarchical structure ensures the marginal population inferences of the resultant RSF will be valid (Berlin *et al.*, 1999; Begg & Parides, 2003; Cam *et al.*, 2002) and will provide appropriate conditional (group) level inferences (eg., Fig. 3-2). Although we focused on marginal effects (population-level) here, mixed effect models provide a powerful approach for examining evolutionary processes and questions related to the fitness consequences of individual-level variation in studies of resource selection (Franklin *et al.*, 2000). For example, relying on marginal (population) inferences for an endangered species may hide important conditional (subpopulation or individual) differences that could have important implications for conservation. Conditional estimates of resource selection could be used to identify which subpopulations to focus conservation efforts on.

Our simulated examples demonstrate that random intercepts can correct for unbalanced designs, but balanced use-availability designs may require both a random intercept and coefficient to detect individual variation in selection. Simulations in other fields (Ten Have *et al.*, 1999) draw similar conclusions regarding the importance of random coefficients. Many wildlife studies thus far, however, have focused on the inclusion of a random intercept without incorporation of random coefficients (Franklin *et al.*, 2002; Cam *et al.*, 2002; Boyce *et al.*, 2005). We caution that in resource selection studies with use-available designs, including only a random intercept will only account for differences in samples sizes but not for differences in selection among individuals. In our unbalanced simulation, adding a random coefficient in addition to a random intercept decreased the random intercept variance and improved model fit slightly. This was likely a result of the random coefficient explaining some of the variance in the random intercept (Skrondal & Rabe-Hesketh 2004) and accounting for slight differences in the coefficient due to the random generation of used and available points.

Perhaps the most compelling argument for considering random coefficients in RSF models comes from the ability of random coefficients to model functional responses (Mysterud & Ims, 1998). Mysterud and Ims (1998) provide a simple framework for assessing functional responses in examples with 2 habitat types (e.g. Osko *et al.* 2004). However, available resources are often more than 2 categories or continuous, and Mysterud & Ims (1998) concluded by urging future studies to consider generalizations of the logit model. Our results suggest that inclusion of a random intercept and coefficient provides a useful generalization. To our knowledge, this is the first demonstration of an approach to effectively model functional responses in resource selection. As a guide in using random effects to uncover functional responses we offer the following suggestions. The isolation of functional responses in continuous covariates may require a multifaceted approach. Consider that after we simulated a functional response in elevation (Table 3-3b), we improved model fit over the fixed effect model by including a random coefficient for open habitat rather than elevation. This is an example of conditionality between the model intercept and the categorical covariate coefficient. When the coefficient for the continuous covariate (elevation) is altered, individual intercepts are altered (see Fig. 3-3b), having an effect on the categorical variable (habitat type) because the effect of habitat type = 0 is absorbed by the intercept. Even so, results in Table 3-3b indicate a functional response in elevation given the magnitude of change in model fit. Thus, we believe measures of model fit will be critical to assessing where functional responses in RSF occur when there is no *a priori* decision to consider particular random effects (see also (Greenland, 2000).

Critical to modeling a functional response in resource selection is identification of a resource type that is limiting in a trade-off situation (Mysterud & Ims 1998). Without a trade-off, constant selection (Fig. 3-1a) will be possible (e.g. a constant proportion of habitat in a home range). However, as in the gray squirrel (*Sciurus carolinensis* Gmelin) example in Mysterud & Ims (1998), gray squirrels made a trade-off once the amount of cropland increased beyond some threshold (Fig. 1 of Mysterud & Ims 1998), showing avoidance for cropland once availability of cropland exceeded 30% of a squirrel's home range. Often, however, ecologists will be faced with the problem of identifying for which covariate the random effect or functional response occurs. Simple approaches include graphical examination of conditional effects (e.g., Fig. 3-2), and dividing animals into two groups for preliminary RSF modeling (Mauritzen *et al.*, 2003; Osko *et al.*, 2004).

An additional challenge for researchers is that in a RSF design as the number of available points increases, the magnitude of the $log(L)$ also increases (unpubl. data), and therefore, model selection using AIC or similar likelihood approaches may be sensitive to the choice of the number of available points. Finding a way to use information-theoretic approaches in RSF studies and in mixed effect models is an issue that deserves future attention.

Conclusions

Animal data often possess nested or grouped data structures, and inclusion of random effects in resource selection and species distribution models will accommodate such data structures, yielding more robust inference. Random effects improve our ability to account for differences in selection or sample size among individuals or groups and their inclusion can affect the conclusions drawn. Conditional inferences from these mixed effect models will allow researchers to make group specific inferences, with obvious applications to endangered species management and other conservation applications where individual level variation is important. By including random coefficients, the assumption that selection patterns remain constant as availability changes need no longer restrict the development and application of RSF models. We believe that relaxation of this requirement will provide increasingly flexible and powerful resource selection models that allow extrapolation beyond study area borders with increasing biological realism, efficiency, and validity. Given the success of existing resource selection modeling approaches in natural resource management, we believe specification of the functional response will increase the utility of these models to ecology and conservation.

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Table 3-1. Number of GPS telemetry locations per grizzly bear used in random effect Resource Selection Function (RSF) models.

Bear ID	Number of GPS locations	Sex
G2	493	F
G3	227	F
G4	388	F
G5	98	M
G6	92	M
G8	89	M
G10	149	F
G16	441	F
G20	494	F
Total	2471	

Table 3-2. Grizzly bear RSF models with a) fixed effects, b) fixed effects with cluster, c) mixed effects with random intercepts, and d) mixed effects fitting a random intercept and coefficients, with parameter estimates (β_i) and standard errors (SE). Elevation is in 100m intervals, and open habitat is a categorical covariate (open=1 or forested=0). Log-Likelihood reflects model fit. The variance estimates represent the variance in the random intercept (Int.) or coefficient (Coef.).

Model Structure	**Log-Likelihood**	**Elevation x_1**			**Open Habitat x_2**			**Variance**	
		β_i	**SE**	p	β_i	**SE**	p	**Int.**	**Coef.**
Grizzly bear RSF parameters									
1) Logistic	-5902.4	-0.005	0.008	0.503	0.572	0.050	<0.001	--	
2) Logistic with Cluster	-5902.4	-0.005	0.089	0.951	0.572	0.288	0.046	--	
3) Logistic with Random Intercept	-5555.7	0.023	0.012	0.065	0.477	0.052	<0.001	0.47	
4) Logistic with Random Intercept & Random x_1	-5426.2	0.026	0.033	0.439	0.417	0.055	<0.001	19.4	0.047
5) Logistic with Random Intercept & Random x_2	-5499.1	0.041	0.013	0.001	0.431	0.145	0.028	0.761	0.300

Table 3-3. Parameter estimates and standard errors for logistic regression models on data simulated with no correlation structure among individuals. Models fit to the data were 1) fixed effects 2) fixed effects with cluster (see text), 3) mixed effects fitting a random intercept 4) mixed effects fitting a random intercept and random coefficient for elevation (x_1), or 5) a random coefficient for open habitat (x_2). Elevation is a continuous covariate and habitat type is a categorical covariate. Estimates are shown for a) a balanced design (100 used and 500 available points for each of 20 animals) and b) an unbalanced design (31 to 181 used and 500 available points for each of 20 animals).

Model Structure	Log-Likelihood	Variable x_1		Variable x_2		Variance	
		β_i	SE	β_i	SE	Int.	Coef.
a) Balanced Design							
1) Logistic	– 5303	0.434	0.043	0.513	0.051		
2) Logistic with Cluster	– 5303	0.434	0.033	0.513	0.039		
3) Logistic with Random Intercept	– 5303	0.434	0.043	0.513	0.051	0.000	
4) Logistic with Random Intercept & Random x_1	– 5303	0.434	0.043	0.513	0.051	0.000	0.000
5) Logistic with Random Intercept & Random x_2	– 5303	0.434	0.043	0.513	0.051	0.000	0.000
b) Unbalanced Design							
1) Logistic	– 5257	0.463	0.044	0.49	0.051		
2) Logistic with Cluster	– 5257	0.463	0.043	0.49	0.043		
3) Logistic with Random Intercept	– 5168	0.467	0.044	0.494	0.051	0.568	
4) Logistic with Random Intercept & Random x_1	– 5167	0.467	0.047	0.496	0.051	0.165	0.000
5) Logistic with Random Intercept & Random x_2	– 5166	0.469	0.044	0.522	0.058	0.214	0.006

Table 3-4. Parameter estimates and standard errors for logistic regression models on data simulated with a) individual variation in their response to elevation (x_1) and b) individual variation in their response to the open habitat (x_2). Availability was constant across all individuals. Models fit to the data were the same as for Tables 3-2 and 3-3.

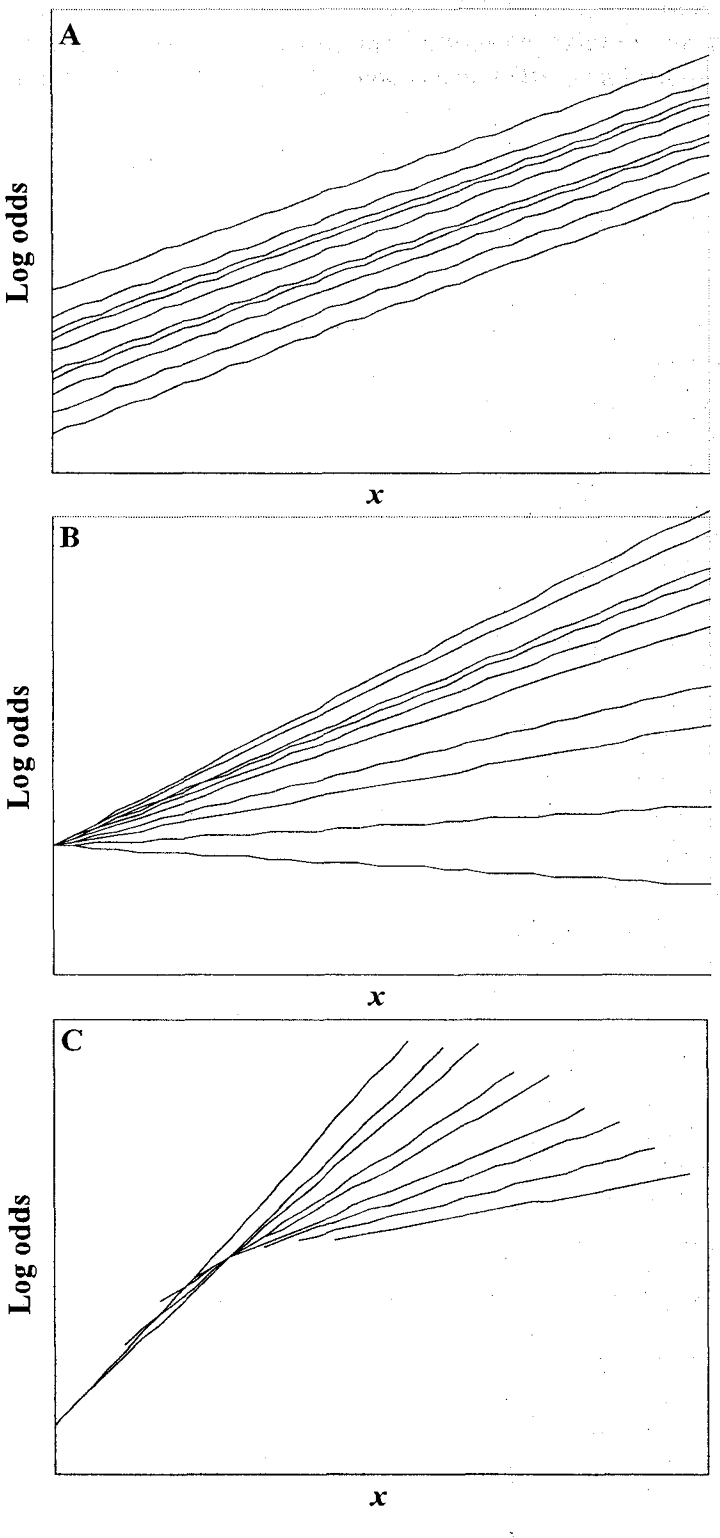
Model Structure	**Log-Likelihood**	**Variable x_1**		**Variable x_2**		**Variance**	
		β_i	**SE**	β_i	**SE**	**Int.**	**Coef.**
a) Random Individual Coefficients for x_1							
1) Logistic	− 5331	0.387	0.043	0.414	0.050		
2) Logistic with Cluster	− 5331	0.387	0.150	0.414	0.036		
3) Logistic with Random Intercept	− 5331	0.387	0.043	0.414	0.050	0.000	
4) Logistic with Random Intercept & Random x_1	− 5250	0.423	0.150	0.426	0.051	0.514	0.408
5) Logistic with Random Intercept & Random x_2	− 5331	0.387	0.043	0.414	0.050	0.000	0.000
b) Random Individual Coefficients for x_2							
1) Logistic	− 5326	0.420	0.043	0.404	0.050		
2) Logistic with Cluster	− 5326	0.420	0.040	0.404	0.158		
3) Logistic with Random Intercept	− 5326	0.420	0.043	0.404	0.050	0.000	
4) Logistic with Random Intercept & Random x_1	− 5326	0.420	0.043	0.404	0.050	0.000	0.000
5) Logistic with Random Intercept & Random x_2	− 5261	0.428	0.044	0.460	0.165	0.199	0.488

Table 3-5. Parameter estimates and standard errors for logistic regression models on data simulated with differing availabilities among individuals and with and without a functional response to these changes in availability. a) constant response to elevation (x_1) with changing availability, b) changing response to elevation (x_1) with changing availability, c) constant response to open habitat (x_2) with changing availability, and d) changing response to open habitat (x_2) with changing availability. Simulation models fit to the data were the same as for Table 4.

Model Structure	**Log-Likelihood**	Variable x_1		Variable x_2		Variance	
		β_i	**SE**	β_i	**SE**	**Int.**	**Coef.**
a) Constant Selection, Changing Availability of x_1							
1) Logistic	– 5335	0.251	0.033	0.465	0.050		
2) Logistic with Cluster	– 5335	0.251	0.037	0.465	0.046		
3) Logistic with Random Intercept	– 5335	0.251	0.033	0.465	0.050	0.000	
4) Logistic with Random Intercept & Random x_1	– 5333	0.310	0.052	0.465	0.050	0.000	0.007
5) Logistic with Random Intercept & Random X_2	– 5334	0.301	0.049	0.465	0.055	0.001	0.010
b) Differing Selection as a Function of Changing Availability of x_1							
1) Logistic	– 5317	0.299	0.033	0.494	0.050		
2) Logistic with Cluster	– 5317	0.299	0.056	0.494	0.042		
3) Logistic with Random Intercept	– 5317	0.299	0.033	0.494	0.050	0.000	
4) Logistic with Random Intercept & Random x_1	– 5305	0.423	0.066	0.496	0.051	0.013	0.038
5) Logistic with Random Intercept & Random x_2	– 5312	0.417	0.048	0.496	0.054	0.046	0.008

Model Structure	Log-Likelihood	Variable x_1		Variable x_2		Variance	
		β_i	SE	β_i	SE	Int.	Coef.
c) Constant Selection, Changing Availability of x_2							
1) Logistic	– 5317	0.468	0.044	0.391	0.049		
2) Logistic with Cluster	– 5317	0.468	0.042	0.391	0.042		
3) Logistic with Random Intercept	– 5317	0.468	0.044	0.391	0.049	0.000	
4) Logistic with Random Intercept & Random x_1	– 5317	0.468	0.044	0.391	0.049	0.000	0.000
5) Logistic with Random Intercept & Random x_2	– 5317	0.468	0.044	0.391	0.049	0.000	0.000
d) Differing Selection as a Function of Changing Availability of x_2							
1) Logistic	– 5253	0.436	0.044	0.717	0.051		
2) Logistic with Cluster	– 5253	0.436	0.035	0.717	0.176		
3) Logistic with Random Intercept	– 5253	0.436	0.044	0.717	0.051	0.000	
4) Logistic with Random Intercept & Random x_1	– 5253	0.436	0.044	0.723	0.055	0.000	0.000
5) Logistic with Random Intercept & Random x_2	– 5154	0.430	0.044	0.741	0.191	0.150	0.679

Figure 3-1. Conceptual plot of the use of a resource unit along a gradient of a continuous covariate *x* for individuals having random intercepts (A), random coefficients (B), or a functional response to the availability of *x* (C).


