



HOME-RANGE AND MOVEMENTS OF *Myrmeciza exsul* (AVES: THAMNOPHILIDAE) IN
TWO FRAGMENTED LANDSCAPES IN COSTA RICA: EVALUATING FUNCTIONAL
CONNECTIVITY

A Dissertation

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Sergio Losada-Prado


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Major Professor: Bryan Finegan, Ph.D.

AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Sergio Losada-Prado, submitted for the degree of Doctor of Philosophy in the area of Biodiversity and Conservation and titled "Home-range and movements of *Myrmeciza exsul* (Aves: Thamnophilidae) in two fragmented landscapes in Costa Rica: Evaluating functional connectivity," has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the Graduate School at CATIE for approval.

Major Professor


 Bryan Finegan (CATIE)

Date

8/5/12

Committee Members


 Fabrice De Clerck (CATIE)

Date

8/5/12


 Fernando Casanoves (CATIE)

Date


8/5/12


 John Dunning (Purdue University)

Date

14 May 2010

Graduate School (CATIE)


 Glenn Galloway (CATIE)

Date

16-5/2012

ABSTRACT

It is well known that fragmentation not only reduces the total amount of habitat available, but also simultaneously isolates the habitat that remains, preventing movement of organisms and processes in previously connected landscapes. Home-range sizes, movements, density, and apparent survival for individual species remains almost entirely unknown for Neotropical birds especially in fragmented landscapes. Likewise, effects of the agricultural matrix on these variables have been little studied and this information is required for conservation planning. We estimated home-range sizes, movements, density, and apparent survival of Chestnut-backed Antbird (*Myrmeciza exsul*), an understory insectivorous bird with limited dispersal; through several methods (telemetry, color-marked individuals, capture-recapture, and observations). We studied two fragmented landscapes in southwestern Costa Rica: Los Cusingos Landscapes (LCL) with a 56% of forest area and Boruca Landscape (BOL) with only 31% of forest area. Each one with different agricultural matrices, thus LCL with sun-grown coffee, shaded coffee, whereas BOL with degraded pastures.

We found significant differences ($t = -3.52, p < 0.05$) between landscapes regarding home-range sizes with averages of 1.85 ha and 1.20 ha in >100-ha forest sites in LCL and BOL, respectively. However, we did not find differences about home-range sizes between landscapes ($t = -1.28, p > 0.05$) in <10-ha forest fragments surrounded by agricultural matrices; in these forest fragments the home-range sizes averaged 1.94 ha and 1.38 ha in LCL and BOL, respectively. The daily movement distance were not significantly different between landscapes ($t = 0.93, p > 0.05$), with average of 149.50 m / day in LCL and 125.00 m / day in BOL. We detected association between *M. exsul*'s occurrence frequencies in forest fragments surrounded by agricultural matrices both in LCL ($X^2 = 33.02, p < 0.05$) and BOL ($X^2 = 11.18, p < 0.05$). Also,

movements of *M. exsul* individuals moving into forest fragments from the agricultural matrix and out of fragments into the agricultural matrix were registered during the study. We did not find significant differences regarding density (Distance Program) between landscapes ($t = -0.34$, $p = 0.7489$), even though LCR registered density average higher than BOR (0.69 ind / ha and 0.61 ind / ha, respectively). Model estimates for apparent survival probabilities (MARK Program) ranged from 0.844 to 1.000 across month in both landscapes.

We considered that LCL is contributing more than BOL on *M. exsul* movements because shade coffee plantations are facilitating movements of individuals among forest fragments. Also, secondary growth vegetation is considered a potential habitat and “soft” barrier for movements of this species, and <1-ha forest fragments can be used as “stepping stones” in fragmented landscapes with agricultural matrices. Finally, we considered that *M. exsul* populations are stable by strategies as territoriality and parental care during post-fledging period which are potential factors influencing the evolution of small clutch sizes in tropical birds.

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CHAPTER 1

INTRODUCTION

Fragmentation reduces the total amount of habitat available and simultaneously isolates the habitat that remains, affecting the movements of organisms and processes in previously connected landscapes. Further, the effects of isolation are often most immediately noticeable for larger animals such as wide-ranging terrestrial carnivores and migratory oceanic species, smaller animals such as birds, small mammals, butterflies, fish, freshwater shrimp, and marine invertebrates (Crooks and Sanjayan 2006) can all suffer when natural levels of connectivity are reduced. Thus, protected areas could be too small or too isolated to maintain viable populations for many wide-ranging species (Newmark 1987, 1995, Gurd et al. 2001) and fragmented landscapes would be contributing to isolation among populations.

There are many mechanisms by which isolation can lead to the reduction of populations and the extinction of species. Demographic, environmental, and genetic forces can act independently or in concert to create a vortex of extinction in fragmented, isolated populations (Gilpin and Soulé 1986), and extinctions may be best avoided by preventing fragmentation and isolation, and ideally by maintaining large populations in large contiguous blocks of quality habitat (Crooks and Sanjayan 2006). However, it is necessary to attempt to maintain connectivity by protecting or restoring linkages in areas where fragmentation has already occurred. Further, at large spatial and temporal scales, maintaining natural levels of connectivity may be essential to allow for natural range shifts in response to long-term environmental transitions.

Despite the obvious benefits of landscape connectivity to conservation, criticism has often been made of the use of corridors as conservation tools to facilitate the movement of organisms among isolated natural areas (Soulé and Simberloff 1986, Simberloff and Cox 1987,

Hobbs 1992, Simberloff et al. 1992, McEuen 1993, Rosenberg et al. 1997). However, corridors enhance population viability of species in patches connected by corridors (Beier and Noss 1998, Levey et al. 2005), though they could also enhance connectivity for invasive species (Crooks and Suarez 2006). Thus, corridors could be assumed but one of the many methods to conserve connectivity.

The structure and heterogeneity of the matrix can also affect the movement of organisms among forest fragments. Gustafson and Gardner (1996) found that although patch size and relative isolation explained most of the variability in dispersal success, with closer and larger patches having the greatest exchange of individuals, the structure of the surrounding matrix also significantly altered transfer among patches. Likewise, dispersal of Fender's blue butterfly could be facilitated by creating small lupine "stepping stones" among lupine patches because butterflies moved more quickly through the matrix habitat (Schultz 1998). Thus, landscape connectivity must be determined based on the organism's perception of, and interaction with the structure and heterogeneity of the landscape.

According to Taylor et al. (2006), managing the matrix could offer an effective means to preserve or restore functional connectivity in fragmented landscapes; thus it would improve the components of landscape connectivity through (a) species movement patterns and behaviors, (b) the size and arrangement of resources patches, and (c) the matrix. Additionally, a range of approaches to manipulating or managing these components is available; it is possible to redirect and manipulate the behavioral responses of species through the use of fences, roadway crossings, and other devices, for example, but these cannot directly alter the inherent behavior of a species (Taylor and Merriam 1995, Pither and Taylor 2000). However, managing the matrix can require decisions with high political or economic costs.

Fragmented agricultural landscapes can form complex mosaics of natural habitats and several land use types. Although cultivated areas may be an inhospitable matrix for many species, these could provide resources for other species and thus help support natural populations (Aizen and Feinsenger 1994, Ricketts 2004). Thus, the ability of individuals to move among these land use types is very important to the persistence of wild populations and communities in nature (Westrich 1996). However, agricultural landscapes can be seen as a common problem of separation between foraging and nesting habitats without effects on species (Saville et al. 1997, Walther-Hellwig and Frankl 2000). Therefore, it is important to separate the effects of connectivity from size or type of adjacent habitat to know the natural dynamics of species in fragmented landscapes (Taylor et al. 2006). Types of habitat adjacent to crop fields may also affect connectivity by altering permeability of the boundary or resistance of the habitat to movement (Schultz 1998, Haddad 1999, Ricketts 2001, Harvey *et al.* 2005). Additionally, maintaining semi-natural conditions of natural habitats in crop fields would be an important strategy for local biota; thereby, Greenberg *et al.* (1997) and Perfecto *et al.* (1997) considered that maintaining a semi-natural canopy of shade trees on coffee farms could provide sites for important pollinators, as well as habitat for a variety of other native species. Therefore, the role of an agricultural matrix must be evaluated not only as a potential reserve of biodiversity, but also for its potential effects on movements, dispersal, and migration of species.

New tendencies in fragmentation studies on species dispersal, movement patterns of organisms and habitat composition in the matrix are being considered owing to its influence on ecological processes which could affect species functionality (Wiens 1995, Kattan 2002). In fragmented landscapes the surrounding matrix directly influences species composition both in mammals and birds (Laurance 1991, Renjifo 2001), and the connectivity function of landscape

matrices must be considered and included in conservation planning to understand how the habitat structure in the matrix influence the permeability to animal movements (Vandermeer and Carvajal 2001, Hannon and Schmiegelow 2002, Castellón and Sieving 2006, Van Houtan et al. 2007, Lindenmayer et al. 2008, Moore et al. 2008). It is known that for many species the matrix is an unsuitable and hostile habitat, but in some cases it is rarely a barrier to dispersal (Arendt 2004, Castellón and Sieving 2006); however, each species responds distinctly to the matrix and few quantitative data on dispersal ability are available (Wiens 1996, Beier and Noss 1998, Hudgens and Haddad 2003, Taylor et al. 2006, Moore et al. 2008, Young et al. 2008). Currently, basic information on territory size, density, and microhabitat requirements is lacking (Stouffer and Bierregaard 1995, Renjifo 2001) and this information is necessary to predict how birds can use a fragment of a given size or second growth of a given structure. Therefore, observations of movements by naturally dispersing animals in already fragmented landscapes can demonstrate the conservation value of both corridors and matrices if efforts are made to document actual travel routes in both corridors and matrix land (Beier and Noss 1998, Bennet 2004).

Among tropical species, understory insectivorous birds are among the most sensitive to fragmentation (Karr 1990, Willson 2004, Sieving and Karr 1997, Stouffer 2007). This sensitivity to dispersal habitat makes the group potentially valuable as focal species for planning the connectivity of landscape design. Additionally, according to Stouffer and Bierregaard (1995) the critical questions for conservation are how far forest dependent understory birds will move through second growth, and whether their use of secondary growth and fragments is indicative of their capacity to maintain viable populations in those areas without depending on colonization from larger areas of forest; thus evaluating movements of birds with limited dispersal abilities in fragmented landscapes will contribute to design conservation strategies to landscape level. For

these reasons, this study evaluated the functional connectivity in two fragmented landscapes to *Myrmeciza exsul* (Aves: Thamnophilidae), an understory insectivorous bird, in southwestern Costa Rica.

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CHAPTER 2

LITERATURE REVIEW

FRAGMENTATION

Deforestation reduces the amount of primary forest available for native flora and fauna and almost inevitably fragments the remaining forest (Bierregaard and Stouffer 1997).

Fragmentation has often been used in the general sense of land transformation that includes the breaking of a large habitat into smaller pieces (Forman 1995). Although an important focus has been on the extinction of species, fragmentation as a spatial process has effects on almost all ecological patterns and processes including the colonization of landscapes by new species. Most of the ecological effects of habitat fragmentation have been examined including patch size, patch number, connectivity, isolation, and species movement (Forman 1995, Murcia 1995, Laurance and Bierregaard 1997, Bierregaard et al. 2001). Likewise, according to Forman (1995) there are six major causes of land transformation: deforestation, suburbanization, corridor construction, desertification, agricultural intensification, and reforestation. Each changing spatial pattern is effectively a mosaic sequence, that is, a series of spatial patterns over time.

Habitat alteration is mostly due to agriculture and forest management practices that reduce ground and mid-story cover (Krementz and Powell 2000). In addition, human modifications could greatly increase fragmentation and the landscapes would be increasingly populated by a mosaic of distinct patches and intervening boundaries (ecotones) as well as more gradual changes in biota, all of which may respond differently to environmental drivers (Noss and Csuti 1997). Likewise, boundaries have been mostly viewed as relatively stable zone of vegetation with differential effects on movements of animals, plants, and materials (Peters et al.

2006). Also, patch size has effects on within-patch processes, such as nitrogen cycling and recruitment, and processes that connect patches, such as animal movement (McIntyre and Wiens 1999). The spatial distribution of patches at broader scales may or may not be in equilibrium through time so that patch dynamics theory has been integrated with hierarchy theory to relate pattern, processes, and scale within the context of the landscape (Wu 1999, Peters et al. 2006).

Three categories of spatial attributes, patch size, connectivity, and boundary length, are considered of particular ecological significance (Forman 1995). In general, larger patches of habitat contain more species and often a greater number of individuals than smaller patches of the same habitat (Turner et al. 2001). Also, the degree of connectivity between patches of equally suitable habitat can constrain the spatial distribution of a species by making some areas accessible and others inaccessible. Once suitable habitat for a species of interest is characterized, determining whether the habitat is or is not spatially connected is often of interest (Turner et al. 2001). Finally, more boundary and edge to area enhance abundance and richness of edge species. Also, more animals move either along the boundary or fewer cross it (Forman 1995).

Many species, including most large mammals and birds, cannot maintain viable populations in small habitat patches, which lead to local extinction and loss of biodiversity (Forman et al. 1976, Kattan 2002). In addition, land fragmentation commonly disrupts the integrity of a stream network system, water quality of an aquifer, the natural disturbances regime in which species evolved and persist, and other ecosystem processes (Schlosser and Karr 1981, Peterjohn and Correll 1984, Pickett and White 1985). According to Forman (1995), fragmentation is a phase in the broader sequence of transforming land by natural or human causes from one type to another. Thus, it is important to examine fragmentation together with other spatial processes in the broader framework of land conversion.

Patterns of land use can alter both the rate and direction of natural processes, and land use patterns interact with the abiotic template to create the environment in which organisms must live, reproduce, and disperse (Turner et al. 2001). Land use refers to the way in which humans employ land surface area and its resources. A related term, land cover refers to the habitat or vegetation type present, such as forest, agriculture, and grassland (Turner et al. 2001). Currently, a related aspect of fragmentation that has received little attention is the effect of changing land use in the matrix surrounding fragments. Moreover, interspecific variations in response to landscape effects are likely to be significant, especially among the sedentary specialized birds of the Neotropics (Stouffer and Bierregaard 1995).

LANDSCAPE CONNECTIVITY

Landscape connectivity is defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993, With et al. 1997). This definition emphasizes that types, amounts, and arrangement of habitat or land use on the landscape influence movement, population dynamics, and community structure. Thus, landscape connectivity combines a description of the physical structure of the landscape with the organism’s response to that structure (Taylor et al. 2006); additionally, landscape connectivity is a property of species-landscape interactions, resulting from the interaction between a behavioral process (movement) and the physical structure of the landscape.

According to Taylor et al. (2006), landscape connectivity considers two types of connectivity: (1) structural connectivity, which describes only physical relationships among habitat patches such as habitat corridors or inter-patch distances, and (2) functional connectivity, which describes the behavioral response of organisms to landscape structure and it increases

when some change in the landscape structure increases the degree of movement or flow of organisms through the landscape. However, a clear distinction between these two concepts is not always possible; habitat does not necessarily need to be structurally connected to be functionally connected because some organisms, by virtue of their gap-crossing abilities, are capable of linking resources across an uninhabitable or partially inhabitable matrix (Dale et al. 1994, Desrochers et al. 2002, Castellón and Sieving 2006). Finally, landscape connectivity must be assessed by determining how organisms move and interact with the structural heterogeneity of the resulting landscape (With et al. 1997).

Urbanization and other human activities often disrupt natural connections among landscapes, and many conservationists have advocated the retention of habitat corridors. Conservation value accrues to corridors only if animals in real landscapes use corridors to bring about connectivity (Beier and Noss 1998). Simulation modeling has been instrumental in the development of general hypothesis about species responses to landscape patterns (Fahrig 1998). A fundamental phase shift in landscape structure occurs at a critical threshold where a single large habitat cluster is suddenly fragmented into many smaller isolated patches. When recolonization is critical for metapopulations persistence, this sudden decrease in connectivity can precipitate the extinction of dispersal-limited species (Bascompte and Sole 1996). The magnitude of these effects depends upon habitat pattern, with spatially aggregated habitats having more connectivity and greater probability of species persistence than spatially random habitats (Hill and Caswell 1999, With and King 1999).

ANIMAL MOVEMENT AND MATRIX COMPOSITION

Animal movement could be defined as daily normal displacements of an individual into a landscape or habitat where food, shelter, or mates for reproduction can be obtained. Thus, movements would be depending both of behavior and internal necessities of each individual. According to Bell (1990) three factors determine searching behavior, (1) the characteristics and abilities of the animal, (2) the resources and risks in the external environment, (3) resource requirements as determined by the internal state of the animal. However, another important factor to facilitate animal movements is related both with landscape and habitat connections. Therefore, movement of individuals and population depends on the major spatial attributes of each landscape.

Most fragmented forest landscapes contain varying degrees of connectivity with variable matrix composition (Bierregaard and Stouffer 1997), and the response of animal movement will depend on the degree of functional connectivity which is in turn related to matrix composition (Tracey 2006). Therefore, the ability to move among remnant forest patches via the landscape matrix redefines the population dynamics within patches. Research about the effect of matrix composition on animal movements (functional connectivity) has demonstrated that older second growth provides more cover and more resources for birds passing through it than does pasture, for example (Stouffer and Bierregaard 1995, Bierregaard et al. 2001). In addition, canopy cover is especially important for many of the understory birds which are generally considered to be poor colonizers and unwilling to cross open areas (Terborgh and Weske 1969, Stouffer and Bierregaard 1995).

Additionally, fragment size is not only an important factor that influences movements of organisms toward the forest fragments. According to Stouffer and Bierregaard (1995), ant

followers were not influenced by fragment size (Manaus, Brazil), but only used fragments surrounded by *Cecropia* at least 6 years old; these species cannot be said to “persist” in the fragments surrounded by *Cecropia*, as they only pass through as they follow ant swarms or move from swarm to swarm. Furthermore, terrestrial insectivorous birds showed little sign of recolonizing fragments possibly because either secondary growth may be inadequate habitat for these species or low vagility probably makes many solitary species unlikely to recolonize (Stouffer and Bierregaard 1995). Vulnerability to fragmentation is compounded by the reluctance of many forest-interior species to cross non-forest matrix, which would reduce gene flow (Stouffer and Bierregaard 1995, Sigel et al. 2006). According to Sigel et al. (2006), species that increased in the census data at La Selva Biological Station (Costa Rica) tended to be forest generalists and omnivores, which may represent a true increase of generalist species because of a greater area of disturbed habitats surrounding the study area.