A
Log odds
x
B
Log odds
x
C
Log odds
x

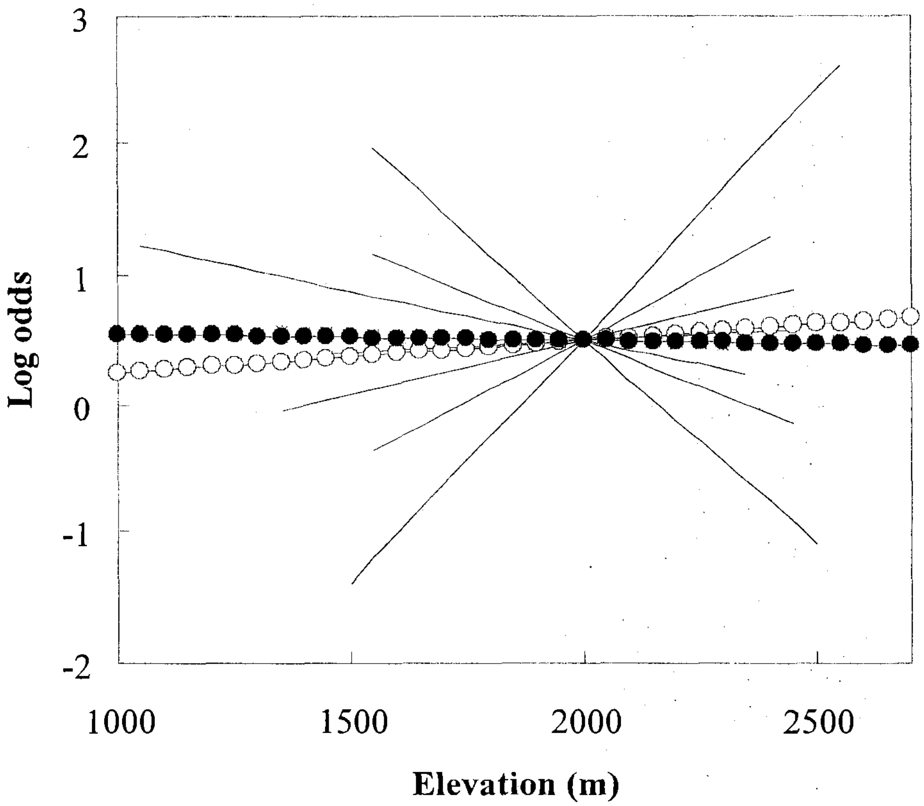
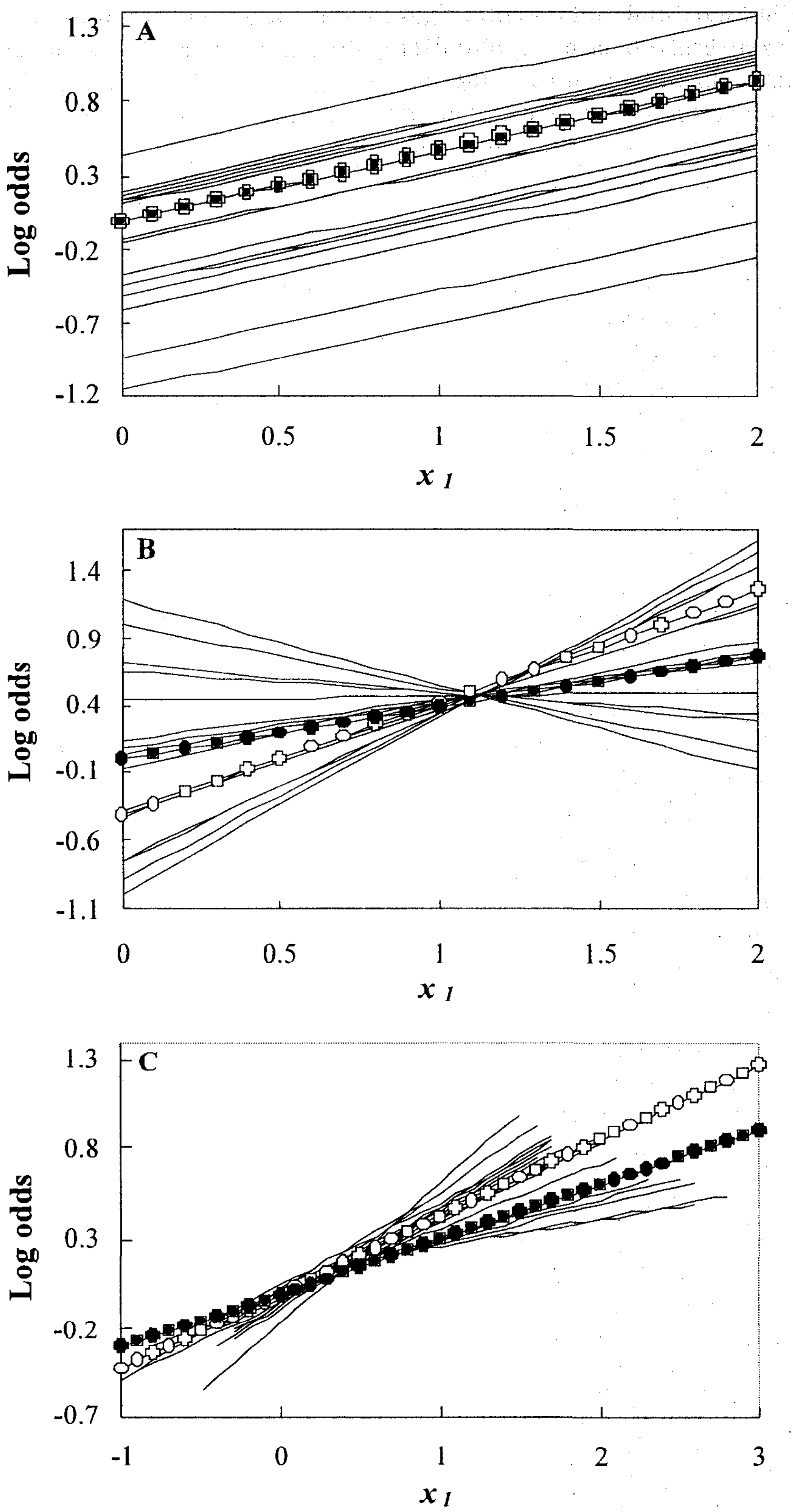


Figure 3-2. Conditional estimates of the relative predicted probability of use as a logit function for individual grizzly bear selection for elevation (thin lines), the marginal population estimate (connected white dots), and the traditional fixed effects logit model estimate (connected black dots) for a grizzly bear RSF model with a random coefficient for elevation.

Figure 3-3. Conditional estimates of the relative predicted probability of use as a logit function for simulated individuals (thin lines), the marginal population estimate (connected white dots), and the traditional fixed-effect logisitic model estimates (connected black dots) for individuals having differing samples sizes and a model with a random intercept (A), differing selection and a random coefficient for elevation (x_1) (B), and a functional response to elevation (x_1) with a random coefficient for elevation (C).


A
Log odds
1.3
0.8
0.3
-0.2
-0.7
-1.2
0
0.5
1
1.5
2
x_1
B
Log odds
1.4
0.9
0.4
-0.1
-0.6
-1.1
0
0.5
1
1.5
2
x_1
C
Log odds
1.3
0.8
0.3
-0.2
-0.7
-1
0
1
2
3
x_1

Chapter 4

Functional responses in habitat selection by tropical birds moving through fragmented forest[1]

Abstract

1. The ability of animals to move through a landscape is a fundamental determinant of population persistence in fragmented habitats. Key contributors to this movement are the responses of moving animals to the composition and configuration of the habitat that remains. To date, there have been few studies of habitat selection by animals moving at landscape scales and none that address the way responses to habitat elements vary as a function of their availability; a functional response (*sensu* Mysterud & Ims 1998).

2. To assess habitat selection during movement, I translocated 60 individuals of two species of birds with differing forest dependency in three configuration treatments in a highly fragmented, tropical dry forest landscape: along a riparian corridor, along a fencerow, or across pasture. I closely followed the return routes of translocated birds to determine their choice of habitat type and proximity to the edges that delineated forest habitat. I then tested whether habitat composition or configuration (treatment) best explained individual variation in habitat selection.

3. Both species exhibited a preference for habitat closer to the forest edge, but this preference was weaker in the forest specialist, the barred antshrike (*Thamnophilus doliatus*). This species selected routes in forest habitat over fencerow and stepping stone habitat, which were all preferred over pasture habitat.

4. By contrast, the forest generalist, the rufous-naped wren (*Campylorhynchus rufinucha*) preferred forested habitat equally to fencerow and stepping stone habitat over pasture habitat. For it, fencerow habitat was selected more strongly than stepping stones.

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[1] I intend to submit this paper to *Journal of Applied Ecology*.

5. Analysis of the individual variation in selection for forest habitat revealed that both species exhibited a functional response to habitat configuration, selecting forest more strongly in riparian corridor treatments where it was also more abundant. The forest specialist also reduced its preference for edge habitat in riparian corridor treatments.

6. *Synthesis and applications*. The unprecedented precision of my route information suggests that forest is the most important habitat for moving forest specialists, relative to fencerow and stepping stone habitat. Forested riparian corridors allowed the forest specialist to travel in what I assume to be safer habitat further from the forest edge. Functional responses to habitat configuration indicate that these species take greater risks when forested corridors are not present.

Introduction

Habitat loss and fragmentation have been widely acknowledged as major contributors to biodiversity loss worldwide. Many of the species affected by habitat loss dwell in forest, which is permanently cleared for urbanization, agriculture and industry. The long-term persistence of forest-dependent species in landscapes that have been anthropogenically fragmented is expected to depend on the success with which individuals move within and among sub-populations (Hanski 1998). The mechanistic basis of this movement is habitat selection and yet there have been very few detailed assessments of the way moving animals select habitat at the landscape scales at which habitat fragmentation occurs (Selonen & Hanski 2006; Chetkiewicz *et al.* 2006).

Habitat selection by animals in fragmented habitats can be influenced by both the composition and configuration of the preferred habitat (e.g. Potvin *et al.* 2000; Stubblefield *et al.* 2006; Radford & Bennett 2007). In general, habitat configuration is expected to be more important to population persistence in landscapes in which small amounts of the original habitat remain (Fahrig 1998), such as those dominated by agriculture. Fundamental components of habitat configuration in these landscapes are those elements facilitating animal movement among isolated populations. Conduits for animal movement may be provided by riparian corridors (Beier & Noss 1998), fencerows (living fences; Rosenberg *et al.* 1997; Şekercioğlu *et al.* 2002), and stepping stones of individual trees (Fischer & Lindemayer 2002a). All of these have been advocated for conservation planning (Rosenberg *et al.* 1997). Because these habitat elements typically create an abrupt edge with the surrounding matrix, edge response is a fundamental part of habitat selection in highly fragmented habitats (McCollin 1998). To date, these responses have been studied in the context of distance from edges within home ranges (e.g. Desrochers & Fortin 2000) or breeding territories (e.g. Mazerolle & Hobson 2003), as directional response to patch edges (e.g. Schultz & Crone 2001; Schtickzelle *et al.* 2007) or as directional response to corridor edges (e.g. Andreassen *et al.* 1996; Haddad 1999; Levey *et al.* 2005). I know of no study that has provided a detailed assessment of habitat selection and the effect of edges on animals traveling at large spatial scales (> 200 m) in fragmented landscapes.

More detailed information about habitat selection for animals moving at landscape scales is particularly important in the tropical dry forests of Mesoamerica where only 2% of the original forest remains (Janzen 1986). Pressure on the remaining forest is likely to continue as the agricultural land area expands to meet growing food demand (Tilman *et al.* 2001). Tropical birds, and insectivores in particular, are considered to be more sensitive to forest destruction than their temperate counterparts (Harris & Reed 2002; Stratford & Robinson 2005) and one contributor to this difference may be greater sensitivity to forest edges (Lindell *et al.* 2007). This sensitivity, in turn, may occur because areas near the edge of tropical forests are very different, physically and climatically, from the forest interior (Laurance *et al.* 2002). Edge habitats are expected to present greater predation risk for forest birds (McCollin 1998; Ries *et al.* 2004).

Where forest birds occur when moving through highly fragmented tropical landscapes likely depends on two main attributes: the type of habitat elements used and the selection or avoidance of habitat edges these elements create. Identifying the responses of birds to both attributes can be achieved using resources selection functions (hereafter RSFs; Boyce & McDonald 1999; Manly *et al.* 2002), which quantify habitat preferences based on the habitats used relative to their availability. RSFs typically examine the mean habitat selection for a sample of individuals. However, this approach can obscure individual differences in selection stemming from variation in their habitat context. It is more likely that the habitat preferences animals exhibit for a particular habitat type varies with habitat abundance (Mysterud & Ims 1998). Mysterud & Ims (1998) termed this difference a functional response to habitat availability and acknowledged that it may also vary with changes in the spatial arrangement, or configuration, of the habitat. They developed a method to examine functional responses in a relatively simple trade-off scenario with two categories of a single habitat variable. Recent advances in the methodology used to analyze resource selection (Gillies *et al.* 2006) make it possible to explore individual-specific habitat selection and examine functional responses for multiple habitat types and continuous variables.

To better understand habitat and edge selection and test whether moving birds exhibit functional responses to habitat configuration or composition, I translocated and then followed the returns of 60 individuals of two species of insectivorous forest birds as they traveled through highly fragmented tropical dry forest in Costa Rica. Translocations were aligned in three treatments of habitat configuration corresponding to common habitat elements in this and other highly fragmented, agriculturally-dominated forests: riparian corridors, fencerows, and open pasture. This experimental approach enabled us to collect information about habitat and edge selection by adult birds moving in novel habitat at a landscape scale. This observed behaviour may reflect the behaviour of the dispersing individuals that are so critical to the persistence of subpopulations (Levey *et al.* 2005). Using translocations allowed us to standardize the bird's motivation for moving, anticipate the direction it would predominantly travel, and choose the configuration of the intervening habitat (Bélisle 2005).

Materials and Methods

Study area

I followed the movement of two species in an agricultural landscape of northwestern Costa Rica near the town of Liberia. This landscape was once comprised of contiguous tropical dry forest, but is now dominated by cattle pasture. Remaining forest is often confined to riparian areas. The landscape also contains fencerows that have been planted at the edges of fields and individual trees or small patches of trees in the pasture that I term stepping stones. These are typically remnants of the original forest cover that have been retained as shade for the cattle. Fencerows and stepping stones are rare relative to forest habitat (Table 4-1).

Translocations and tracking

I followed moving forest birds in real time at a landscape scale, collecting information about their route and habitat use. I translocated 30 territorial barred antshrikes (*Thamnophilus doliatus*, hereafter antshrikes) and 30 rufous-naped wrens (*Campylorhynchus rufinucha*, hereafter wrens) between 0.7 and 1.9 km. Both are common insectivores that hold territories year-round, but antshrikes are forest specialists, typically being found only the in the understory of the most intact forest in this region (Stiles & Skutch 1989). Birds were moved away from their territory in one of three treatments: along riparian corridors, along fencerows, and through pasture. I conducted translocations from June to August 2000 and January to June 2002. All individuals were caught by 0940 local time (mean capture time = 0659 hours ± 65 min) by attracting them into a mistnet with a playback of a conspecific song. I moved male antshrikes and both male and female adults of the monomorphic wrens. I attached a radio transmitter using eyelash adhesive to trimmed feathers on the backs of translocated individuals. Birds were captured in forest and released in fencerow or forest habitat. Birds were translocated along unique configurations except I used each of three fencerows for two trials of differing distances due to the relative rarity of that habitat type in the study area. Most wrens (23 of 30) were sexed by extracting DNA from a whole tail feather (Griffiths *et al.* 1998). The remaining individuals were sexed by comparing their weight, tarsus length, and exposed culmen length to measurements of individuals of known sex using a discriminant function analysis (Desrochers 1990). I translocated 14 female and 16 male wrens.

Following release, I recorded with radio-telemetry and hand-held GPS units the location of each translocated bird approximately every 15 minutes (mean=14.8 min ± 8.2 min standard deviation) for up to 4 days and daily thereafter for 10 days or until they returned, whichever was earlier. Two observers closely followed individuals by simultaneously triangulating their location from a mean distance of 27 m ± 13 m. These positions provided trajectories of moving birds, which I used to assess the habitat used during movement. Sixty individuals were translocated; one bird from each species was translocated in each treatment at each of ten distances (0.7-1.3 km in 0.1 km intervals, then 1.45, 1.6, and 1.9 km). Even the shortest translocations were well outside the home range of these birds. Although empirical information for the home range size of these species is not available, home range radius was ~ 60 m for a : cogener to the antshrike in Brazil (*T. caerulescens*; Duca *et al.* 2006) and ~ 75 m for a cogener to the wren in Venezuela (*C. nuchalis*; Yaber & Rabenold 2002). Riparian corridors were typically between 50 m and 150 m wide. Fencerows were typically 15 m to 30 m wide with little understory.