For understory insectivorous birds it appears that isolated fragments without surrounding secondary growth are analogous to true islands, with some individuals trapped by isolations, and new individuals only rarely colonizing (Willis 1974). Thus, terrestrial insectivorous birds are affected by a separation of only 70-100 m from continuous forest and this was sufficient to cause species loss after isolation within each fragment in lowland rain forests in Manaus (Stouffer and Bierregaard 1995). Additionally, Laurance (2004) found that in the lowland rain forest of central Amazonia a small unpaved road (<40 m wide) caused a major alteration in the distribution and abundance of many understory birds; also many understory insectivorous birds exhibited strong edge avoidance, with captures of many terrestrial species, solitary species, army ant followers, members of mixed-species flocks declining sharply near road margins, whereas edge/gap specialists increased near the road. On the other hand, Castellón and Sieving (2006)

demonstrated as wooded corridors and shrubby vegetation functioned similarly as movement habitat for dispersing Chucaos, *Scelorchilus rubecola*, a forest understory bird endemic to South American temperate rainforest. Thus, these habitat types (secondary growth vegetation, wooded corridors, and shrubby vegetation) may be similarly viable to use in landscape management both to enhance connectivity and animal movements.

RADIO TELEMETRY

Wildlife biologists commonly use radio-telemetry to obtain descriptions of movement and estimates of survival (Pollock et al. 1989, White and Garrott 1990) and mark-recapture methods to estimate population size, survival, and movement patterns (Pollock et al. 1990, Kremenetz and Powell 2000). Also, Bibby et al. (1992) noted that distribution data obtained by radio-telemetry are less biased by the observer than similar data collected by other study methods. Likewise, according to Kenward (2001) radio-telemetry has the potential to reduce potential bias in studies of nesting birds. Usually, radiomarked animals are also marked with bands, tags, or some other form of identification during the course of the study (Powell et al. 2000). According to Powell et al. (2000), there are several advantages to the simultaneous use of data from both mark-recapture data and radiomarked animals, (1) precision of survival estimates should be increased by combining two sources of information about the same parameter, (2) incorporating mark-recapture data into a combined data structure allows for tests of potential radio effects on survival or other parameters, and (3) a combined design allows to separate inference on movement, emigration, and mortality rates that are often confounded in complex ways, particularly in studies at broad spatial scales.

Radio-telemetry studies applied to birds such as that by Powell et al. (2000) at the Piedmont National Wildlife Refuge in central Georgia, U.S.A. during the 1996 breeding season using *Hylocichla mustelina*, were able to estimate the weekly fidelity rates in the study area and its complement (off study area). Also, it was shown that precision of recapture and movement parameters increased under a combined model (banded and radiomarked animals). Likewise, these models can provide important information to help manage populations at the landscape level. Also, Krementz and Powell (2000) reported daily movements during breeding season of 100 m/day by *Pipilo erythrophthalmus* at the Savannah River Site (South Carolina). In addition, they found that excursions away from the central activity area were common, sometimes long (1250 m), and crossed through different aged pine stands. However, middle age pine stands were the usual target of these movements.

In the tropics, Roberts (2007) evaluated the movements of *Hylocichla mustelina*, a Neotropical-Nearctic songbird, at La Selva Biological Reserve. Using radio telemetry, individuals of *H. mustelina* showed home ranges between 0.99 and 1.02 ha. In other region, Stouffer (2007) evaluated 13 species of understory insectivorous birds in Manaus (Brazil), these species recorded different territory sizes, densities, and biomass; likewise, he found territory sizes in the range of 6-7 ha for species like *Myrmeciza ferruginea*, *Formicarius colma*, *Corythopis torquatus*, and *Conopophaga aurita* whereas at the other extreme, the territories of *Sclerurus mexicanus*, *S. rufigularis*, and *Myrmornis torquatus* sometimes exceeded 20 ha. In Barro Colorado Island (Panamá), Stutchbury et al. (2005) described movements, singing, and territorial behavior of two antbirds, *Myrmeciza exsul* and *M. longipes*, two congeneric species; they found that *M. longipes* made off-territory forays during the dry season while they did not detect off-territory forays in *M. exsul*.

Currently, no study has registered *Myrmeciza exsul*'s movements and home-range sizes in fragmented landscapes with agricultural matrices of coffee crops and pastures.

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CHAPTER 3

Home-range size and movements of Chestnut-backed Antbird (*Myrmeciza exsul*), a forest specialist bird, in fragmented landscapes in southwestern Costa Rica

Sergio Losada-Prado¹, Bryan Finegan¹, Fernando Casanoves¹, Fabrice Declerck¹, John Dunning²

¹Department of Natural Resources and Environment, CATIE, Turrialba, Costa Rica.

²Purdue University, Indiana, USA.

ABSTRACT

The effect of fragmented landscapes on species dispersal is receiving significant attention with the aim of maintaining connectivity among animal populations. Landscape connectivity influences the spatial distribution of a species by making some areas accessible and others inaccessible. Among tropical birds, understory insectivorous species are among the most sensitive to fragmentation owing to their limited dispersal abilities. This sensitivity to dispersal makes the group potentially valuable as focal species for planning the connectivity of landscapes. Through telemetry methods, banded individuals, capture-recapture, and observations we evaluated individuals Chestnut-backed Antbird (*Myrmeciza exsul*), a common non-migratory understory insectivore with low mobility and a forest specialist, to determine its home-range size and movements within the agricultural matrix in two fragmented landscapes of southwestern Costa Rica. Los Cusingos Landscape (LCL) had 56% forest area, woodland, and pasture with trees; additionally, crops such as coffee, sugar cane, and pasture occupied 34% of the land area. On the other hand, Boruca Landscape (BOL) had 31% forest cover, 23% pastures without trees, and 3% permanent crops such as coffee. We found significant differences ($t = -3.52$, $p = 0.0018$) between landscapes regarding home-range sizes, although daily movement distance was not different ($t = -0.93$, $p = 0.3640$) between landscapes. We estimated average home-ranges sizes with a 95% probability between 1.02 and 2.76 ha in LCL and between 0.77 and 1.80 ha in BOL. Additionally, average core areas (50% probability) were estimated between 0.14 and 1.08 ha in LCL and between 0.05 and 0.52 ha in BOL. Daily movement distances were 149 m/day and 125 m/day at LCL and BOL respectively. We registered movements of *M. exsul* through shaded coffee and across secondary roads (~12 m wide). To our knowledge this study is the first information regarding use of agricultural matrices by *M. exsul* in fragmented landscapes. We

concluded that *M. exsul*'s home-range size was greater in LCL than in BOL, while daily movement distance was not different between landscapes.

Key words: Chestnut-backed Antbird, antbirds, home-range size, movements, agricultural landscape.

INTRODUCTION

Myrmeciza exsul is a common non-migratory understory insectivore that ranges from eastern Nicaragua to western Ecuador, has low mobility, prefers treefall tangles as nest sites (Willis and Oniki 1972, Sieving and Karr 1997, Zimmer and Isler 2003), and can be found throughout the year (Stiles 1983). The species is found in lowland forests, forest edges, and older secondary forests throughout its range to about 1000 m elevation (Skutch 1969, Willis and Oniki 1972, Zimmer and Isler 2003, Losada-Prado *pers. obs.*). This species forages almost entirely on arthropod prey taken from the leaf litter (Stouffer 2007). Using the system proposed by Stiles (1983), *M. exsul* is categorized as Ap4acd (A = abundant, many can be recorded daily; p = permanent resident, breeds in the area, can be seen at any time of year; 4 = wooded habitats; a = forest interior; c = forest edge, including light gaps of various types; d = old second growth, with a more or less distinct “canopy” stratum). Clutch size is two eggs, and mated pairs remain paired year-round; also, *M. exsul* can produce up to three successful broods per year (Skutch 1960, Willis and Oniki 1972).

Among tropical birds, understory insectivorous birds like *M. exsul* are among the most sensitive to fragmentation owing to their limited dispersal abilities (Willis 1974, Karr 1990, Sieving and Karr 1997, Stouffer 2007). This sensitivity to dispersal makes the group potentially valuable as focal species for planning connectivity landscape design. Recently, the effects of

fragmentation on species dispersal have received increased attention with the aim of maintaining connectivity among animal populations (Hannon and Schmiegelow 2002, Cullen et al. 2004, Frankman 2006, Paquet et al. 2006, Marra et al. 2006, Ruiz-Gutiérrez et al. 2008) and ecosystem services (Pearce and Mourato 2004, Ricketts et al. 2006) to enhance the persistence of animal populations. Thus, the connectivity of suitable habitat can determine the spatial distribution of a species by making some areas accessible and others inaccessible (Turner et al. 2001, Levey et al. 2005, Lindenmayer et al. 2008). Once suitable habitat for a species of interest is characterized, determining whether the habitat is or is not spatially connected is often of interest (Turner et al. 2001, Fahrig 2003). Basic information on territory size, density, and microhabitat requirements of *M. exsul* does not exist (Stouffer and Bierregaard 1995, Renjifo 2001) and this information is necessary to predict how birds can use a fragment of a given size or second growth of a given structure.

Data on individual movements are important for understanding dispersal, habitat selection, and foraging techniques, particularly in areas where habitat is not contiguous (Colwell and Oring 1989, Krebs and Inman 1992, Fahrig and Merriam 1994, Reed et al. 1998a, Reed et al. 1998b, Gordon 2000). Likewise, conservation biology requires knowledge about individual movements (abilities and patterns) because of their relationships to population persistence in fragmented landscapes and parameters of metapopulations (Hansson 1991, Reed et al. 1998b, Crooks and Sanjayan 2006, Moilanen and Hanski 2006). Also, it is necessary to evaluate how human-altered habitat may restrict dispersal movement among habitat fragments (Dunning et al. 1995, Sieving et al. 1996, Antongiovanni and Metzger 2005, Van Houtan et al. 2007, Lindenmayer et al. 2008).