Land cover information

Land cover information for the study area was developed from a series of high-resolution (~1 m pixel size) infrared images taken by the Airborne Sensor Facility at the National Aeronautics and Space Administration (NASA) as part of the CARTA program during March 2003 (http:\\asapdata.arc.nasa.gov). Images were orthorectified using a digital elevation model and the coordinates of known locations in the field with the OrthoBASE package in ERDAS IMAGINE 8 (ERDAS Inc. 2002). Land cover was delineated on these images using ArcGIS (ESRI 2005) as pasture, forest, fencerow, or stepping stone habitat. The calculation of total tree cover (forest, fencerow, and stepping stone habitat combined) for each individual was measured inside an ellipse with foci on the release and capture points and an eccentricity of 1.4. This ellipse approximated the region in which these birds typically moved while returning. For the habitat selection analysis, used locations were intersected with the land cover and I sampled the available habitat at 1000 random locations within each individual's ellipse using 'Hawth's Tools' (Beyer 2007). Similarly, I measured the distance to the forest edge for those observed locations that occurred in forest and I sampled the available distance from the forest edge at 200 random points in forest within each individual's ellipse.

Data analysis

Habitat selection and edge selection were both analyzed using Resource Selection Functions (RSF; Manly *et al.* 2002) using mixed-effects logistic regression. The RSF for habitat selection compared the used habitat types to their availability. The RSF for Edge selection examined whether the birds selected or avoided areas closer to the forest edge. I included random effects in all models to account for the correlation inherent in taking multiple samples from the same individual and to correct for differing samples sizes among individuals (Gillies *et al.* 2006). The inclusion of a random intercept for each individual helps account for differences among individuals in the number of used and available points. Inclusion of a random coefficient allows individuals to vary from the population coefficient estimate in the strength of selection for a covariate. This approach also made it possible to assess individual-specific responses to habitat variables in addition to the estimate of population-level responses (Gillies *et al.* 2006).

Statistical models for the individual-specific (random) coefficients were built using forward step-wise entry of variables ($p < 0.1$ for the coefficient for addition). Because $n = 30$ for these two analyses, I felt it was inappropriate to include all the covariates in a single model. I considered variables to be statistically significant at $p < 0.05$, but used $p < 0.1$ for addition to include variables that may have been significant with a larger sample size. The candidate variables for inclusion in the model are in Table 4-2. Variables describing the amount of forest cover and the mean distance from the edge for the random points were included to investigate how birds responded to habitat availability in the habitat and edge selection, respectively. I tested for the addition of interaction terms once there were no more univariate variables to add at $p < 0.1$. For the analysis of edge selection I included only those individuals that had 10 or more used points in forest (antshrikes $n = 29$; wrens $n = 26$). I removed one outlier from the analysis of the antshrike edge selection coefficients because the value for forest selection was greater than five standard deviations different than the mean for the rest of the individuals in that treatment. Mean available distances to the forest edge ranged from 16 m to 141 m (mean = 38 m) for the antshrikes and 8 m to 76 m (mean = 33 m). All analyses were performed using Stata 10.0 (Statacorp 2007). The mixed-effects logistic regressions used the *GLLAMM* package in Stata (Rabe-Hesketh & Skrondal 2004) and the analyses of the individual-specific coefficients used linear regression. Post-hoc tests for group membership used the *test* procedure in Stata (Statacorp 2007).

Results

Habitat Selection

To determine which habitats birds selected or avoided in their return paths, I built a resource selection function (RSF; Manly *et al.* 2002) for each species. In these initial analyses, a single categorical variable described the habitat elements birds could select in their return journeys: forest, fencerow, stepping stones, with pasture as the reference category. There were 2441 used locations for the antshrikes and 2295 for the wrens, with a range of 12 to 175 per individual for the antshrikes and 11 to 248 for the wrens.

The forest specialist antshrikes selected all three habitats relative to pasture (Fig. 4-1; Table 4-3). Predictably, they exhibited significantly stronger selection for forest than for either fencerow or stepping stone habitat. The forest generalist wrens also selected all three habitats relative to pasture (Fig. 4-1; Table 4-3), but this generalist species selected fencerow habitat more strongly than stepping stone habitat and showed an intermediate preference for forest habitat, which did not differ significantly from either fencerow or stepping stone habitat (Table 4-3). For both species, I included in these initial models a random intercept and a random coefficient for forest habitat which revealed substantial individual variation in the strength of selection (Fig. 4-1).

To better understand whether habitat composition (forest cover) or configuration (treatment) was affecting the strength of an individual's selection for forest, I next regressed their individual-specific coefficients against my candidate predictor variables (Table 4-2). For both species, configuration treatment and whether the bird returned were significant predictors of the variation in selection for forest (Table 4-4; overall model for antshrikes $F_{3,26} = 11.55$, $P = 0.0001$, $r^2 = 0.57$; wrens $F_{4,25} = 9.41$, $P = 0.0001$, $r^2 = 0.60$). This effect of forest configuration indicates that selection for forest habitat increased in riparian corridor treatments and decreased in fencerow treatments relative to pasture treatments. Put another way, these birds exhibited greater preference for forest habitat when forested routes were available, the requirement of a functional response. When they were in a fencerow or pasture treatment, they were using the forest less than in riparian corridor treatments, and this change is greatest in fencerow treatments. Non-returning birds selected forest more strongly than returning birds of both species. Finally, female wrens selected forest more strongly than males.

Edge selection

There were a total of 2224 used points in forest for the antshrikes and 1669 for the wrens with which I examined selection for edge proximity. Sample sizes ranged from 11 to 171 per individual for the antshrikes and 11 to 202 for the wrens. Both species selected positions closer to the edge relative to the random locations, but this preference was stronger in the wrens than the antshrikes (Table 4-3). Inclusion of a random intercept and a random coefficient for distance to the edge improved the fit of the models for both species, again indicative of substantial variation in edge preference among individuals.

For the antshrikes, the individual-specific coefficients for edge selection were related to treatment, which is my measure of habitat configuration (Table 4-5; overall model $F_{2,25} = 6.59$, $P = 0.005$, $r^2 = 0.35$). The other candidate variables (Table 4-2) were not significant predictors and were not added to the model. Antshrikes selected edges more strongly in pasture and fencerow treatments than riparian corridor treatments. In riparian corridor treatments, their selection for edge was neutral, they neither selected nor avoided edge habitat when they had a forested route to their territory. For wrens, increases in forest cover were slightly associated with a lesser preference for edge habitat, but this effect was shy of conventional statistical significance (Table 4-5; overall model $F_{1,22} = 3.88$, $P = 0.0617$, $r^2 = 0.15$). In landscapes with low forest cover, wrens selected edge habitat, but their response to edges became approximately neutral in landscapes with higher amounts of forest cover (max. = 58% forest cover). In sum, both species selected edges in treatments with less forest and the antshrikes were less selective of edge or neutral in the more forested corridor treatments.

Discussion

Closely following the movement of translocated birds allowed us to examine the habitat preferences and edge selection of two species of tropical forest birds as they moved through novel, fragmented landscapes. Differences in their habitat selection were consistent with differences in what is known of their breeding habitat. The forest specialist consistently selected more forested locations relative to the other habitat elements. The generalist selected the three habitats similarly although it preferred fencerow habitat to stepping stone habitat. While habitat preferences are typically related to food availability (Buler *et al.* 2007), few studies have examined the habitat selection of moving birds. I assume that preference for forest by the forest specialist is related to both food availability and the need for security cover while moving. Indeed, animals may select habitat for movement similarly to what they select for breeding or home range purposes (Chetkiewicz *et al.* 2006). This may explain why understory and terrestrial insectivores are consistently some of the most sensitive species to fragmentation. Their unwillingness to enter or cross open habitat (Develey & Stouffer 2001; Harris & Reed 2002; Stouffer *et al.* 2006) or to travel in areas with little understory (Sieving *et al.* 2000) may be caused by the fact that these habitats do not contain usable habitat for foraging or other activities. Preference for fencerow habitat by the generalist suggests that they select these habitats to provide a direct route of mostly continuous trees through the open matrix, but it may also be that their more generalist foraging strategies make the habitat more suitable in other contexts. Despite these average differences between the two species, there was also large individual variation in the strength of selection for forest cover within species.

The application of random effects to my models of habitat selection made it possible to examine the sources of variation among individuals. In my context and other applications of resource selection functions, random effects also make it possible to determine whether selection changes with availability (Gillies *et al.* 2006), the essence of a functional response (Mysterud and Ims 1998). Mysterud & Ims (1998) developed a method to recognize functional responses in cases with two categories of a single habitat variable. In addition to this difference in habitat composition, they suggested that animals could also exhibit a functional response to the spatial arrangement of habitat, its configuration. Although there has been much attention paid to the relative effects of habitat composition and configuration on abundance of forest birds on breeding territories (e.g. Villard *et al.* 1999; Betts *et al.* 2007; Radford & Bennett 2007), this is, to my knowledge, the first investigation of their relative importance to habitat selection by animals moving in a novel landscape. My analyses of the individual-specific coefficients suggested that both species adjusted their selection of habitat elements in response to habitat configuration, but not habitat composition. By contrast, when predicting returns rather than habitat selection, results from previous translocation studies suggested that composition was important in some cases (Bélisle *et al.* 2001; Gobeil & Villard 2002), but configuration affected the return of birds in other contexts (Bélisle *et al.* 2001; Bélisle & St. Clair 2001; Chapter 2). In this study, both species used non-forest habitat (fencerows and stepping stones) more when they did not have a direct forested route home, possibly adjusting their habitat selection as a compromise to be able to return home. This trade-off is suggested by the observation that returning birds of both species had weaker selection for forest than did non-returning birds. Male wrens also had weaker selection for forest habitat than did females. The sex difference may reflect greater fitness consequences of territory loss for males. In a cooperatively breeding congener, males had higher reproductive success if they stayed on territories to inherit breeding positions than if they dispersed from their natal territory (Yaber & Rabenold 2002). This effect was reversed in females. Thus males may have stronger motivation to return to their territories to retain their breeding position rather than move to a new territory.

Similar to the overall measures of habitat selection, there were differences between species in edge selection. Other studies have examined edge selection on breeding territories (e.g. Restrepo & Gomez 1998; Mazerolle & Hobson 2003; Laurance 2004) and winter home ranges (Desrochers & Fortin 2000), but it has been difficult to collect such information from forest birds as they move through novel landscapes, a context with much relevance to the value of corridors for conservation. In my study, both the specialist and generalist exhibited preference for areas closer to the edge, though this preference was weaker in the forest specialist. This result contrasts with other work in the Neotropics where insectivores have been found to avoid areas near the forest edge (Restrepo & Gomez 1998; Laurance 2004). Nonetheless, there is some consistency in the extent of edge avoidance within guilds. Similar to my results, Laurance (2004) found that midstory insectivores, which occupy a more generalized niche, were indifferent to edges, whereas solitary understory species – specialists – actively avoided edges. However, much variation in edge preference in my study was attributable to individuals and this variation is typically obscured in assessments of the mean response of all individuals.

Examining correlates of individual-specific coefficients for edge selection in my study revealed how individuals adjust their edge selection to broad landscape differences and provides insight on how corridors may facilitate bird movement more generally. By moving closer to edges in landscapes without a direct forested corridor home (in pasture and fencerow treatements), the forest specialist exhibited a functional response to habitat configuration, but not to the availability of distances to the edge or measures of habitat composition. In riparian corridor treatments, their behaviour was neutral, neither selecting nor avoiding edge. In contrast, Levey *et al.* (2005) found that edges channeled birds along the edges of corridors. Consistent with this finding, several authors have suggested that observed behaviour at edges would channel bird movement in corridors (Machtans *et al.* 1996; Desrochers & Fortin 2000) or have found evidence for reflection off boundaries facilitating corridor function in other taxa (Andreassen *et al.* 1996; Haddad 1999).

In my study, it appears that specialist birds moved closer to the forest edge, and hence potentially directed by it, only when they did not have the option of traveling directly home via riparian corridors. Within corridors, they traveled at greater distance from the edge (mean = 34 m, range 17 m to 59 m, n = 10), where it was less likely they were channeled by edge habitat, but successfully used other mechanisms to home. For the generalist, the slight trend for edge selection to decline with increasing forest cover (the only measure of habitat composition that neared significance) suggests that they avoided edges when it had the option of doing so. Together, these results argue against an automatic predation disadvantage of edges in corridors (*sensu* Simberloff *et al.* 1992). Even if predation risk is higher at forest edges (McCollin 1998), the presence of riparian corridors in this landscape presumably allowed birds to travel with less risk relative to fencerow or pasture configurations.

Fencerow and stepping stone habitat were not the preferred habitat for the forest specialist, but they were on par with forest habitat for the forest generalist and they were important for the specialist outside of riparian corridor treatments. These findings may have important implications for the retention of these features. Fencerows and stepping stones are relatively rare habitats compared to forest and are easily influenced by human activity. Fencerows are planted by farmers at the edges of their fields whereas stepping stones are created primarily when farmers leave large trees or patches of trees from the original forest as shade for cattle. Interviews with farmers in my study area indicated that some of them planned to intensify their operations, using methods that would require fields with fewer or no obstacles to accommodate the use of machinery (unpublished data). This could result in the clearing of stepping stones especially, which has been observed in other areas following agricultural instensification for mechanized irrigation (Maron & Fitzsimons 2007). Beyond their value to traveling birds, these remnant trees can also be very important for birds living in the agricultural landscape (Fischer & Lindenmayer 2002b; Şekercioğlu *et al.* 2007). Fischer *et al.* (2006) promoted the retention of stepping stones as a general principle of conservation in agricultural landscapes. Because many of the existing stepping stone are in cattle pasture where natural regeneration is unlikely (Manning *et al.* 2006), active planting of stepping stones is likely needed to retain them in the landscape. Loss of stepping stones could have substantial impacts on the permeability of this landscape and they are likely to be similarly important in other landscapes, particularly for forest generalists.

In sum, this study provided some of the first detailed information on habitat and edge selection and associated functional responses for animals moving at a landscape scale. Although my information was collected from birds moving under an artificial stimulus (translocation and homing), the differences among and within species I reported are likely suggestive of the ways habitat fragmentation influences dispersing tropical birds. Moreover, my results are likely to be conservative. A dispersing bird would have less motivation to reach a final destination than would birds returning to a territory and mate. The forest specialist in particular is likely to take fewer risks while dispersing; selecting forest habitat more strongly and avoiding edge habitat. Consequently, I expect dispersing forest specialists to be even more reliant on forest and forested corridors and show weaker edge selection or even avoidance than my results demonstrated.

Despite these caveats, my study demonstrated that forested habitat is likely critical to the movement of forest specialist birds. The presence of forested corridors increased selection for forest habitat and is likely to minimize the predation risk encountered by moving birds. The shifts in habitat and edge selection I reported represented functional responses to habitat configuration, suggesting that habitat configuration may be as important or more important than habitat composition to the movement of animals in highly fragmented habitats. For the forest generalist, both fencerows and stepping stones appeared to be important contributors to movement and stepping stones were also important to the specialist species when forest routes were not available. These findings support suggestions that these habitat elements are important contributors to connectivity and deserving of more attention in conservation planning (Fischer *et al.* 2006; Manning *et al.* 2006).

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Table 4-1. Habitat amounts in each of the three treatments, including means and standard deviations, measured in the 20 ellipses for each treatment.

Treatment	Forest	Fencerows	Stepping Stones	Total
Riparian corridor	35.3% ± 13.5%	2.9% ± 2.1%	1.9% ± 1.0%	40.2% ± 13.7%
Fencerow	21.8% ± 11.6%	6.3% ± 2.9%	2.6% ± 1.2%	30.6% ± 10.9%
Pasture	16.8% ± 7.9%	3.1% ± 2.8%	4.0% ± 2.1%	23.8% ± 7.9%

Table 4-2. Candidate variables for inclusion in the forward step-wise addition of variables to the models explaining individual-specific (random) coefficients. Measures of cover were the proportion of the ellipse around the capture and release points that contained that habitat (forest, fencerow or stepping stone). Pasture treatments were the reference category for the treatment variable. I considered treatment as a measure of habitat configuration and measures of cover as measures of habitat composition.

Analysis	**Candidate variable**
Habitat selection	Treatment (2 levels; riparian corridor and fencerow)
	Forest cover
	Treatment*forest cover
	Fencerow cover
	Stepping stone cover
	Whether returned
	Translocation distance
	Sex (wrens only)
Edge selection	Treatment (2 levels; riparian corridor and fencerow)
	Mean available distance to edge
	Treatment*mean available distance
	Forest cover
	Fencerow cover
	Stepping stone cover
	Whether returned
	Translocation distance
	Sex (wrens only)

Table 4-3. Table of model coefficients, standard errors, significance, and random effect variance for habitat and edge selection. Pasture habitat provides the reference category to which the other habitat types were compared. Superscripts denote group membership for posthoc comparisons.

Analysis	Species	Variable	Coefficient	SE	P	Random effect variance
Habitat Selection	Antshrikes	Forest	6.48^{A}	0.52	<0.001	5.42
		Fencerow	5.23^{B}	0.22	<0.001	
		Stepping Stone	5.08^{B}	0.22	<0.001	
		Constant	-7.99	0.47	<0.001	4.03
	Wrens	Forest	5.48^{AB}	0.48	<0.001	5.11
		Fencerow	6.04^{A}	0.21	<0.001	
		Stepping Stone	5.24^{B}	0.22	<0.001	
		Constant	-7.64	0.37	<0.001	2.44
Edge Selection	Antshrikes	Distance to edge	-0.0185	0.0040	<0.001	0.00825
		Constant	-0.748	0.165	<0.001	0.942
	Wrens	Distance to edge	-0.0285	0.0088	0.001	0.00154
		Constant	-1.231	0.243	<0.001	1.284

Table 4-4. Models predicting the individual-specific coefficients for forest habitat from the habitat selection analysis. Treatment coefficient superscripts denote group membership ($p \geq 0.05$). For the categorical variable treatment, pastures provide the reference category.

Species	Measure	Variable	Coefficient	SE	P
Antshrikes	Forest Coefficients	Treatment-riparian corridor	2.54^{A}	0.73	0.002
		Treatment-fencerow	-1.47^{B}	0.70	0.045
		Returned	-1.38	0.61	0.032
		Constant	0.47	0.54	0.393
Wrens	Forest Coefficients	Treatment-riparian corridor	1.86^{A}	0.72	0.016
		Treatment-fencerow	-1.61^{B}	0.70	0.029
		Returned	-1.74	0.59	0.007
		Sex – males	-1.33	0.59	0.034
		Constant	1.78	0.63	0.009

Table 4-5. Models predicting the individual-specific coefficients from the edge selection analysis. Treatment coefficient superscripts denote group membership ($p \geq 0.05$) and pasture is the reference category.

Species	Variable	Coefficient	SE	P
Antshrikes	Treatment-riparian corridor	0.0495^{A}	0.0145	0.002
	Treatment-fencerow	0.0103^{B}	0.0149	0.494
	Constant	-0.0319	0.0105	0.006
Wrens	Forest Cover	0.090	0.046	0.062
	Constant	-0.023	0.014	0.105

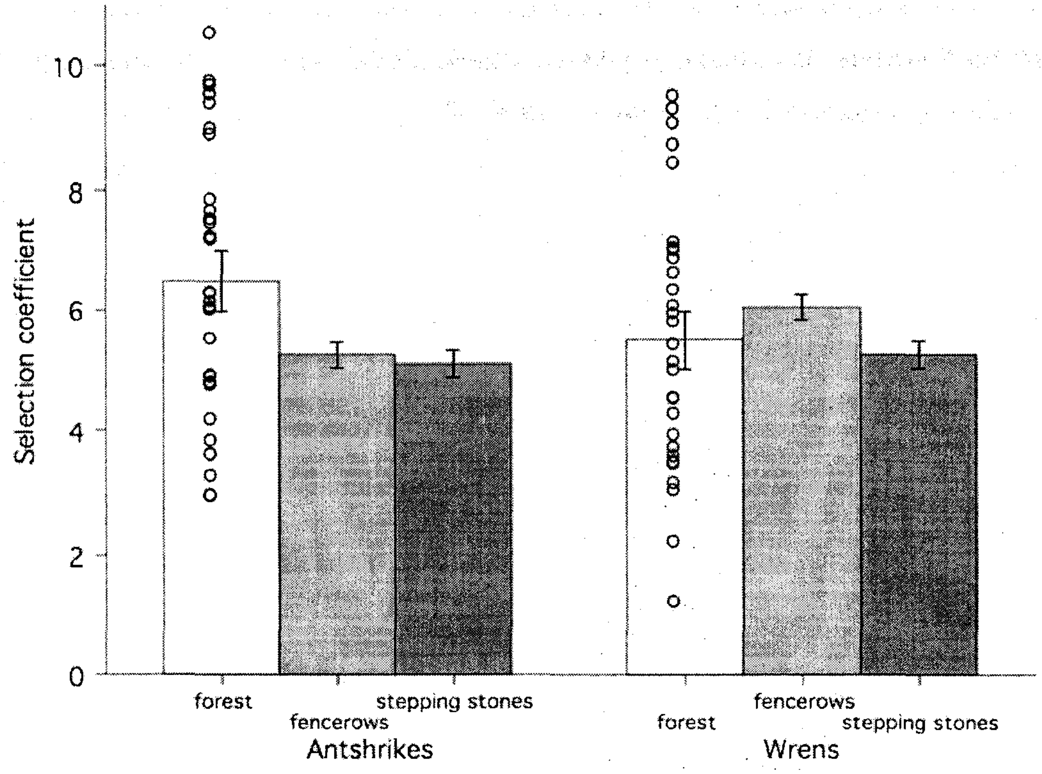

Figure 4-1. Coefficient values for habitat selection for both species for the three habitat types. Pasture was the reference category. Error bars are standard errors on the coefficient estimates (Table 4-3). Open circles are the individual-specific values of selection for forest used in the examination of functional responses.

Chapter 5

Fine-scale movement decisions of tropical forest birds in a fragmented landscape[1]

Abstract

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

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[1] I intend to submit this paper to *Ecology*. Hawthorne Beyer is a co-author on this paper. He created the ArcGIS program to generate random steps and collect land cover information about the used and random steps.

remaining forest cover. We expect that naturally dispersing birds and species with greater forest dependence would exhibit even stronger selection for forested routes than did the birds in our experiments.

Introduction

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

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

Movement by forest birds through the agricultural matrix is impeded by gaps between forested patches (Desrochers and Hannon 1997, St. Clair et al. 1998, Develey and Stouffer 2001, St. Clair 2003, Castellón and Sieving 2006). For many forest bird species, these open habitats represent areas of high predation risk (Rodríguez et al. 2001, Turcotte and Desrochers 2003) and this may be the reason that forest birds generally avoid them

(Lima and Dill 1990). Response to risky habitats likely affects where birds choose to travel in the habitat they encounter. These fine-scale movement decisions can affect the broader pattern of movement (Bowne et al. 1999) and, in simulations, can have impacts that scale up to population dynamics (Russell et al. 2003).

Despite the importance of movement to the conservation of birds, the behavioral decisions of free-moving forest birds are almost completely unknown (Harris and Reed 2002). This stems primarily from the difficultly of tracking moving birds (Desrochers et al. 1999, Bélisle 2005), but it may also stem from a traditional emphasis on habitat selection at points of occurrence over path selection. Indeed, where there is detailed information about the location and habitat use of birds or other vertebrates, analyses typically consider only characteristics of the location (Boyce and McDonald 1999) or the area around the location (e.g., Johnson et al. 2002). More recently, some authors have developed techniques to assess the characteristics of the path segment between successive locations (e.g., Whittington et al. 2004, Fortin et al. 2005). Fortin et al. (2005) developed step selection functions (SSF), which are similar to resource selection functions (RSF's; Manly et al. 2002), to compare used path segments to randomly generated 'available' segments. Like RSF's, these step selection functions are flexible enough to examine the effects of complex covariates, including situations where an animal's response to a covariate varies with habitat availability.

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

Methods

Study area

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

Translocations and tracking

We followed moving forest birds in real time at a landscape scale, collecting information about their route and habitat use. We translocated 30 territorial barred antshrikes (*Thamnophilus doliatus*, hereafter antshrikes) and 30 rufous-naped wrens (*Campylorhynchus rufinucha*, hereafter wrens). Both are common insectivores that hold territories year-round, but antshrikes are forest specialists, typically being found only in the understory of the most intact forest in this region whereas wrens are forest generalists, being found in a wider range of habitats (Stiles and Skutch 1989). Birds were moved away from their territories in one of three treatments: along riparian corridors, along fencerows, and through pasture. One bird from each species was translocated in each of the three treatments at each of ten distances (0.7-1.3 km in 0.1 km intervals, then 1.45, 1.6, and 1.9 km). We conducted translocations from June to August 2000 and January to June 2002. All individuals were caught by 0940 local time (mean capture time = 0659 hours ± 65 min) by attracting them into a mistnet with a playback of a conspecific song. We moved male antshrikes and both male and female adults of the monomorphic wrens. We attached a radio transmitter using eyelash adhesive to trimmed feathers on the backs of translocated individuals. Birds were captured in forest and released in fencerow or forest habitat. Due to the rarity of fencerows in the study area, the same fencerow was used for two treatments (one of each species) on three occasions. In these cases, we moved an individual of each species different distances. All other treatments were used only once. Most wrens (23 of 30) were sexed by extracting DNA from a whole tail feather (Griffiths et al. 1998). The remaining individuals were sexed by comparing their weight, tarsus length, and exposed culmen length to measurements of individuals of known sex using a discriminant function analysis.

Following release, we recorded with radio-telemetry and hand-held GPS units the location of each translocated bird approximately every 15 minutes (mean = 14.8 min ± 8.2 min standard deviation) for up to 4 days and daily thereafter for 10 days or until they returned, whichever was earlier. Two observers closely followed individuals by simultaneously triangulating their location from a mean distance of 27 m ± 13 m. These positions provided trajectories of moving birds with unprecedented precision and with which we assessed the habitat used during movement. Even the shortest translocations were well outside the home range of these birds. Although empirical information for these species is not available, home range radius was ~ 60 m for a cogener to the antshrike in Brazil (*T. caerulescens*; Duca et al. 2006) and ~ 75 m for a cogener to the wren in Venezuela (*C. nuchalis*; Yaber and Rabenold 2002). Riparian corridors were typically between 50 m and 150 m wide. Fencerows were typically 15 m to 30 m wide with little understory.

Land cover information

Land cover information for the study area was developed from a series of high-resolution (~1 m pixel size) infrared images taken by the Airborne Sensor Facility at the National Aeronautics and Space Administration (NASA) as part of the CARTA program during March 2003 (http:\\asapdata.arc.nasa.gov). Images were orthorectified using a digital elevation model built from 1:20,000 topographic information and the coordinates of known locations in the field with the OrthoBASE package in ERDAS IMAGINE 8

(ERDAS Inc. 2002). Land cover was delineated on these images using ArcGIS (ESRI 2005) as pasture, forest, fencerow, or stepping stone habitat.

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

Data analysis

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

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

Results

Antshrikes

For the forest-specialist antshrikes, the best model included the proportion of the step in forest as the risk variable (Table 5-1). This model fit the data better than the competing models including the other three risk variables (proportion of the step in pasture, number of gaps crossed, and total distance of gaps crossed). This model included univariate covariates for the proportion of the step in stepping stone habitat, the distance home as well as steps ending in both forest and stepping stone habitat (Table 5-2). The coefficients comparing used to available steps for the three univariate terms that were not part of interaction terms revealed the direction of their effects (Table 5-2). The antshrikes were more likely to select steps that took them closer to home and that, on average, contained lower proportions of stepping stone habitat. Relative to availability, antshrikes avoided steps that ended in fencerow. The effect of proportion of forest in this best-fit model was adjusted by its interaction with three other variables: distance from the home territory to the start of the step, starting the step in forest, and ending the step in a stepping stone.

The interaction terms in the best-fit model indicate that selection for forest by antshrikes was context dependent. We explored these interactions by generating linear predictors for each pair of terms from the best model (Table 5-2) with the other covariates held constant at their means. The linear predictor is the linear component of the logit equation predicting probability of use. Higher values indicate a greater relative probability of use. Antshrikes selected steps with more forest when they were distant from their territory, but selected steps with less forest when they were close to their territory (Fig. 5-1a). There was a similar effect of starting habitat. Antshrikes selected more forested steps when the step started in forest, but selected less forested steps when starting in the non-forest habitat of fencerows and stepping stones (Fig. 5-1b). Finally, they selected less forested steps when the step ended in a stepping stone, but selected more forested steps when the step ended in fencerow or forest (Fig. 5-1c). Put another way, given the choice between two steps ending in stepping stone habitat, they were more likely to choose the step with less forest, but if the step ended in forest or fencerow habitat, they were more likely to choose the more forested step. In addition, the intersection of the lines in Fig. 5-1c indicates that when the available steps had low amounts of forest cover, antshrikes preferred steps ending in stepping stones, whereas when steps had high amounts of forest, antshrikes preferred steps ending in forest or fencerow.

The variance in the random coefficient for the proportion of forest was of a similar magnitude to the coefficient estimate (Table 5-2), indicating there was substantial variation among individual antshrikes in their selection for the proportion of the step in forest. However none of the candidate variables were significant predictors of these individual-specific coefficients (Table 5-3).

Wrens

The best model for the forest generalist wrens included a different risk variable than the best antshrike model; the proportion of the step in pasture (Table 5-1). Like the antshrikes, wrens responded to the distance home at the end of the step and the presence of fencerow at the end of the step. Model coefficients revealed that wrens selected steps that: took them closer to home, had more fencerow habitat, and ended in fencerows (Table 5-2). However, their selection for the proportion of the step in pasture was context dependent. When starting from forest, the amount of pasture did not affect their choice of steps. In contrast, when they started from fencerow or stepping stone habitat, wrens selected steps with more pasture (Fig. 5-1d).

Like the antshrikes, the magnitude of the random coefficient variance indicates there was substantial variation among individual wrens in their response to the proportion of the step in pasture (Table 5-2). Males selected steps with greater proportions in pasture more strongly than females (Table 5-3). Selection for steps with more pasture was stronger in individuals that had available steps with more pasture. In other words, the strength of selection increased with increasing availability of pasture in the landscape. This measure of the mean amount of pasture in the available steps varied from 4% to 42% across the 30 individuals.

Discussion

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

Of the four risk variables we examined (proportion of step in pasture, proportion in forest, number of gaps crossed and cumulative gap-crossing distance), the proportion of forest was the most important predictor of the movement of the antshrikes, whereas the proportion of pasture best explained the movement of wrens. This suggests that antshrikes view forest habitat as more secure for movement than fencerow or stepping stone habitat, but the wrens view all three similarly. This matches the habitat selection information for these species (Chapter 4), which showed that antshrikes preferred forest habitat over fencerow and stepping stone habitat, whereas wrens selected non-pasture habitats similarly (forest, fencerow, and stepping stone habitat). The response of our forest specialist to forest habitat was similar to the work of Sieving et al. (2000) where the availability of understory was the primary predictor of whether forest specialist birds were willing to travel in treed corridors. A treed corridor without understory would be similar to the fencerows in our study area. Thus, conservation planning for generalist species in this and other similar landscapes could consider all of the non-pasture habitats when planning for landscape connectivity. In contrast, planning for the more sensitive forest specialists would need to be based on the amount and configuration of forested habitat.

An important variable predicting the steps selected by both species was the distance from the end of the step to the home territory. Because birds consistently selected step endpoints that were closer to home than the available choices, it is apparent that they were homing during their paths. We expect this because the majority of the translocated individuals for both species successfully returned (Chapter 2).

One implication of the differing dependency on forest for movement by the forest generalist vs. specialist is the utility of living fencerows for conservation purposes. An earlier examination of entire return paths (Chapter 2) showed that fencerows are not effective travel routes for antshrikes, whereas they were often used by wrens. At the finer spatial scale of the analyses here, antshrikes avoided steps ending in fencerow, whereas wrens selected steps both that contained more fencerow habitat and that ended in fencerow habitat. The avoidance of fencerows by the antshrikes may be the mechanism causing antshrikes to travel longer paths in forest around fencerows (Chapter 2). For the wrens, the fencerows may represent a very effective means to travel in their desired direction, covering a small area, but providing mostly continuous tree cover. Living fencerows have been advocated as a means to provide connectivity in fragmented landscapes (Rosenberg et al. 1997, Şekercioğlu et al. 2002) and structurally similar hedgerows are used extensively in the United Kingdom with support of agricultural subsidies (Oldfield et al. 2003). These results suggest that the utility of fencerows may be limited to forest generalists. For the specialist we studied, the structural connectivity afforded by fencerows did not generate functional connectivity (sensu Taylor et al. 1993, Bélisle 2005). The response of these birds to forest and stepping stone habitat was more complex and was dependent on the context of the step.

The importance of context for step selection was demonstrated in our results by the several significant interaction terms included in best models for both species. Antshrikes selected steps with more forest when they were far from their home territory, when they started the steps in forest, and when they ended steps in stepping stones. The effect of distance home on selection for forest probably reflects a change in risk-taking behavior. Crossing open habitat exposes forest birds to the risk of predation (Lima and Dill 1990, Rodríguez et al. 2001, Turcotte and Desrochers 2003). Far from their home territories, birds may have had less motivation to take risks by using non-forested habitat relative to when they were closer to home and might have had stronger motivation to return. Homing pigeons show a similar pattern whereby their flights become more directed when they are closer to home perhaps because they make greater use of landmarks then (Guilford et al. 2004).