Besides connectivity, estimates of either territory or home-range sizes are important to bird conservation in fragmented landscapes. They have been suggested as possible indices of habitat quality and are sometimes an issue of management and regulatory concern (Yosef 1993, Atwood 1998, Linkhart et al. 1998). Home range can increase with body mass, decrease with increased habitat productivity, and may change over the season (Lindstedt et al. 1986, Peery 2000, Duca et al. 2006). According to Myers et al. (1979) individuals establish territories that contain adequate resources to meet their energetic needs and individuals will defend as large an area as it can, constrained by competition with other individuals. However, these hypotheses do not include the influence of matrix types on the species' territory size in fragmented landscapes, a factor that has been studied very little. Contrarily, Duca et al. (2006) did not find a relationship between territory sizes and distances to forest edges or roads on three antbirds in southeastern Brazil.

Little is known about *M.exsul*'s movements (Barnett et al. 2007) and home-range sizes in fragmented agricultural landscapes. Willis and Oniki (1972) estimated territory size of a male at ~2.5 ha in mature forest at Barro Colorado Island; whereas Stutchbury et al. (2005) registered territories of 1 ha at the same site for the same species. Sigel et al. (2006) demonstrated that *M. exsul* decreased in abundance in continuous forest at La Selva Biological Station (Costa Rica) together with other insectivorous species possibly due to multiple ecological factors, but unfortunately these researchers were unable to test interactions among factors. Roberts (2007) evaluated *M. exsul*'s presence in forest fragments (~10 ha) surrounded by pastures around La Selva Biological Station and found that abundance was influenced by the interaction of fragment area and forest cover. However, she did not register movements either among or within forest

patches. None of these studies estimated both home-range sizes and movements of *M. exsul* in fragmented landscapes with different agricultural matrices.

In this study we estimated the home-range size and movement (daily movement distance) of 38 *M. exsul* individuals in two fragmented landscapes in southwestern Costa Rica. The Los Cusingos landscape (LCL) had 56% forest cover and Boruca landscape (BOL) 31%. Our hypothesis was that average home-range size and daily movement distance of *M. exsul* were smaller in BOL than in LCL. This is because BOL has degraded pastures near the forest edge that might limit the *M. exsul*'s movements among forest patches, while LCL is dominated by different vegetation types (e.g., coffee and shaded coffee) that we believe might facilitate *M. exsul*'s movements. We predicted this because both degraded pastures and open areas are a potentially hostile habitat to the movements of understory insectivorous birds and some habitat types near forest could be permeable to a variety of species that require minimum conditions to move across the landscape.

MATERIALS AND METHODS

Study sites

We conducted the study in two fragmented landscapes of southwestern Costa Rica: (a) Los Cusingos Landscape (LCL) located in the Alexander Skutch Biological Corridor which included the Los Cusingos Natural Reserve (Canet 2005), and (b) Boruca Landscape (BOL) located in the proposed AMISTOSA Biological Corridor (Cespedes 2006) which included the Boruca Indigenous Reserve (Figures 1 and 2).

In the Los Cusingos Landscape, the most representative life zones according to the Holdridge Life Zone classification system (Holdridge 1978) are Premontane wet forest (P-wf) and Premontane rain forest (P-rf), the average annual temperature is 24°C and annual precipitation of 3237.8 mm, and the corridor has an area of 6,010 ha and altitudes from 600 to 2500 m (Canet 2005, Morera et al 2006). The Chirripo National Park and Las Nubes Biological Reserve border the corridor in high altitudes (>1000 m) (Canet 2005) and borders with the Biosfera-La Amistad Reserve in the Talamanca mountains (Canet 2005). Also, it belongs to the Perez Zeledon canton, San José Province (Morera et al. 2006). Fifty-six percent of the landscape comprised woodlands, pastures with trees, and forest areas (Table 1). Permanent crops (e.g., coffee), sugar cane, and pasture which occupy 34% of the land area, consequently this landscape is highly fragmented and dominated by coffee crops (Morera et al. 2006). According to the McIntyre and Hobbs (1999) classification this landscape is considered fragmented (~10-60% forest cover).

BOL is located in the Boruca Indigenous Reserve in Buenos Aires canton, Puntarenas Province. This reserve is the second most important in the AMISTOSA Biological Corridor, and includes undisturbed high priority habitats within the structural connectivity network proposed by Céspedes (2005). The reserve is located between the Biosfera-La Amistad Reserve and the protected areas of the Osa peninsula. The 34,479 ha, area encompassing BOL, ranges from 0 to 3290 meters above sea level and is considered a fragmented landscape (McIntyre and Hobbs 1999) with a forest cover of 31% within a matrix of pastures, fallow growth, and shaded coffee (ITCR 2004, Céspedes 2005). The most representative life zones are Premontane wet forest (P-wf) and Tropical moist forest (T-mf), Premontane belt transition with an average annual temperature of 24°C.

Data for this study were gathered during both dry and rainy seasons from April 2008 to March 2009 in both landscapes. There is almost no rain from November to December, and there is less rain in the middle of the year than in the months just before or after July-August or August-September. Likewise, a main dry and hot season on the Pacific occurs between December and May. Peak annual rainfall occurs in September and October (Coen 1983).

In LCL we selected three forest sites >100 ha in continuous forest and five forest fragments (0.16-10 ha) surrounded by either shaded coffee or sun-growth coffee. In BOL three forest sites were selected using the former criterion (>100 ha) and three forest fragments (2-10 ha) surrounded by pastures (Table 2). In each landscape the forest sites >100 ha were separated from each other ~1 km. Thus, we compared home-range sizes of *M. exsul* in landscapes with different matrices and forest fragments.

Capture method of *M. exsul*

We captured *M. exsul*, in each forest site and forest fragment, by placing 5-10 mist-nets (2 × 12-m, 36-mm mesh) in a circle and using tape playback to lure individuals into them (Stouffer 2007, S. Woltmann *pers. com.*). Each day, 30 minutes before sunrise, we opened the nets for 5 hours and these were checked at 30 minutes intervals. For each captured bird, we recorded age and sex, and individuals were banded with a unique colored leg bands combination to identify each one. We netted each forest site and forest fragment for two days and registered banded individuals within and among capture sites through recaptures and resighting individuals with color bands.

***M. exsul*'s locations in forest sites and forest fragments**

We marked four individuals with radio transmitters and 26 individuals with color leg bands in forest sites >100 ha; additionally, eight individuals were radio-marked in forest fragments (0.16 and 10 ha) surrounded by agricultural matrix in both landscapes. Radio-marked individuals were fitted with a radio transmitter TXB-003B (*TELENAX*, Mexico) weighing about 1.8 g each (<5% of body weight). Radio transmitters were attached using a figure-eight harness (Rappole and Tipton 1991) made of light-weight cotton embroidery floss. We monitored each individual's status (alive or dead) and location daily over three weeks (Krementz and Powell 2000). We used a RA-14K hand-held antenna (*TELONICS*, Arizona, USA) and a TR-4 radio receiver (*TELONICS*, Arizona, USA) to locate each radio-marked bird. The frequencies were in the 150-151 MHz band and separated at least 20 MHz to avoid overlapping among signals.

The individuals locations were obtained on a grid system (25 × 25 m) using a GPS (Garmin *eTrex*), a compass, a metric tape, and spending the time necessary to improve the accuracy of the location records at each site (Verner and Ritter 1988, Bibby et al. 1992, Buckland 2006, Stouffer 2007). With this technique birds can be placed within an area of 0.25 ha and it is considered an adequate sampling method for terrestrial insectivores (Stouffer 2007). Also, following Stouffer (2007) each individual was located at least 63 times over three weeks with a mean of 21 locations per week. In addition, we registered locations at intervals of not less than 20 minutes (Swihart and Slate 1985, Atwood et al. 1998) to ensure independent observations. Thus, we located each individual at least eight times per day during a three-hour period and took bearings from at least three points on three sides near each bird. Individuals were followed for three weeks.

Statistical analyses

With the locations from both observations and telemetry we estimated *M. exsul*'s kernel home-range using the utilization distribution function (Worton 1987, 1989) in Arcview GIS version 3.3 and the Animal Movement (USGS 1998) and Distances and Bearings between Matched Features extensions (Jenness 2007). The home-range size obtained through the Kernel method was reported as the minimum area that includes a fixed percentage of the volume in the distribution of use (Silverman 1986, Fuller et al. 2005). Thus, the home-range size was estimated as 95% probability polygon (with default smoothing parameter) which includes the location points to delineate home-range boundaries and a 50% probability to represent core areas within each home-range (UGSD 1998, Bennett and Bloom 2005). Additionally, each home-range size was analyzed with the Site Fidelity Test where a Monte Carlo simulation and parameters from the original data are used to determine if the observed movement pattern has greater site fidelity than could occur randomly if the pattern is random (UGSD 1998). Home-range size is reported as mean \pm SD.

We registered the daily movement distance as a response variable (Krementz and Powell 2000) by using Arcview GIS version 3.3 and the Pathmatrix extension obtaining a distance matrix for estimating distance traveled per day. The home-range size and daily movement distance were estimated from both color-marked and radio-marked individuals. Thus, locations concerning home-range size and daily movement distance were independently collected using the radio-telemetry and color-bands methods. Daily movements are reported as mean distance \pm SD.

Normal distribution and variance homogeneity were analyzed for both the home-range size and daily movement distance (Zar 1996). We did not find a correlations between home-

range sizes and the numbers of locations ($r = 0.02$, $n = 30$), thus home range was not affected by the number of locations for each individual. Overall, statistical tests were evaluated with a significance level of 0.05. A t-test (Zar 1996) was used to determine whether home-range sizes and daily movement distance differed between landscapes in the forest sites >100 ha and <10 ha forest fragments. Additionally, the home-range size was analyzed with vegetation variables through Principal Component Analysis. The vegetation variables (canopy cover, diameter at breast height, tree density, basal area, habitat vertical structure) were obtained from Losada-Prado and Finegan [Chapter 5]. These analyses were carried out with InfoStat version 2009 (Di Rienzo et al. 2009).

RESULTS

We registered 5,236 locations (2,895 from LCL and 2,341 from BOL) to obtain the mean home-range size of *M. exsul* in forest sites >100 ha. Of these locations 4,277 were with color-marked individuals and 959 were from radio-marked individuals (481 from LCL and 478 from BOL). Overall, we estimated 30 home-range sizes, 15 from LCL and 15 from BOL, of which four were from radio-marked individuals. Each individual averaged 175 locations with ~ 8 locations / day. Overall sampling effort was 1,890 hours and a mean of 63 hours / individual.

Home-range sizes in forest sites (>100 ha)

The 95% home-range sizes were significantly different ($t = -3.52$, $p = 0.0018$) between landscapes with color-marked individuals with higher values at LCL than at BOL (Table 3, Appendix 1). There were also significant differences ($t = -5.13$, $p = 0.0359$) between landscapes with radio-marked individuals with home-range sizes greater at LCL than at BOL. Data from

radio-marked individuals showed less variance (LCL = 0.0046, BOL = 0.00051) than color-marked individuals (LCL = 0.39, BOL = 0.14) for both landscapes. However, the mean home-range sizes between color-marked individuals and radio-marked individuals were not significantly different in either LCL ($t = 0.60$, $p = 0.5588$) or in BOL ($t = -0.67$, $p = 0.5132$) (Figure 3). This supports the notion that the color leg band method provides the same results as the telemetry method. Additionally, 95% home-range size between males and females did not show significant difference in either LCL ($t = -0.41$, $p = 0.6902$) or in BOL ($t = 0.48$, $p = 0.6399$) (Table 4).

Core areas. Core areas estimated by 50% probability were significantly different ($t = -4.13$, $p = 0.0007$) between landscapes with color-marked individuals, but with radio-marked individuals there were not significant differences ($t = -3.02$, $p = 0.0942$) between landscapes. Core areas were always higher in LCL than in BOL (Table 3, Appendix 1). For males, the core areas were significantly different ($t = -2.74$, $p = 0.0228$) between landscapes with color-marked individuals and the same for the females ($t = -2.78$, $p = 0.0273$) (Table 4).

Home-range sizes in forest fragments (<10 ha)

We registered 973 locations at LCL and 966 locations at BOL (eight radio-marked individuals in both landscapes) in forest fragments surrounded by agricultural matrix (shaded-coffee at LCL and pastures at BOL). The 95% home-range sizes were not significantly different ($t = -1.28$, $p = 0.2482$) between landscapes with different matrices, even though the values were the highest in LCL (Table 3, Figure 4, Appendix 2). Likewise, core areas were not significantly different ($t = 0.90$, $p = 0.4363$) between landscapes. We did not register correlation between forest fragment sizes and home-range sizes ($r = -0.01$, $n = 8$). Through correlation analysis the

home-range size was correlated with the habitat vertical structure ($r = 0.85$, $n = 30$) and these variables were spatially closed in the Principal Component Analysis by indicating a significant relation (Figure 5).

Daily movement distances

The daily movement distances were not significantly different with either color band-marked individuals ($t = -0.93$, $p = 0.3640$) or with radio-marked individuals ($t = -2.85$, $p = 0.1045$) in both landscapes. However, individuals from LCL (149 m / day) registered higher values than BOL (125 m / day) regarding this variable (Table 5). The daily movement distances of males ($t = -1.11$, $p = 0.2829$) nor of females ($t = -0.10$, $p = 0.9203$) were not significantly different between landscapes, with color-marked individuals. Additionally, there was no significant difference between males and females ($t = -1.47$, $p = 0.1540$).

We observed *M. exsul* individuals spending 2-3 hours in areas of $\pm 1000 \text{ m}^2$ making a careful examination of either food or in the nest. For instance, seven individuals in LCL and eight individuals in BOL showed this behavior. Most locations were registered in forest (99.26%) with the rest in secondary shrubland (0.74%). No movements were registered in shaded coffee or pastures. However, two radio-marked individuals from $<10 \text{ ha}$ forest fragments at LCL moved toward other forest fragments (10 ha) by crossing through a shaded coffee plantation and adjacent secondary shrubland. These individuals moved $\pm 1,058 \text{ m}$ until another forest fragment. They spent five days in the 0.16 ha forest fragment. Two color-marked individuals were also observed in that same small 0.16 fragment, for four days. These were not subsequently observed, so that these two individuals were assumed to have moved to another fragment through the shaded coffee.

DISCUSSION

Home-range sizes

Our home-range sizes were close to those registered by Willis and Oniki (1972) and Stutchbury et al. (2005) in mature forest at Barro Colorado Island (2.5 and 1 ha, respectively). However, home-range data from LCL, the less fragmented landscape, are closer to Willis and Oniki (1972)'s value than BOL home-range sizes. The differences between home-range sizes on Barro Colorado Island were not specified by Stutchbury et al. (2005), but it could be related to habitat variations. Additionally, core areas were not higher than 0.90 ha indicating that *M. exsul* might use small habitat areas, although its persistence in fragments of this area is not guaranteed over long periods of time. This was observed with the two radio-marked individuals at LCL which passed five days in a 0.16 ha forest fragment, and with two color-banded individuals who stayed four days in the same forest fragment.

For congeneric species, Fedy and Stutchbury (2004) found home-range sizes of *Myrmeciza longipens*, a second growth species, ranging from 0.7 to 2.3 ha in Soberania National Park and Gamboa, Panama. Other studies with other species have found much larger home-range sizes. Willson (2004) estimated a home-range size of 15.4 ha for *Myrmeciza fortis* an obligate army-ant-following bird, in lowland rain forest of Manu National Park, Peru. Stouffer (2007) registered home-range size of 6.62 ha in lowland rain forest of Manaus, Brazil, for *Myrmeciza ferruginea*, a species of small gaps and undisturbed forest. Stouffer (2007) also recorded small home ranges for other terrestrial insectivores such as *Formicarius colma* (6.58 ha), *Conopophaga aurita* (6.28 ha) and *Corythopsis torquatus* (6.00 ha). Although, the home-range sizes could depend on body mass in terrestrial insectivorous birds, Willson (2004) did not find

support for this hypothesis and in a literature review we did not find any direct relation ($r^2 = 0.03$, $n = 27$) between home-range sizes and body mass for twenty five terrestrial insectivorous birds (Appendix 3). Thus, our data indicated that *M. exsul* have smaller home-range sizes than similar species (between 20 and 30 grams) living in Amazonian forests with exception of *Thamnophilus caerulescens* and *Pyriglena leucoptera* (Duca et al. 2006). In Central America, *Thryothorus rufalbus* in Nicaragua seems to have similar home-range sizes, from 0.33 to 1.58 ha (Martinez 2008), to *M. exsul* (from 0.83 to 1.80 ha) at BOL in Costa Rica, which share fragmented landscape and degraded pastures and it could indicate an effect of the agricultural matrix on home-range sizes of forest-specialist birds.

Movements

M. exsul's movements in the forest occur near the ground in heavy or dense cover (*personal observations*) with similar descriptions from Willis and Oniki (1972). Also, we only observed this species moving (twice in LCL and once in BOL) occasionally with three swarms of army ants and always foraging between the ground and 0.5 m up, confirming the observation by Willis and Oniki (1972) that *M. exsul* individuals are not regular or frequent ant-followers. Contrary to Willis and Oniki (1972)'s descriptions we never registered *M. exsul* in mixed bird flocks. In addition, we often netted *M. exsul* between 0 and ~1 m height when individuals flew short distances in the forest. We registered two occasions where *M. exsul* crossed secondary roads (~12 m wide) between two secondary forest fragments.

Although the agricultural matrix can be an unsuitable and hostile habitat for many species, it also might be permeable to some (Beier and Noss 1998, Arendt 2004, Procheş et al. 2005, Castellón and Sieving 2006) and affect dispersal distances after isolation in fragmented

landscapes (Van Houtan et al. 2007). Castellon and Sieving (2006) showed that movements of *Scelorchilus rubecola*, a terrestrial insectivore of temperate forests, were facilitated by shrubby vegetation and wooded corridors; in addition, that vegetation cover was the relevant factor rather than species composition. Likewise, *S. rubecola* was reluctant to cross gaps ≥ 60 m and few crossed gaps ≥ 80 m although this species demonstrated strong resistance to dispersing to open areas (Castellón and Sieving 2006). Van Houtan et al. (2007) with information from BDFFP (Manaus, Brazil) through dispersal models demonstrated how habitat fragmentation influenced bird dispersal among forest fragments before and after isolation. *Myrmornis torquata*, a terrestrial antbird, decreased dispersal after plot isolation and tended to move shorter distances. Conversely, *Myrmotherula axillaris*, a flock dropout insectivore, tended to move further after isolation than before, and Van Houtan et al. (2007) estimated dispersal beyond 5 km for some species after isolation (e.g., *M. axillaris*, *Automolus infuscatus*, *Glyphorhynchus spirurus*, and *Xiphorhynchus pardallotus*). With radio-marked individuals we demonstrated that *M. exsul* is capable of dispersing $\pm 1,058$ m by crossing shaded coffee and secondary shrubland to access other forest fragments; however, we do not have information regarding *M. exsul*'s movements before isolation in Costa Rican fragmented landscapes. Contrarily to our results, Moore et al. (2008) evaluated dispersal of understory birds on open-water gaps in Barro Colorado Island and classified *M. exsul* as a poor disperser because this species registered a mean distance flown between 34 and 48 m with a maximum distance of 90 m across open water; although we must consider the open-water matrix completely hostile to movements of this species and very different from the agricultural matrix. In relation to daily movement distance (81.25-149.50 m / day) in both landscapes, we demonstrated that *M. exsul*'s movements are reduced and this species spends a lot of time in small areas (± 1000 m²) in the forest; in addition, our results are

close to the found by Stutchbury et al. (2005) where *M. exsul* spend one hour in $\pm 1600 \text{ m}^2$ in the primary forest of Barro Colorado Island.