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

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

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

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

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

Using step selection functions, we provide the first detailed information about route selection of forest birds moving at a landscape scale. We showed that the reliance on forested habitat, one measure of the risk in route choice, is context dependent. The forest specialist preferred forested routes, particularly when moving from forest habitat and while traveling in novel areas. This species avoided both fencerow and stepping stone habitat, except when forest cover was low. The forest generalist showed what we consider to be riskier movement behavior by exhibiting preference for routes with more pasture when moving from non-forest habitats. For conservation planning, forested routes (i.e. corridors) through fragmented landscapes are likely the best option to facilitate the movement of sensitive forest specialists. Fencerow and stepping stone habitat is unlikely to be enough to conserve these species. However, stepping stones appeared to have particular utility for movement when forest cover was low and this may mean that their conservation will be important in this and other landscapes.

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Table 5-1. The candidate models for each of the four risk variables, their AIC values, difference from the best model, and Akaike weights. The best model for each species is in bold. Candidate models were built using forward step-wise addition. The four risk variables are proportion of the step in forest habitat (PF), proportion of the step in pasture habitat (PP), total amount of gap crossed (TotGap), and the number of gaps crossed (Gaps). Other variables included in the models are; distance home at the end of the step (Dhome), distance home at the start of the step (Dstart), proportion of the step in fencerow habitat (PFR), proportion of the step in stepping stone habitat (PSS), start in forest (StartFor), start in fencerow (StartFR), end in fencerow (EndFR), end in stepping stone (EndSS). The best model was the model with the lowest AIC plus a random coefficient for the risk variable minus non-significant terms ($P > 0.1$).

Species	Model	k	logL	AIC	ΔAIC	Weight
Antshrikes	Dhome + PF + PSS + EndFR + EndSS	5	-4869	9748.3	32.5	<0.001
	Dhome + PF + PSS + EndFR + EndSS + Dstart*PF + StartFor*PF + EndSS*PF	**8**	**-4850**	**9715.9**	**0**	**0.80**
Best	**Same as above + random coefficient PF**		**-4834**			
	Dhome + PP + EndFR + EndSS	4	-4870	9747.6	31.7	<0.001
	Dhome + PP + EndFR + EndSS + Dstart*PP + EndSS*PP	6	-4853	9718.9	3.0	0.17
	Dhome + TotGap + EndFR + EndSS	4	-4870	9748.0	32.1	<0.001
	Dhome + TotGap + EndFR + EndSS + Dstart*TotGap + EndSS*TotGap	6	-4859	9731.0	15.1	<0.001
	Dhome + Gaps + PSS + EndFR	4	-4869	9745.7	29.9	<0.001
	Dhome + Gaps + PSS + EndFR + Dstart*Gaps	5	-4856	9722.5	6.6	0.03
Wrens	Dhome + PF + PSS + EndFR + EndSS	5	-5355	10719.3	55.1	<0.001
	Dhome + PF + PSS + EndFR + EndSS + StartFor*PF + EndSS*PF	7	-5331	10676.6	12.4	0.001
	Dhome + PP + PFR + EndFR + EndSS	5	-5356	10721.1	56.9	<0.001
	Dhome + PP + PFR + EndFR + EndSS + Dstart*PP + StartFor*PP + StartFR*PP + EndFR*PP + EndSS*PP	**10**	**-5322**	**10664.2**	**0**	**0.60**
Best	**Dhome + PP + PFR + EndFR + StartFor*PP + random coefficient PP**		**-5312**			
	Dhome + TotGap + PSS + EndFR + EndSS	5	-5354	10718.4	54.2	<0.001
	Dhome + TotGap + PSS + EndFR + EndSS + Dstart*TotGap + StartFR*TotGap + EndSS*TotGap	8	-5339	10693.6	29.4	<0.001
	Dhome + Gaps + PSS + EndFR + EndSS	5	-5352	10713.1	48.9	<0.001

Species	Model	k	logL	AIC	ΔAIC	Weight
	Dhome + Gaps + PSS + EndFR + EndSS + Dstart*Gaps + StartFor*Gaps + EndSS*Gaps	8	-5325	10665.0	0.8	0.40

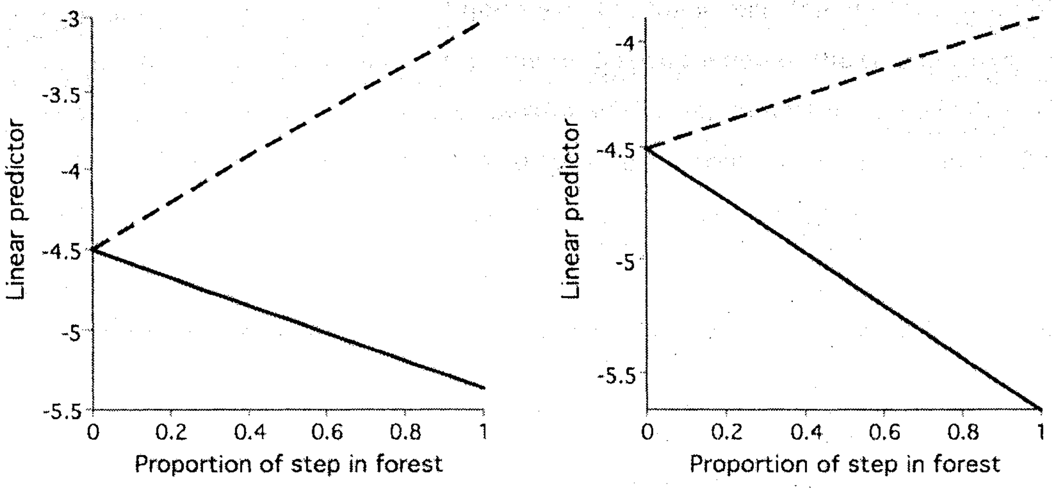
Table 5-2. Table of final model coefficients, standard errors, significance, and random coefficient variance for the step selection by both species from the best model in Table 5-1.

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

Table 5-3. Table of final models predicting the individual specific coefficients from the SSF models (Table 5-2). No variables were added to the model for the antshrikes.

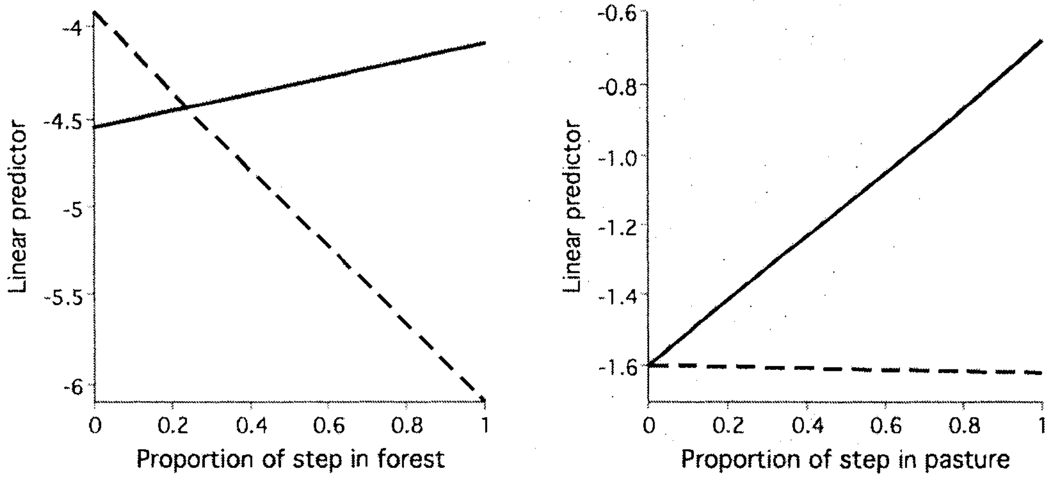
Species	**Variable**	**Coefficient**	**SE**	***P***
Antshrikes	Constant	-0.00076	0.223	1.000
Wrens	Sex – males	1.057	0.433	0.022
	Mean proportion pasture in available steps	4.340	1.844	0.026
	Constant	-1.391	0.499	0.010

Figure 5-1. The linear prediction of the probability of use by antshrikes (a-c) in relation to the proportion of the step in forest and by wrens (d) in relation to the proportion of the step in pasture. Antshrikes selected steps with more forest when distant from their territory (a; dashed line = 2 km), but avoid steps with more forest when close to their territory (a; solid line = 0.2 km). They selected steps with more forest when their step starts in forest (b; dashed line) vs. non-forest (b; solid line = fencerow and stepping stone habitat). They selected steps ending in stepping stones (c; dashed line) at low amounts of forest cover, but select steps ending in non-stepping stone habitat at higher amounts of forest cover (c; solid line = forest and fencerow). Wrens selected steps with more pasture when the step started in non-forest habitat (d; solid line = stepping stone and fencerow habitat), but the proportion of the step in pasture did not affect step choice when the step started in forest habitat (d; dashed line). These values were generated from the best models (Table 5-2) with the other covariates held constant at their mean.



a) Antshrikes - distance

b) Antshrikes – starting habitat



c) Antshrikes – ending habitat

d) Wrens – starting habitat

Chapter 6

General Discussion

The preceding chapters presented results and analyses of the movement of forest birds at three distinct spatial scales. At the coarsest scale of whole paths, forest birds used corridors for their return paths when homing. Forested corridors were particularly important for the forest specialist and fencerows were not sufficient for their movement. For the forest generalist, forested corridors had little benefit. At an intermediate scale, I examined the occurrence of these birds in the landscape, comparing their locations to the available habitat in the landscape. The forest dependence that is assumed of these birds in breeding contexts was suggested by their habitat selection while traveling. The specialist preferred forest habitat, but still used fencerow and stepping stone habitat to a lesser degree. Both species selected positions closer to the edge, but the specialist was further from the edge than the generalist. Treatment (habitat configuration) predicted individual variation in the strength of selection for forest habitat for both species and edge by the specialist. At the finest scale, I examined the movement decisions of these birds. These analyses suggested that birds chose their routes based on the land cover characteristics available to them and the distances to their territories. Selection for forested routes by the specialist was strongest when individuals were far from their territories, started their steps in forest or ended their steps in either forest or fencerow.

Several of these findings provided novel information for others interested in movement behaviour in fragmented habitats. Most of this information was dependent on the broader ecological context in which I studied movement and I believe that my study system offered several advantages for the mechanistic investigation I conducted. The first of these advantages was the year round territoriality exhibited by my study birds. Several other translocation studies have focused on migrant birds in temperate regions (e.g. Bélisle *et al.* 2001, Bélisle and St. Clair 2001, Gobeil and Villard 2003). Using birds that were territorial year round on small home ranges meant that their knowledge of their surrounding environment was limited so their homing was slower and more exploratory, which probably made it easier to follow them. In temperate regions, the movement of migratory birds appears to be influenced mainly by landscape composition (e.g. Bélisle *et al.* 2001, Bélisle and St. Clair 2001, Gobeil and Villard 2003). The ability of these birds to colonize new habitats may not depend on their ability to disperse locally if they can simply migrate to a new area the following spring. A second advantage was the scale of the translocations in my study. This scale is similar in magnitude to the majority of dispersal movements by tropical forest birds. In a review of the extensive dataset from the Biological Dynamics of Forest Fragments Project, Van Houtan *et al.* (2007) found 360 dispersals from 21 species of forest birds. Approximately 30 % of these movements were > 300 m, but only a 'small fraction' were > 5 km. Similarly, Yaber and Rabenold (2006) found that dispersal of juveniles and adults of a cogener to the wren I studied dispersed an average of ~360 m with a maximum dispersal distance of approximately 1500 m (n = 214). My own translocations were all within the range of these natural dispersal events. A third advantage is that this study system is relevant to other highly fragmented forest landscapes in a way that some studies are not. A number of manipulative studies have reversed corridor (open habitat) and matrix (forest; e.g. Haddad 1999, Tewksbury *et al.* 2002, Haddad *et al.* 2003, Levey *et al.* 2005, Damschen *et al.* 2006). This reversal limits the generality of some of the results from these studies. For example, Levey *et al.*'s (2005) observed that open habitat birds used corridors by flying along their edges, just inside the matrix, which was forest. Yet it is unlikely that the corollary would be true; that forest dwelling birds would fly along a forested corridor just within a matrix of open habitat (see also Sieving *et al.* 1996, Develey and Stouffer 2001, Stouffer *et al.* 2006, Chapter 5). A final advantage of my study system is the comparison it provided between two seemingly-similar species. The use of two species with differing forest dependence provided several additional insights about selection for and use of corridors, fencerows, and stepping stones.

The difference between the two species is one of the primary themes in the results of all three chapters comparing these two species. The preference for breeding in more intact forest that characterizes the antshrike appeared to translate into a preference for forest habitat while moving at all three scales. Compared to the generalist, individuals of this forest specialist were more dependent on riparian corridors for their returns, selected locations in forest more strongly, traveled further from the forest edges, and selected forested routes more strongly when traveling in forest habitat that was distant from their territories. Thus, it appears that the natural history that governs breeding habitat preferences may also predict the importance of forest and forested corridors for movement.

Within the broad ecological group described by tropical, forest-dwelling, insectivorous birds, there is a wide range of guilds supported by different forest niches. Occupied niches range from the forest canopy to the midstory, understory, and terrestrial habitats. Not surprisingly, the nature of impacts stemming from forest fragmentation vary among these niches, but understory and terrestrial species are consistently the most likely to disappear following fragmentation (e.g. Renjifo 1999, Şekercioğlu *et al.* 2002, Ribon *et al.* 2003, Stouffer *et al.* 2006, Cleary *et al.* 2007), to avoid edges (e.g. Laurance 2004), and to avoid crossing gaps (e.g. Laurance *et al.* 2004). The forest specialist in my study is known to occupy the most intact forest within the dry forests ecosystem (Stiles and Skutch 1989). However, in wetter forests, this species appears to be much less forest-dependent, being found at the forest edge or even in forest gaps (Stiles and Skutch 1989). In these wetter forests, there are other species that are much more forest dependent than my forest specialist antshrikes. For example, scaled antpitta (*Grallaria guatimalensis*) and thicket antpitta (*Hylopezus dives*) are found only deep in the forest in the understory or on the forest floor. Many of these species, such as antthrushes, antpittas (both Formicariidae), and tapaculos (Rhinocryptidae) are very weak fliers and appear to be highly unwilling to cross into open habitat (Sieving *et al.* 1996, Laurance *et al.* 2004). For example, Castellón and Sieving (2006) translocated chucao tapaculos (*Scelorchilus rubecula*) into very small patches and several of them stayed ≥ 30 days, seemingly because they were unwilling to cross gaps of as narrow as 120 m. This extreme sensitivity to gaps may be the reason birds in these groups are so endangered. Indeed, 20 of the 62 species of Formicariids (32%) and 11 of the 57 species of Rhinocryptids (19%) are described as near threatened, vulnerable or endangered by the IUCN (IUCN 2007). Thus, the considerable forest dependence that was apparent from my forest specialist is actually less dependency than would probably be exhibited by these hardcore forest specialists. For these more sensitive species, I expect the importance of forested routes for movement would be even stronger.

Regardless of the position of a species on a continuum of forest specialization, identifying preferred habitat is critical to conservation action. For many species, habitat selection is obscured by so-called 'noise' variation among individuals. With the application of random effects, it is now possible to better understand and predict individual variation in the strength of selection for different habitat features (Chapter 3) and to identify functional responses to both habitat composition and configuration (*sensu* Mysterud and Ims 1998). Because functional responses are probably quite common in nature (Mysterud and Ims 1998), this techniques holds promise for exploring habitat selection in many other conservation contexts. My results also invite reassessment of the assumption that composition is generally more important than configuration to the persistence of populations in fragmented habitats (Fahrig 1998). My measure of configuration (treatment) was important in three cases where composition was not; it affected the strength of selection for forest habitat by both species and the strength of selection for edge habitat by the antshrikes. The effects of changes in habitat configuration with ongoing changes in land cover will have important consequences for movement of these species in the future. Predicting these effects requires not only the understanding of movement I have promoted, but also a greater understanding of the changes in land cover that are rapidly occurring throughout the tropics.

In the dry forest of Costa Rica, land cover has changed dynamically during the past 50 years. Whereas very little of the original dry forest habitat in Mesoamerica remains (Janzen 1986), there is actually quite a lot of regenerated secondary dry forest (Arroyo-Mora *et al.* 2005). Most forest clearing in northwestern Costa Rica occurred in the period 1960 to 1980. Following this period, declining beef prices, fewer incentives for cattle farming, and possibly Costa Rica's system of payment for environmental services (Calvo 2000) resulted in substantial regeneration in northwestern Costa Rica (Arroyo-Mora *et al.* 2005). Regeneration has occurred primarily in areas that were marginal for raising cattle due to shallow soils and steep slopes. Currently, the majority of these regenerating forests are still too young to harbour the forest specialist I studied, and regeneration has been more limited in the flat intensively farmed areas where my research was concentrated. Nonetheless, this regeneration presents an opportunity to restore forested corridors in this landscape presumably increasing both structural and functional connectivity in future.

Land use change is one factor affecting future biodiversity and some of its effects, as discussed above, may be positive. Another unknown factor with potential implications for habitat quality and connectivity is climate change. As important as climate change is likely to be as an individual factor, its greatest impact on biodiversity may be in the form of synergy with other factors (Sala *et al.* 2000). In my study system, the interaction between changes in land cover and climate are likely to be particularly important. While the majority of temperature rise associated with climate change is expected to occur at high latitudes (IPCC 2001), the tropics are also likely to see substantial changes, primarily decreased precipitation (IPCC 2001). In Central America, runoff and tree cover are both expected to decline under a range of future scenarios (Scholze *et al.* 2006). Several farmers that I interviewed[1] reported that the climate is drier now making it more difficult to graze cattle on their land through the entire dry season. A recent study found that the dry season was shorter and wetter during the Little Ice Age, also suggesting that the dry season will be longer and drier under a warming climate (Lozano-García *et al.* 2007). The effects of a warming climate are likely to include multiple factors that affect the distribution of forest in the tropics. For example, warmer nighttime temperatures are increasing respiration and speeding tree mortality and hence decomposition. Due to this increased mortality, large areas of lowland forest may actually become atmospheric carbon sources rather than carbon sinks (Clark *et al.* 2003). In addition, greater tree mortality could substantially open forest structure making the understory less suitable for

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[1] I interviewed 19 farmers or land managers in March 2003 about past and future land cover change with plans to use this information to create realistic scenarios of land cover change in a simulation model of bird movement in this landscape. There was little consensus about future land cover change and other aspects of the model were intractable to me. The resource selection functions in Chapter 3 replaced this earlier plan.

birds that inhabit the darkest refugia of the forest. Deforestation also appears to reduce precipitation in downwind areas (Lawton *et al.* 2001). A drier climate may make the dry forest habitat too dry for the forest specialist on two counts: it may make it unsuitable as breeding habitat and it may also reduce the effectiveness of forested corridors by reducing leaf cover. The majority of trees in the dry forest are deciduous (Murphy and Lugo 1986) and this is particularly true in younger secondary forest. If the tree cover in the forested habitat has fewer leaves during longer dry periods, forest birds may be less willing to use them if they do not feel as secure traveling in them. Finally, a drier climate may increase the mortality of stepping stones, which could reduce the permeability of the matrix for movement.

Whether by climate change or more direct anthropogenic effects, the loss of stepping stones could have some important consequences to the movement of forest birds. Seen as a component of the matrix, the role of stepping stones in connectivity supports the notion that 'the matrix matters' (Ricketts 2001). Stepping stones are a rare element in this landscape, but they were used during translocation-induced movement by both species. Although they were not preferred when more forested routes were available (Chapter 4), and they may not be used by the most forest dependent birds in other landscapes (e.g. Fischer and Lindenmayer 2002a), they appear to have an important role for permeability in the landscapes with very low forest cover; exactly the kind of landscape where connectivity for forest-dwelling species is most constrained. Because this kind of landscape is projected to increase in future (Laurance 1999), the importance of stepping stones to movement may continue to increase. Unfortunately, at the same time stepping stones may themselves be threatened through the combined effects of climate change (above) and mechanized farming (Maron and Fitzsimmons 2007). Conversion from cattle pasture to other crops such as sugarcane, rice, or melon plantations would presumably eliminate the stepping stones that are currently used to shade cattle. Removal of stepping stones has occurred elsewhere following agricultural intensification (Pulido *et al.* 2001, Maron and Fitzsimons 2007). The use of stepping stones and their potential removal illustrates another important generalization from my thesis: the matrix is not homogenous and completely inhospitable. Only recently has the nature of the matrix been recognized as an important part of connectivity (e.g. Bowne *et al.* 1999, Baum *et al.* 2001, Ricketts 2001, Fischer and Lindenmayer 2002a, Bender and Fahrig 2005, Castellón and Sieving 2006). In addition to facilitating movement, the matrix may be used as breeding habitat by forest species where the intensity of the agriculture is low or sufficient forest remnants remain (e.g. Daily *et al.* 2003, Fischer and Lindenmayer 2002b, Şekercioğlu *et al.* 2007). Conservation of stepping stones in this and similar fragmented landscapes is likely to benefit the permeability for forest-dependent birds. Predicting the rate at which stepping stones will be lost by indirect (e.g. climate change) or direct (e.g. mechanization) means is a topic that merits attention in future.

Like stepping stones, fencerows are a relatively rare element in this landscape. Whereas the forest specialist used stepping stones under conditions of low forest cover (Chapter 4), these birds traveled around fencerows even when they provided a direct route home (Chapter 2) and avoided steps that ended in fencerow habitat (Chapter 5). The use of fencerows to promote biodiversity has only recently been advocated in the tropics (Şekercioğlu *et al.* 2002). In contrast, structurally similar hedgerows are used extensively in the United Kingdom and are supported by agricultural subsidies (Oldfield *et al.* 2003). There, much of their justification comes from their role as corridors, but a recent review by Davies and Pullin (2007) suggested the evidence for their value as corridors is equivocal. My results also do not lend much support to their value as corridors. While the forest generalist used them during their returns, there was no benefit over pasture treatments. This finding may be dependent on the availability of stepping stones in my study system (above), once more advocating for their retention. The contrast between the utility of stepping stones vs. fencerows provides a poignant reminder of the difference between structural and functional connectivity. For the forest specialist I studied, it was not important for habitat elements to be physically connected to provide connectivity in the landscape. Indeed, this discrete habitat element appeared to be more useful than the structurally connected habitat element of fencerows.

In contrast to fencerows, the benefits of forested corridors were clear, particularly for the forest specialist. Forested corridors facilitated the returns of individuals (Chapter 2), but also allowed them to spend more time in forest habitat and travel further from the forest edge, presumably with less risk (Chapter 4). Additionally, corridors provided the preferred habitat for individual steps in those return paths (Chapter 5), perhaps indicative that forest-dependent birds generally employ the same behavioural rules for selecting habitat regardless of whether it is to move, forage, or breed. While there is strong evidence for the benefits of corridors for a number of ecological processes including species richness (Gilbert *et al.* 1998, Damschen *et al.* 2006), population persistence (González *et al.* 1998), interpatch movement (Beier and Noss 1998, Tewksbury *et al.* 2002), pollination and seed dispersal (Tewksbury *et al.* 2002, Levey *et al.* 2005), this study is the first to closely track the movement of forest birds using corridors at a landscape scale. These conclusions support the contention that corridors will be important in agricultural landscapes for the conservation of tropical birds (Stratford and Robinson 2005, Fischer *et al.* 2006). The conservation and restoration of forested corridors is likely to have substantial benefits for functional connectivity in this and other fragmented tropical landscapes. Despite the uncertainty that has dogged their development in the conservation literature (Simberloff and Cox 1987, Simberloff *et al.* 1992), my work contributes to an emerging consensus that corridors are good conservation investments.

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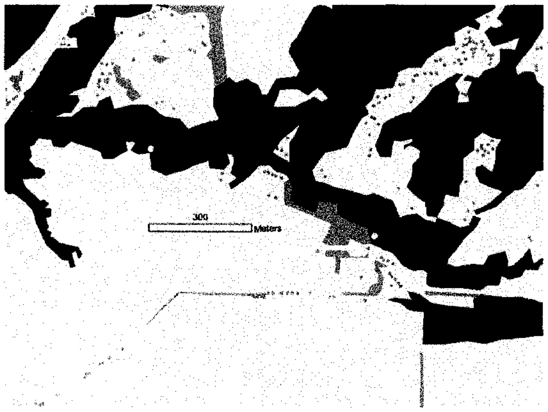
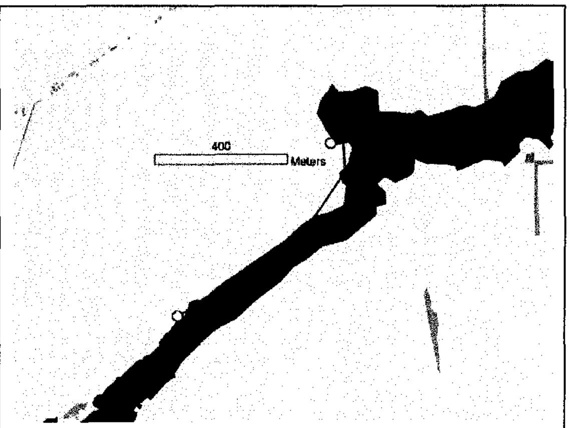
Appendix 1. Movement Paths

Movement paths are overlaid on land cover information. Capture and release points are shown by yellow circles. Land covers are: dark green = forest, tan = pasture, bright medium green = stepping stones, and dull medium green = fencerows. Below each map are the translocation distance, species, and treatment.



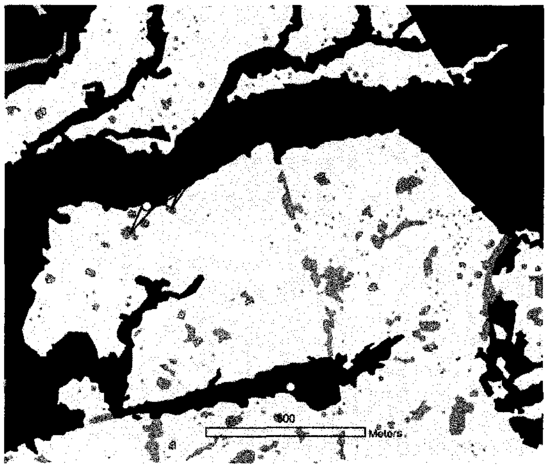
0.7 km Antshrike corridor



0.7 km Wren corridor

0.7 km Antshrike fencerow

0.7 km Wren fencerow



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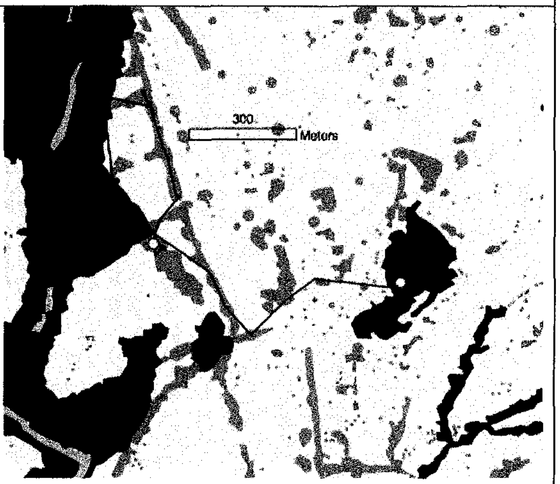
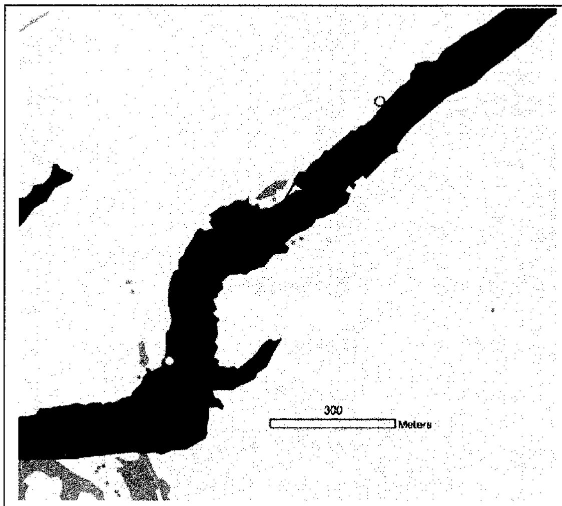
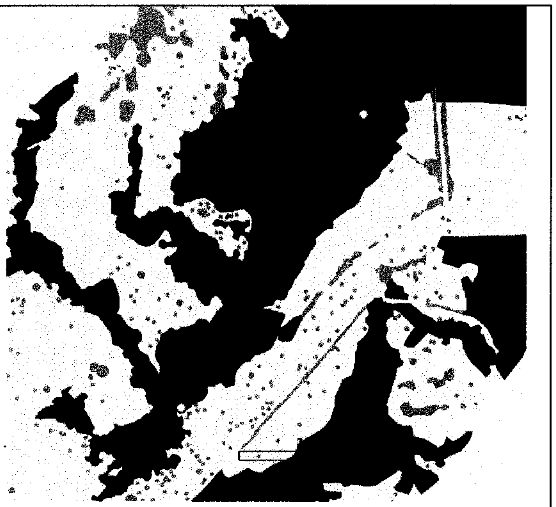


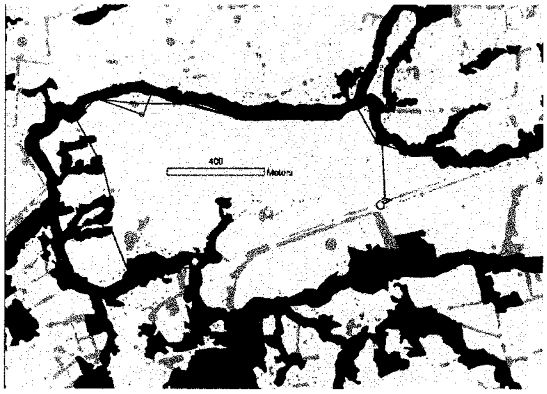
0.7 km Wren pasture



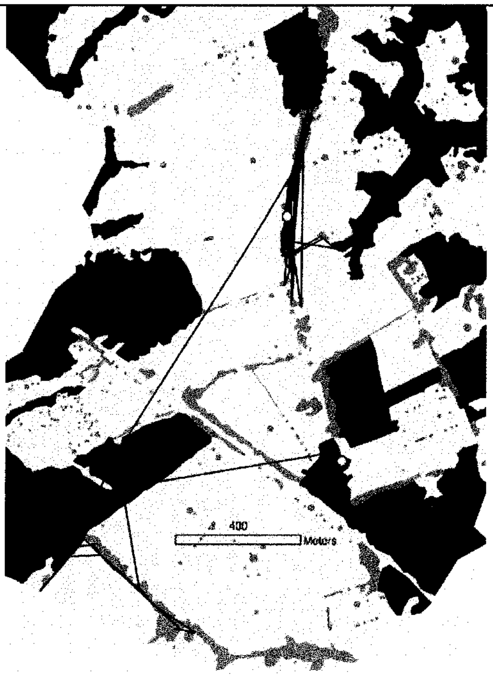
0.8 km Antshrike corridor



0.8 km Wren corridor



0.8 km Antshrike fencerow



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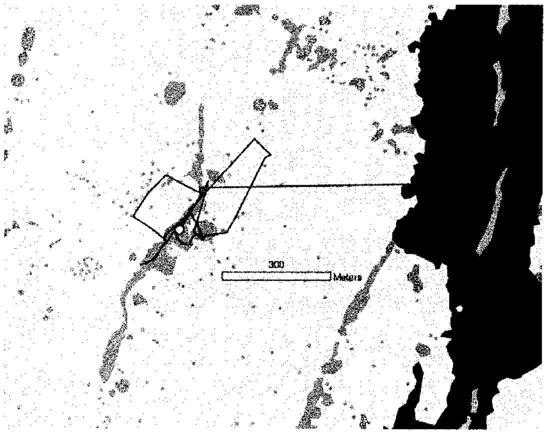
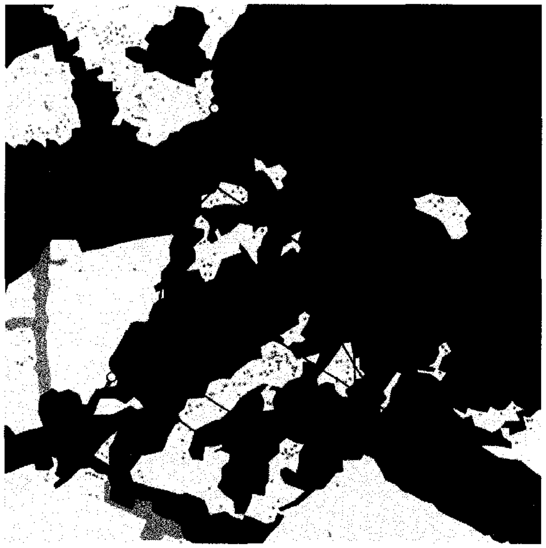