Finally, we concluded that *M. exsul*'s home-range size was greater in LCL than in BOL, while daily movement distance was no different between landscapes. However, in relation to home-range size this response could be attributed to vertical structure of the forest rather than to the fragmented landscape. Therefore, it would be indicating that habitat disturbances (e.g., anthropogenic use, abiotic factors [Becker et al. 1991, Brosi et al. 2008]) on the habitat vertical structure are affecting the home-range size and no fragmentation effects.

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TABLE 1. Percentage of land uses in both LCL and BOL according to Canet (2005) and Céspedes (2006) in southwestern Costa Rica.

Landscape	LCL (Canet 2005)	BOL (Céspedes 2006)
Forest	56.0	31.0
Permanent crops	23.6	3.1
Annual crops		3.9
Pastures	17.9	23.2
Pastures with woody plants		5.5
Secondary shrublands	2.1	20.5
Different uses	8.4	
Others	0.6	8.4

TABLE 2. Forest fragments in LCL and BOL in southwestern Costa Rica (2008-2009).

Fragment code	Area (ha)	Description
LCL-FF1	1.5	It is surrounded by shaded coffee toward all directions. The shade tree is Poro (<i>Erythrina poeppigiana</i>). According with the landowners this forest fragment was isolated ~20 years ago.
LCL-FF2:	0.16	It is surrounded by shaded coffee toward all directions. The shade trees are Poro (<i>Erythrina poeppigiana</i>) and Guaba (<i>Inga</i> sp.). Two trees (~30 cm dbh) were extracted during our study time.
LCL-FF3	3.0	It is surrounded by shaded coffee to north, west, and east, and by sugar cane toward southeast. The shade trees are Poro (<i>Erythrina poeppigiana</i>) and Guaba (<i>Inga</i> sp.). This forest fragment is crossed for a small stream and there is shrub vegetation to at each side of this water body.
LCL-FF4	10	It is surrounded by shaded coffee with Poro and Guaba and is crossed by a small stream.
LCL-FF5	2.5	It is surrounded by shaded coffee to southeastern, pastures to western, and shrub vegetation to southwestern.
BOL-FF1	2.0	It is surrounded by pastures to cattle. We registered cattle in Sep/08 inside and around of this fragment, but in Oct/08 the cattle were in other pasture land.
BOL-FF2	2.5	It is surrounded by pastures.
BOL-FF3	5.0	It is surrounded by pastures

TABLE 3. Home-range sizes and core areas in hectares (mean \pm SD) of *Myrmeciza exsul* in two fragmented landscapes in Costa Rica, 2008-2009. LCL: Los Cusingos Landscape, BOL: Boruca landscape, N: number of individuals, HR: 95% home range, CA: 50% core area, ^a: color-marked individuals, ^b: radio-marked individuals.

Landscape	Sites	N	HR	CA
		13 ^a	1.88 \pm 0.62	0.53 \pm 0.27
LCL	Forest sites >100 ha	2 ^b	1.61 \pm 0.07	0.93 \pm 0.16
	Forest fragments <10 ha	4 ^b	1.95 \pm 0.78	0.28 \pm 0.07
		13 ^a	1.18 \pm 0.37	0.19 \pm 0.12
BOL	Forest sites >100 ha	2 ^b	1.36 \pm 0.02	0.39 \pm 0.20
	Forest fragments <10 ha	4 ^b	1.38 \pm 0.42	0.40 \pm 0.27

TABLE 4. Home-range sizes and core areas in hectares (mean \pm SD) of *Myrmeciza exsul* by sex in forest sites >100 ha in two fragmented landscapes in Costa Rica, 2008-2009. LCL: Los Cusingos Landscape, BOL: Boruca landscape, N: number of individuals, HR: 95% home range, CA: 50% core area, ^a: color-marked individuals, ^b: radio-marked individuals.

Landscape	Sex	N	HR	CA
LCL	Males	8	1.94 \pm 0.60	0.50 \pm 0.29
		1*	1.56	0.82
	Females	5	1.79 \pm 0.71	0.58 \pm 0.27
		1*	1.66	1.04
BOL	Males	9	1.14 \pm 0.35	0.20 \pm 0.12
		1*	1.38	0.24
	Females	4	1.25 \pm 0.46	0.16 \pm 0.14
		1*	1.34	0.52

TABLE 5. Daily movement distances (m / day) (mean \pm SD) of *Myrmeciza exsul* in forest fragments >100 ha in two fragmented landscapes in Costa Rica, 2008-2009. LCL: Los Cusingos Landscape, BOL: Boruca landscape, N: number of individuals, ^a: color-marked individuals, ^b: radio-marked individuals.

Landscape	Sex	N	m / day
LCL	Males	8 ^a	171.40 \pm 77.22
		1 ^b	130.35
	Females	5 ^a	114.46 \pm 45.68
		1 ^b	106.88
	Total	13 ^a	149.50 \pm 70.75
		2 ^b	118.62 \pm 16.60
BOL	Males	9 ^a	131.12 \pm 71.88
		1 ^b	75.36
	Females	4 ^a	111.22 \pm 47.82
		1 ^b	87.14
	Total	13 ^a	125.00 \pm 64.09
		2 ^b	81.25 \pm 8.33

FIGURE 1. Los Cusingos Landscape in southwestern Costa Rica. Location of Los Cusingos Natural Reserve and forest fragments <10 ha (1, 2, 3, 4, 5).

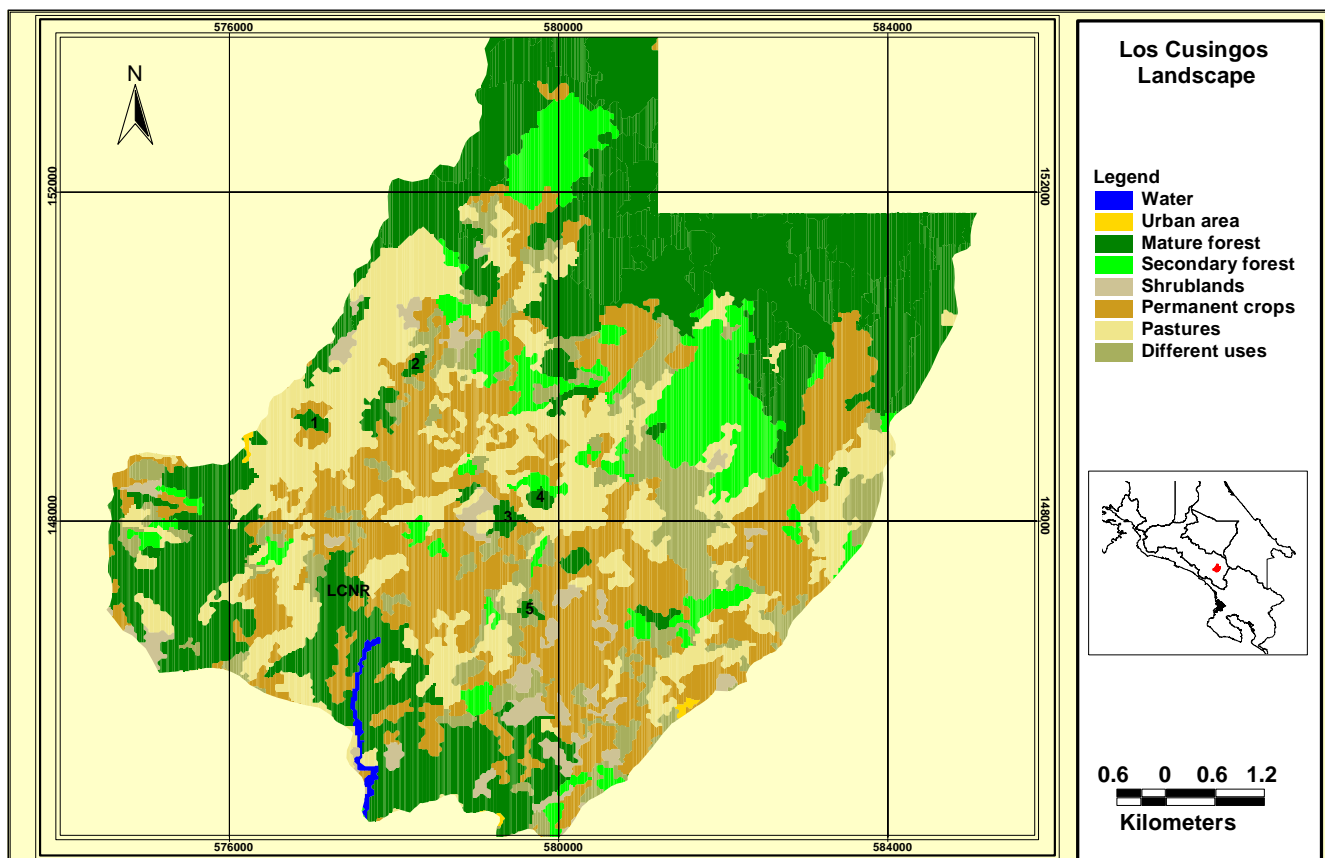


FIGURE 2. Boruca Landscape in southwestern Costa Rica. Location of Boruca forest and forest fragments (1, 2, 3, 4).

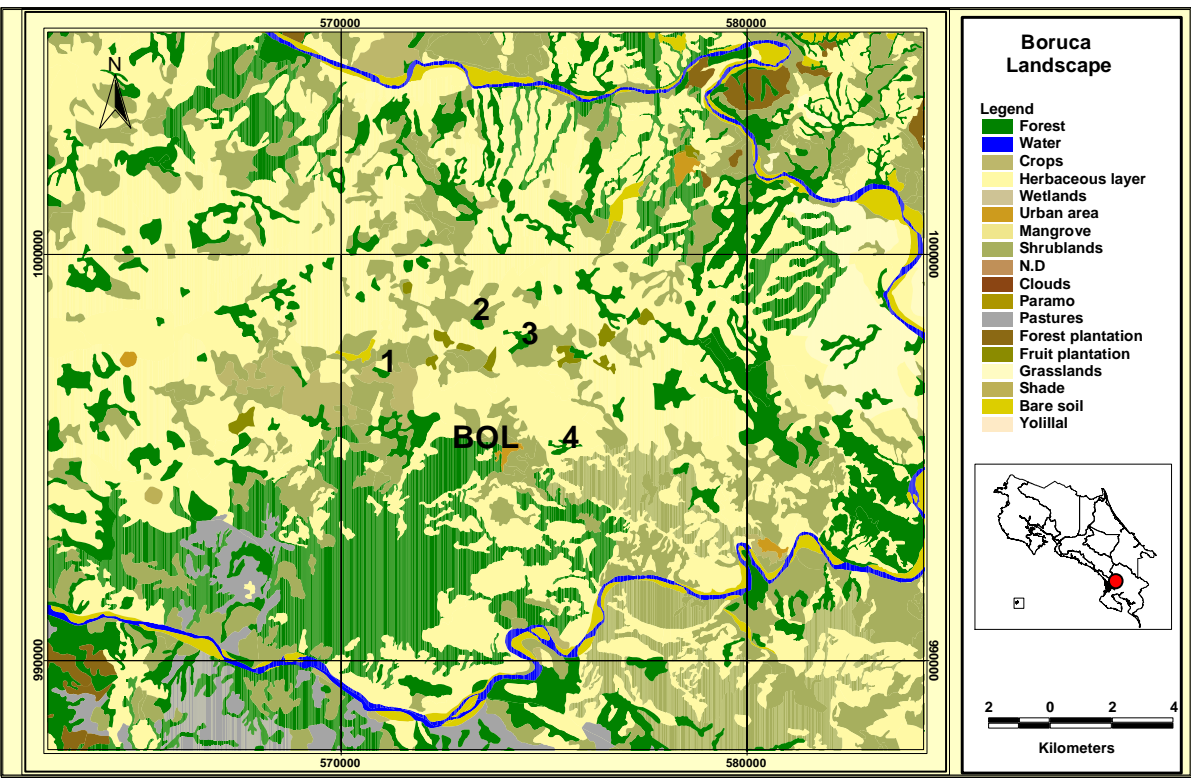


FIGURE 3. Home-range sizes (red color) and core areas (blue color) in hectares (mean \pm SD) of *Myrmeciza exsul* in two fragmented landscapes in Costa Rica, 2008-2009. LCL: Los Cusingos Landscape, BOL: Boruca landscape. ^a: color-marked individuals, ^b: radio-marked individuals.

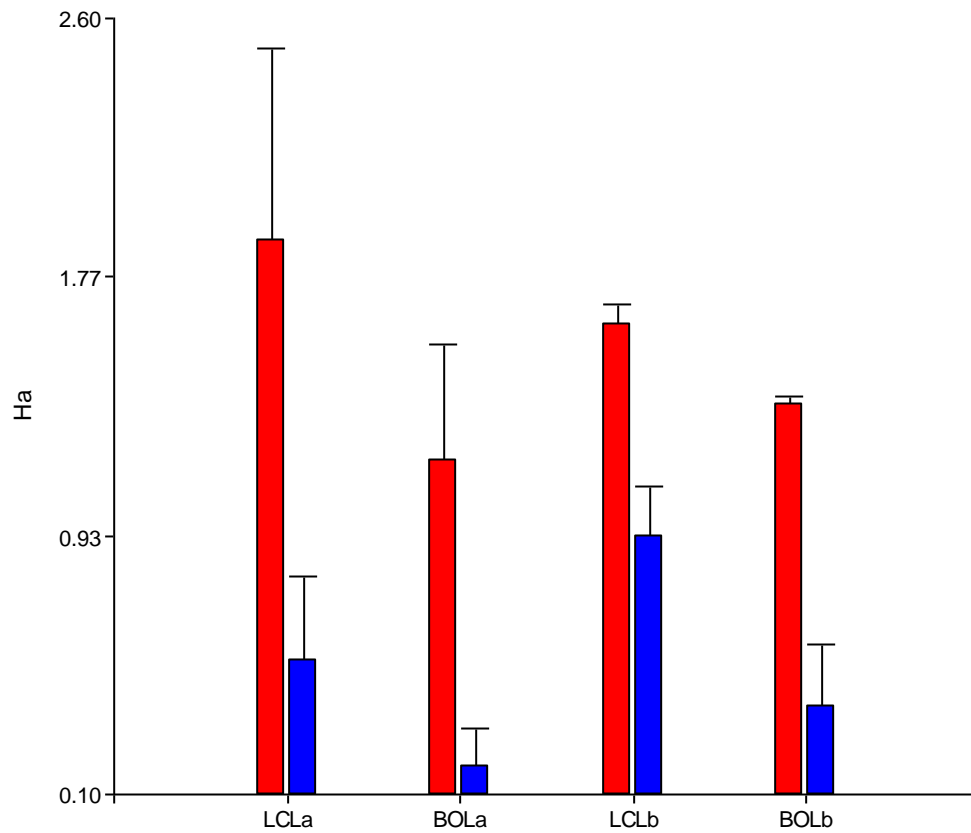


FIGURE 4. Home-range sizes (red) and core areas (blue) in hectares (mean \pm SD) of *Myrmeciza exsul* in Forest sites >100 ha and Forest fragments <10 ha in two fragmented landscapes in Costa Rica, 2008-2009. LCL: Los Cusingos Landscape, BOL: Boruca landscape.