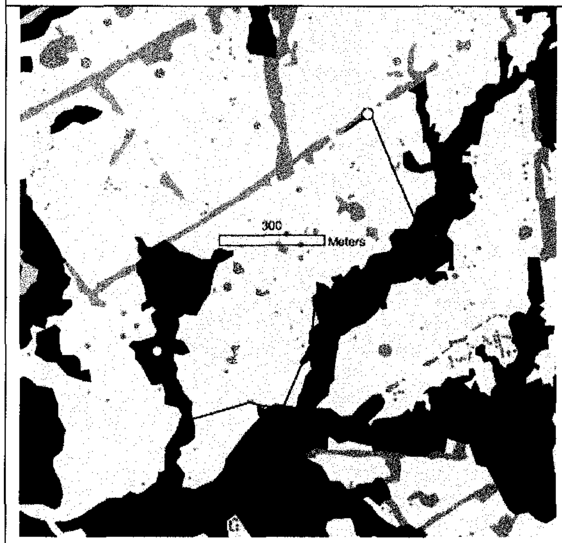
0.8 km Antshrike pasture

0.8 km Wren pasture



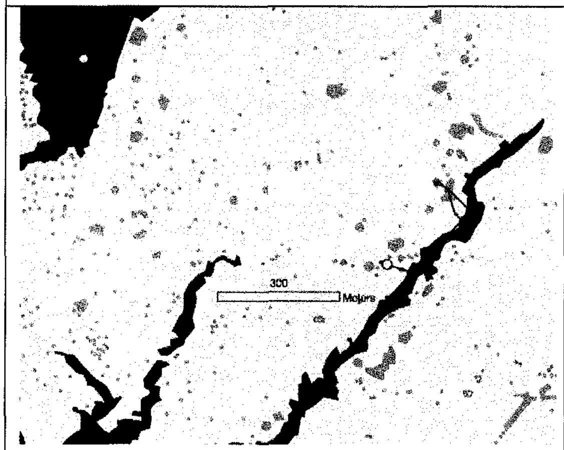
0.9 km Antshrike corridor

0.9 km Wren corridor



0.9 km Antshrike fencerow

0.9 km Wren fencerow



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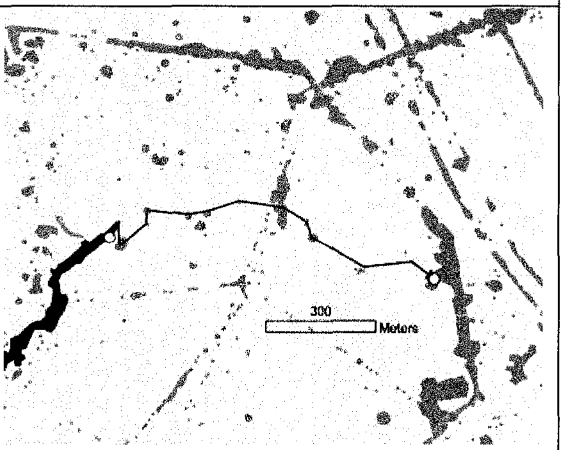
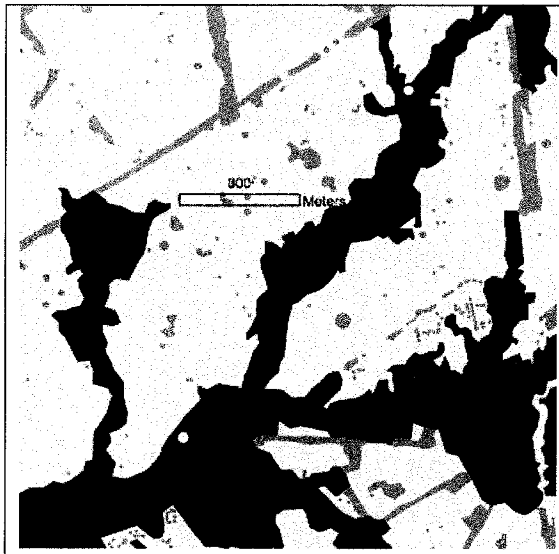
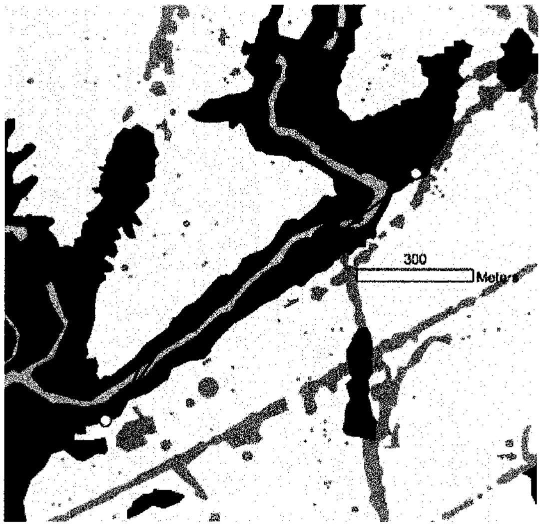


0.9 km Wren pasture

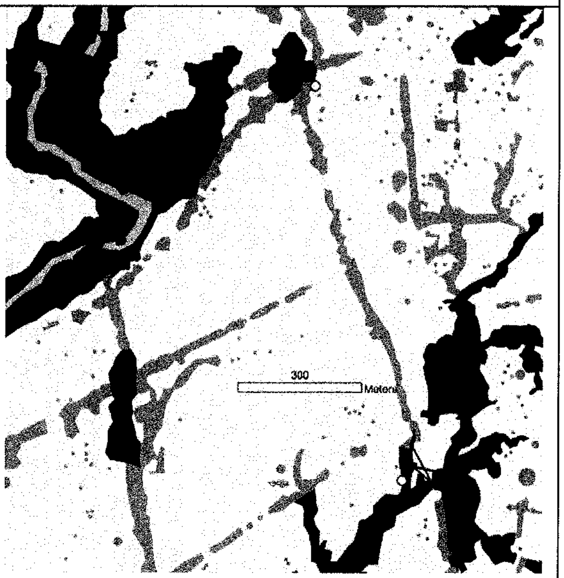


1.0 km Antshrike corridor



1.0 km Wren corridor

1.0 km Antshrike fencerow



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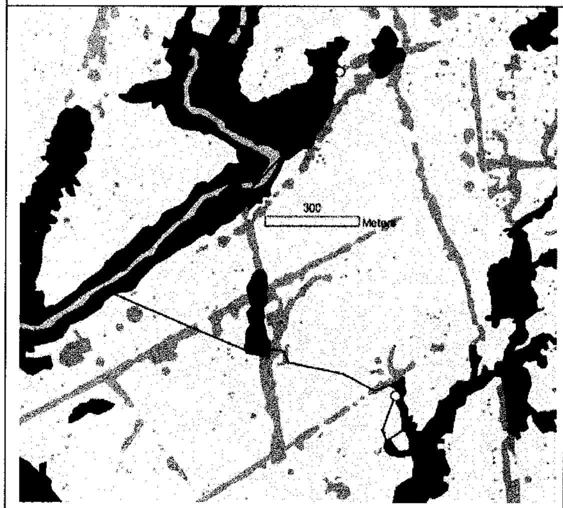

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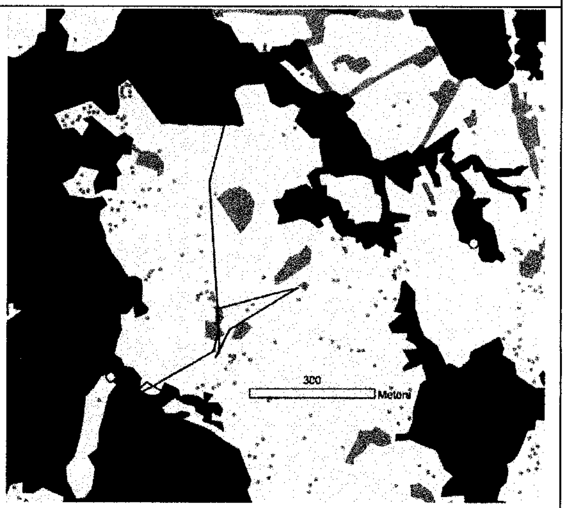
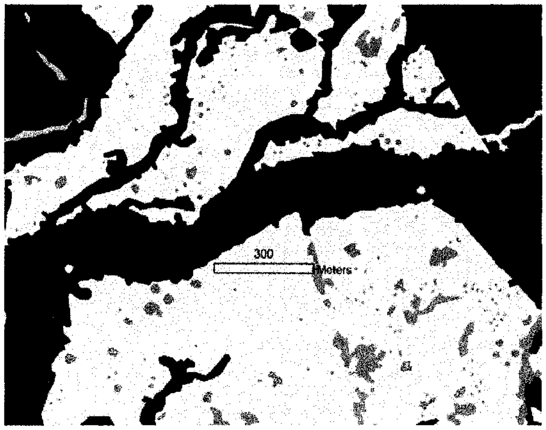
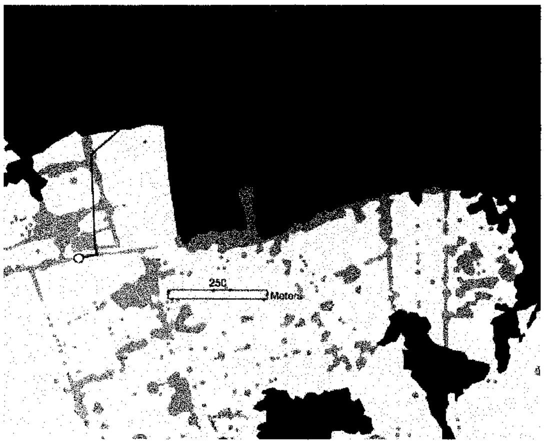


1.0 km Wren pasture



1.1 km Antshrike corridor

1.1 km Wren corridor



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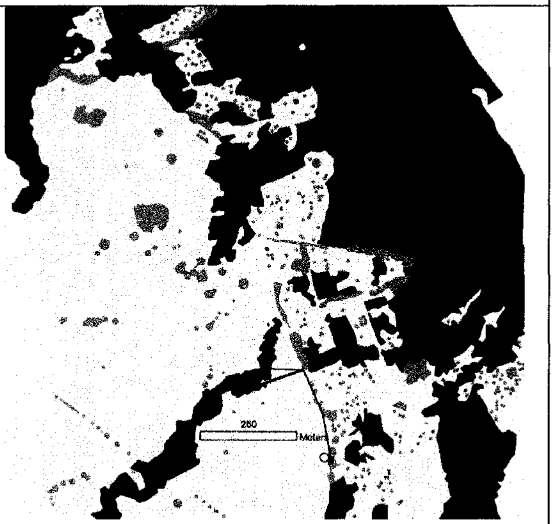
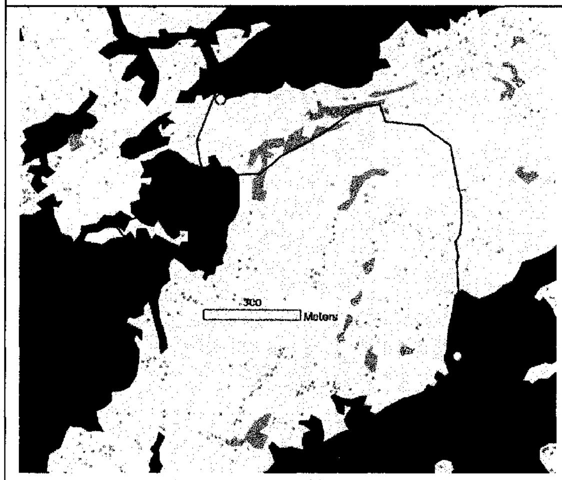
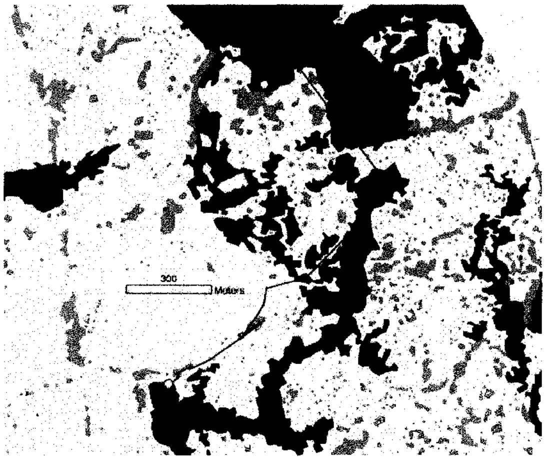


1.1 km Wren fencerow

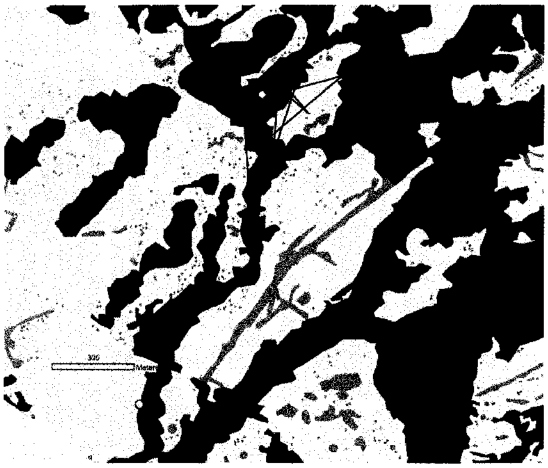


1.1 km Antshrike pasture

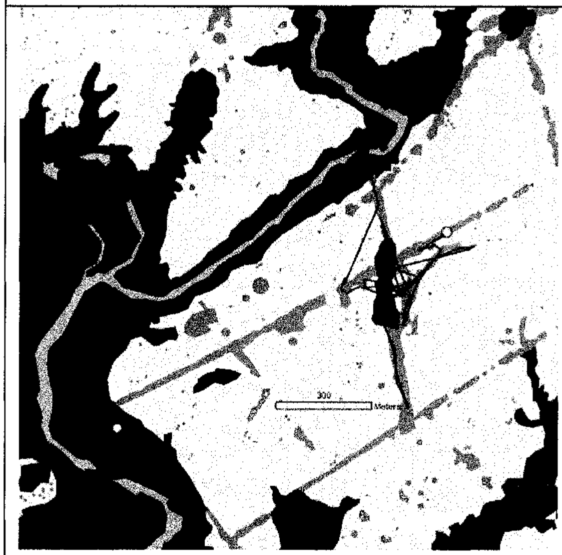


1.1 km Wren pasture

1.2 km Antshrike corridor



1.2 km Wren corridor



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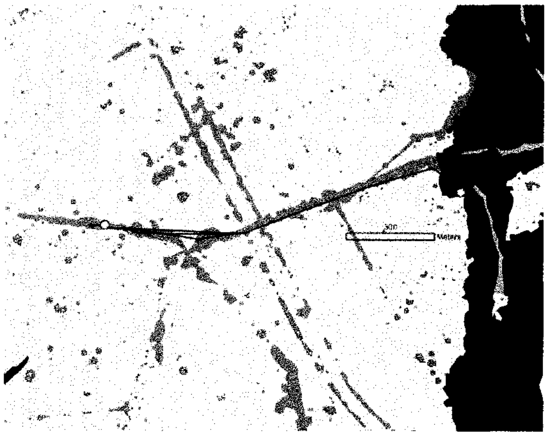

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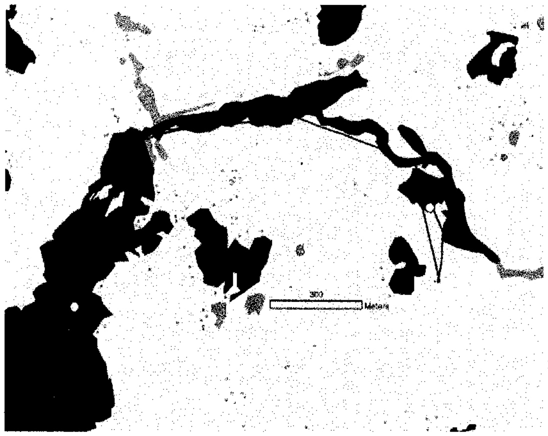
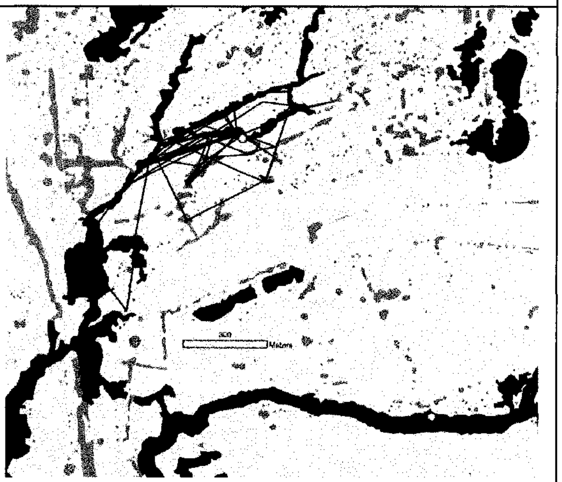
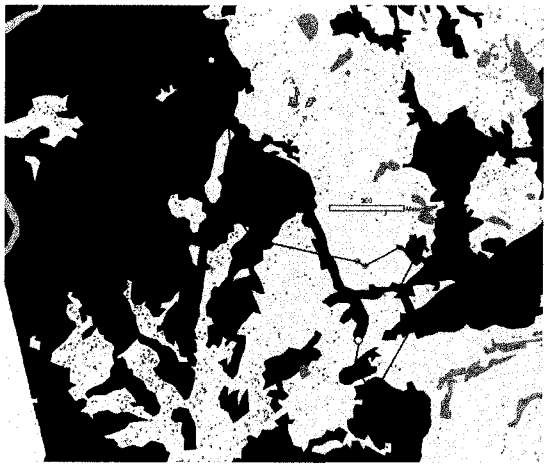


1.2 km Antshrike pasture

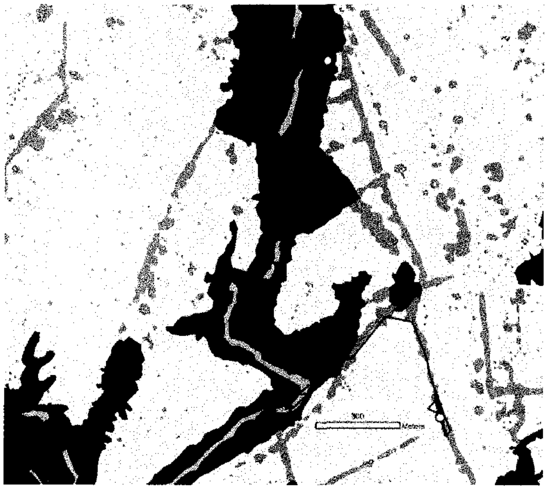


1.2 km Wren pasture

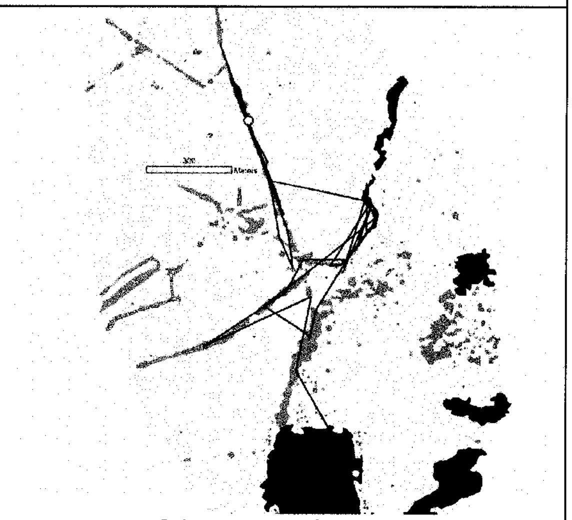


1.3 km Antshrike corridor

1.3 km Wren corridor



1.3 km Antshrike fencerow



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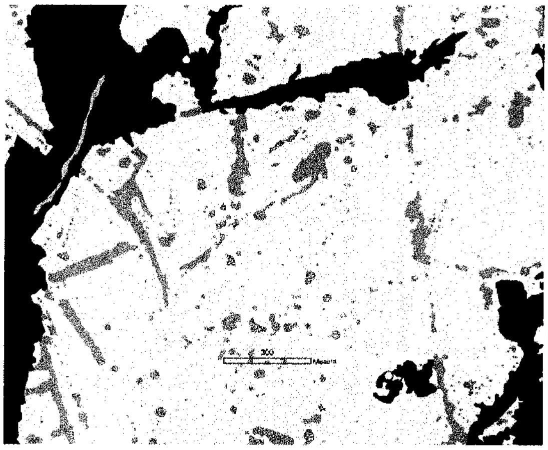
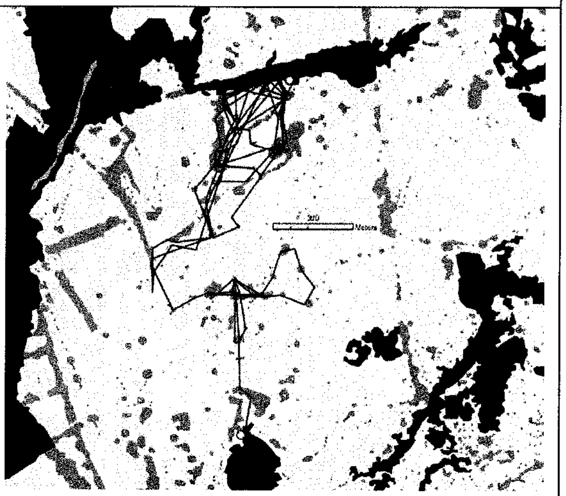
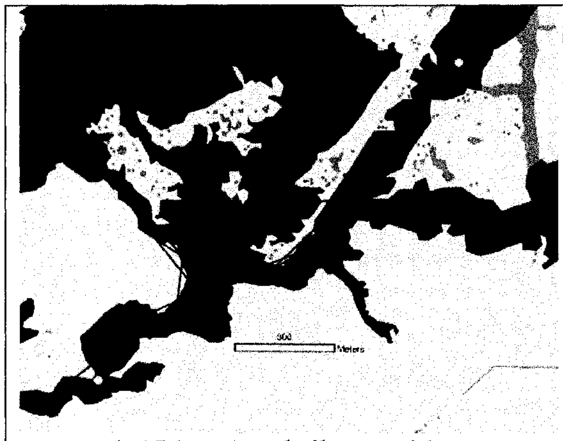


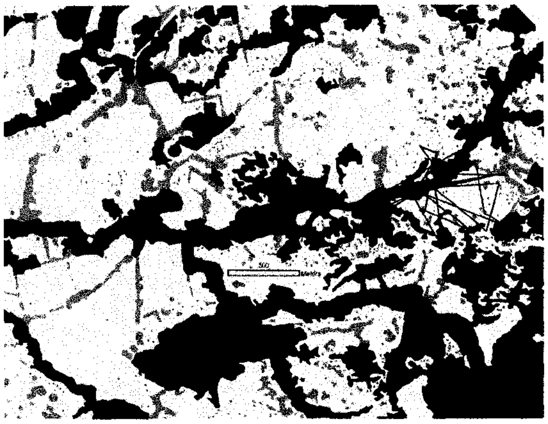
1.3 km Antshrike pasture



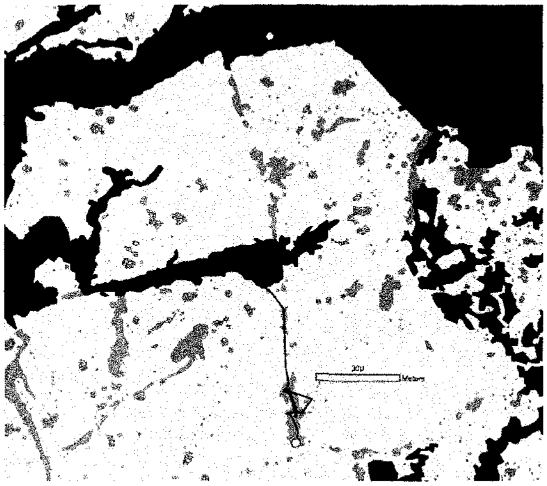
1.3 km Wren pasture



1.45 km Antshrike corridor

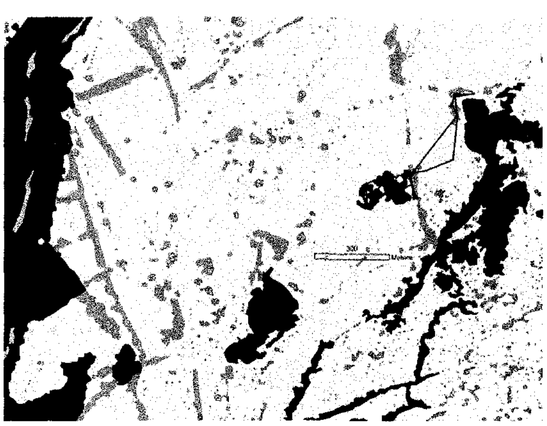


1.45 km Wren corridor



1.45 km Antshrike fencerow

1.45 km Wren fencerow



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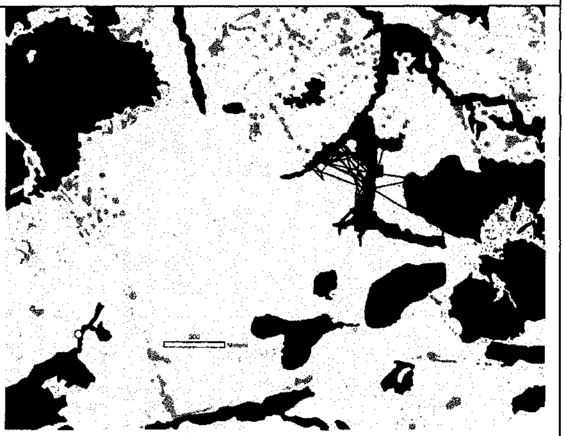

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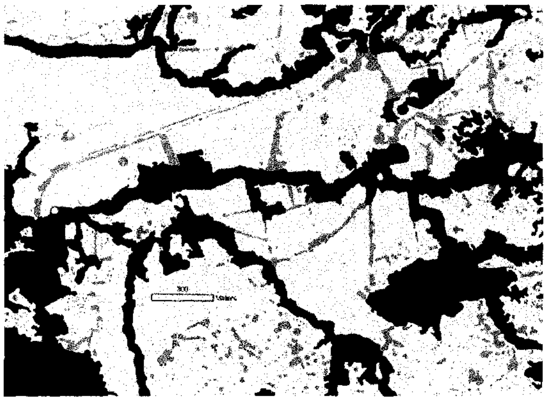
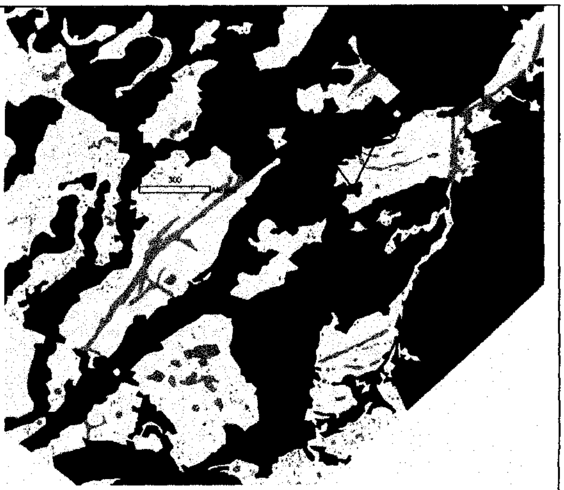
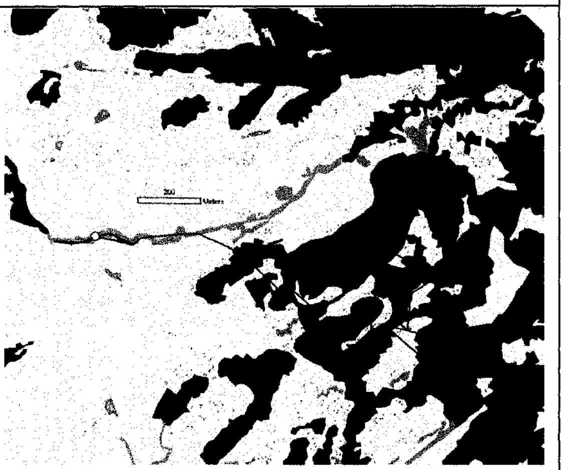


1.6 km Antshrike corridor



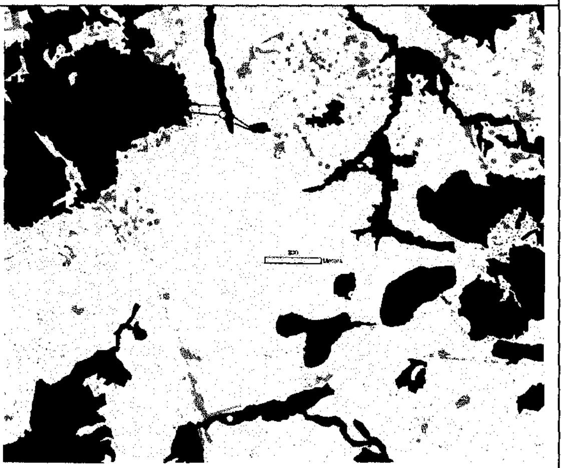
1.6 km Wren corridor

1.6 km Antshrike fencerow

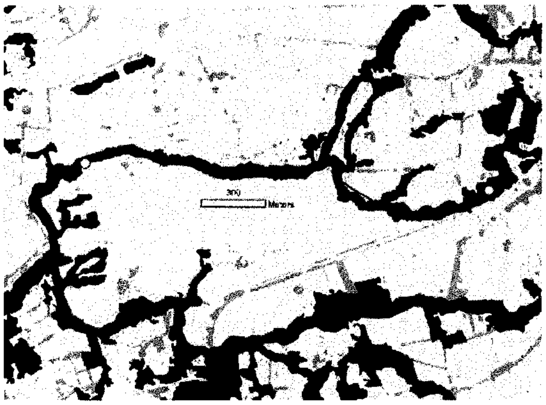


1.6 km Wren fencerow

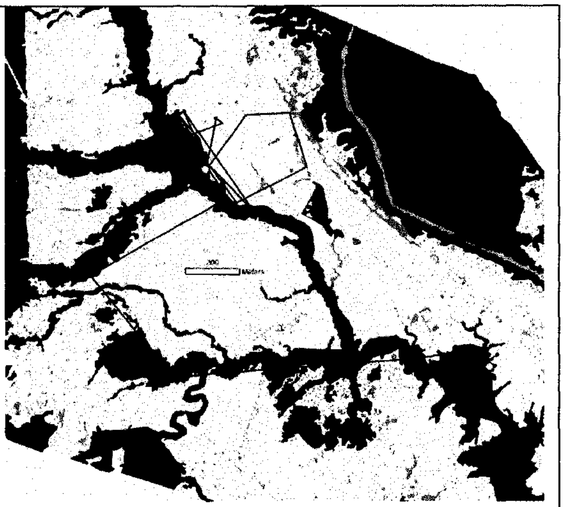
1.6 km Antshrike pasture



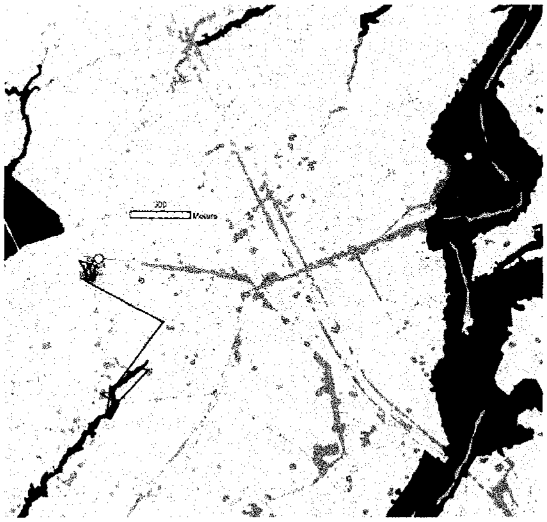
1.6 km Wren pasture



1.9 km Antshrike corridor

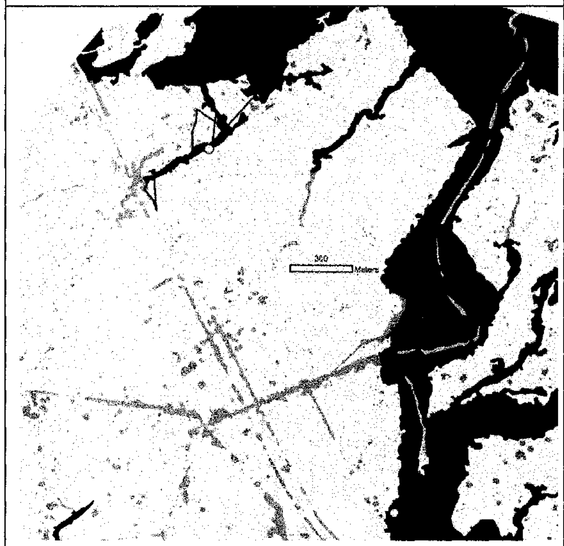


1.9 km Wren corridor

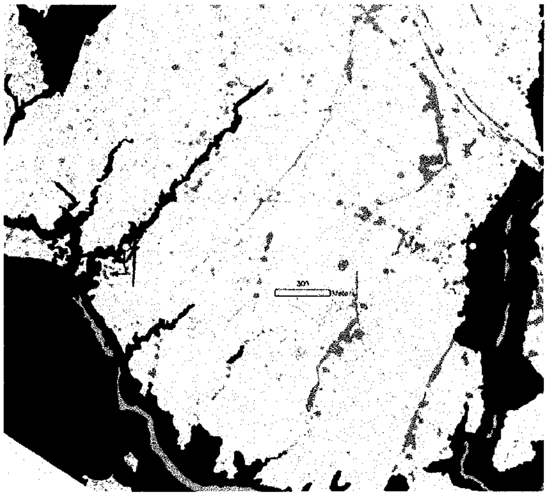


1.9 km Antshrike fencerow

1.9 km Wren fencerow



1.9 km Antshrike pasture



1.9 km Wren pasture