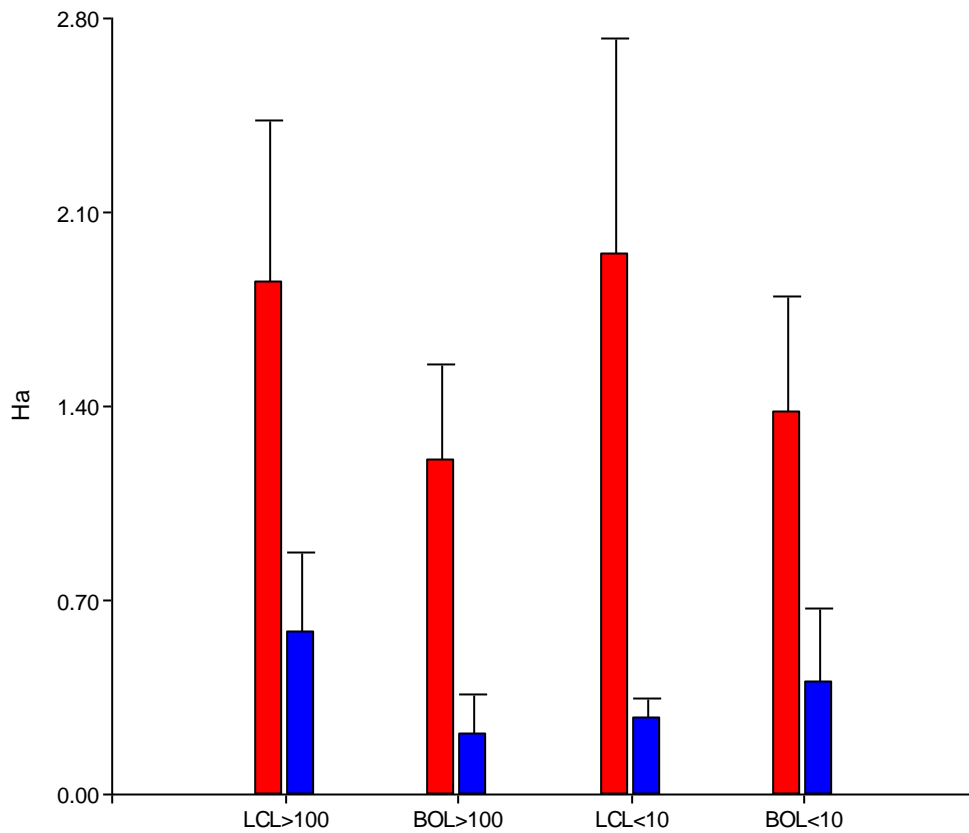
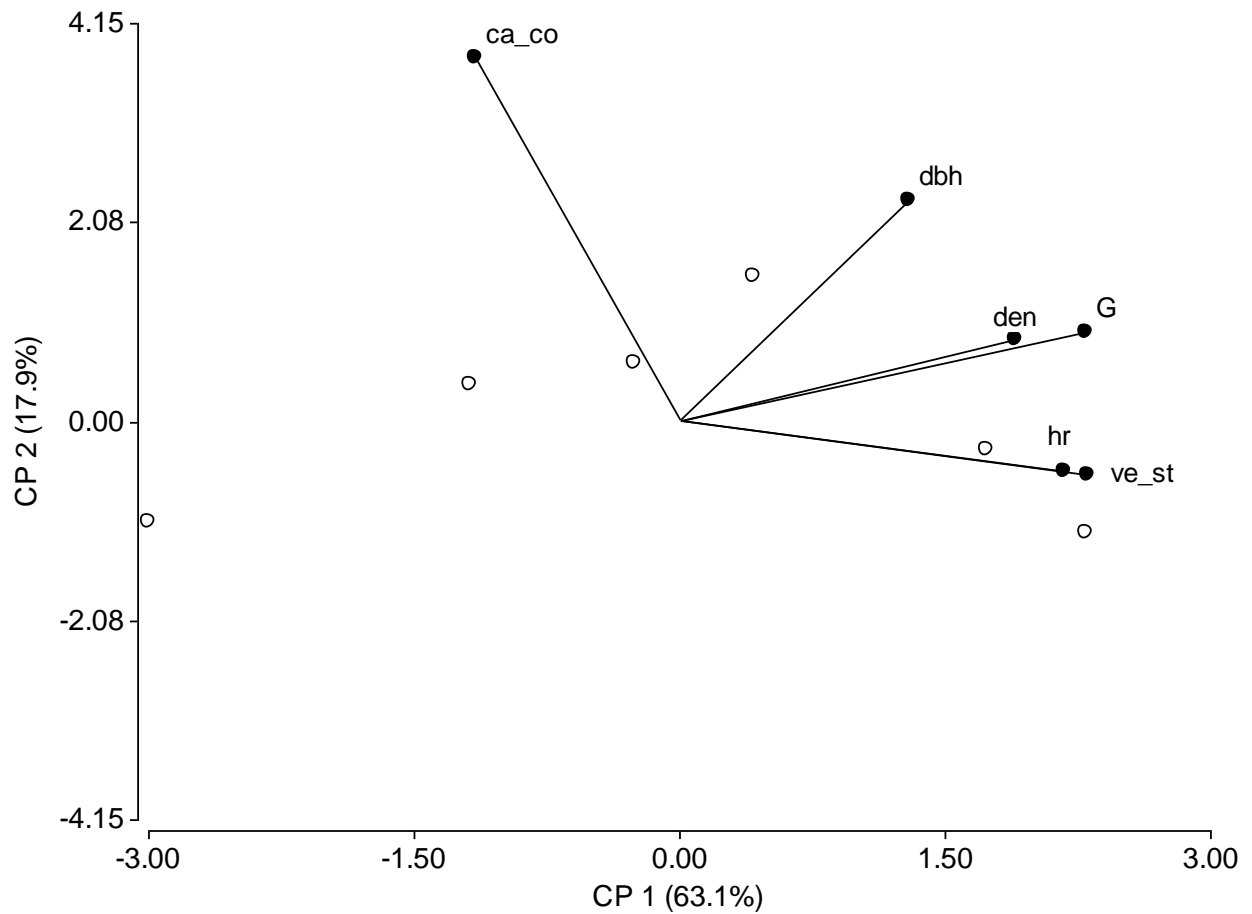


FIGURE 5. Principal Component Analysis of *M. exsul*'s home-range size and vegetation variables in two fragmented landscapes in southwestern Costa Rica. Ca_co = canopy cover, dbh = diameter at breast height, den = tree density, G = basal area, hr = home-range, ve_st = vertical structure.



APPENDIX 1. Home-range sizes and core areas in hectares of *Myrmeciza exsul* in two fragmented landscapes in Costa Rica, 2008-2009. LCL: Los Cusingos Landscape, BOL: Boruca landscape, Ind: individual, HR: 95% home range, CA: 50% core area, N°. Loc: number of locations, M: Male, F: Female, ^a: color-marked individuals, ^b: radio-marked individuals.

Landscape	Site	Ind	HR	CA	N°. Loc
LCL	Queb Cusingos	01M ^a	2.62	0.57	180
LCL	Queb Cusingos	01F ^a	2.65	0.92	175
LCL	Site B Cusingos	02M ^a	1.84	0.39	192
LCL	Site B Cusingos	02F ^a	1.64	0.78	187
LCL	Site B Cusingos	03M ^a	2.38	0.43	210
LCL	Site B Cusingos	03F ^a	2.40	0.35	198
LCL	Escondida	05M ^a	2.01	0.51	195
LCL	Escondida	05F ^a	1.25	0.32	187
LCL	Escondida	06M ^a	1.29	0.14	189
LCL	Chober	10M ^a	1.25	0.23	185
LCL	Chober	10F ^a	1.02	0.52	185
LCL	Chober	11M ^a	1.39	0.64	136
LCL	Chober	18M ^a	2.76	1.08	195
LCL	Escondida	19M ^b	1.56	0.82	235
LCL	Escondida	19F ^b	1.66	1.05	246
BOL	Kantan	01M ^a	1.52	0.39	138
BOL	Kantan	01F ^a	1.79	0.35	140
BOL	Kantan	02M ^a	1.00	0.18	176
BOL	Kantan	03M ^a	1.29	0.29	65
BOL	Kantan	04M ^a	0.77	0.10	65
BOL	Kantan	05M ^a	0.91	0.12	176
BOL	Kantan	06M ^a	0.87	0.07	216

BOL	San Joaquin	11M ^a	0.88	0.06	232
BOL	San Joaquin	11F ^a	0.83	0.05	158
BOL	Changuina	12M ^a	1.25	0.34	82
BOL	Changuina	12F ^a	0.90	0.06	210
BOL	Changuina	16M ^a	1.80	0.26	105
BOL	Changuina	16F ^a	1.50	0.19	100
BOL	Kantan	17M ^b	1.38	0.24	233
BOL	Kantan	17F ^b	1.34	0.53	245

APPENDIX 2. Home-range sizes and core areas in hectares of *Myrmeciza exsul* in forest fragments <10 ha in two fragmented landscapes in Costa Rica, 2008-2009. LCL: Los Cusingos Landscape, BOL: Boruca landscape, Ind: individual, HR: 95% home range, CA: 50% core area, M: Male, F: Female, ^b: radio-marked individuals.

Landscape	Fragment Code	Fragment size (ha)	Ind	HR	CA
LCL	LCL-FF2, LCL-FF2a	0.16, 10.00	14M ^b	1.42	0.27
LCL	LCL-FF2, LCL-FF2a	0.16, 10.00	14F ^b	1.30	0.25
LCL	LCL-FF3	3.0	12M ^b	2.99	0.37
LCL	LCL-FF4	10.0	13M ^b	2.07	0.21
BOL	BOL-FF1	2.0	09M ^b	1.07	0.21
BOL	BOL-FF1	2.0	09F ^b	0.98	0.37
BOL	BOL-FF2	2.5	08M ^b	1.76	0.23
BOL	BOL-FF3	5.0	15M ^b	1.72	0.79

APPENDIX 3. Home-range sizes (ha) and body mass (g) of some terrestrial insectivores in Neotropical forests. HR: home range; MA: Manaus, Brazil; AP: Amazonian Peru; MG: Minas Gerais, Brazil; VE: Venezuela; MA: Matiguas, Nicaragua; LA: La Selva Biological Station, Costa Rica; BCI: Barro Colorado Island, Panama; LCL: Los Cusingos Landscape, Costa Rica; BOL: Boruca Landscape, Costa Rica.

Species	Site	Weight (g)	HR 95%	Source
<i>Sclerurus mexicanus</i>	MA	25.0	25.50	Stouffer (2007)
<i>S. rufigularis</i>	MA	21.2	17.10	Stouffer (2007)
<i>S. caudacutus</i>	MA	38.9	21.30	Stouffer (2007)
<i>Myrmeciza ferruginea</i>	MA	24.7	6.62	Stouffer (2007)
<i>Myrmornis torquata</i>	MA	44.6	16.02	Stouffer (2007)
<i>Formicarius analis</i>	MA	62.2	12.02	Stouffer (2007)
<i>F. colma</i>	MA	46.0	6.58	Stouffer (2007)
<i>Grallaria varia</i>	MA	122.0	8.00	Stouffer (2007)
<i>Hylopezus macularius</i>	MA	42.3	11.70	Stouffer (2007)
<i>Myrmothera campanisoma</i>	MA	47.7	9.00	Stouffer (2007)
<i>Conopophaga aurita</i>	MA	23.7	6.28	Stouffer (2007)
<i>Corythopsis torquatus</i>	MA	14.9	6.00	Stouffer (2007)
<i>Cyphorhinus arada</i>	MA	20.2	22.70	Stouffer (2007)
<i>Phlegopsis nigromaculata</i>	AP	46.0	49.50	Willson (2004)
<i>Myrmeciza fortis</i>	AP	46.5	15.40	Willson (2004)
<i>Dendrocincla merula</i>	AP	47.5	64.60	Willson (2004)
<i>Rhegmatorhina melanosticta</i>	AP	31.4	50.80	Willson (2004)
<i>Gymnopithys salvini</i>	AP	25.9	27.50	Willson (2004)
<i>Thamnophilus caerulescens</i>	MG	20.6	1.00	Duca et al. (2006)
<i>Dysithamnus mentalis</i>	MG	12.2	0.70	Duca et al. (2006)

<i>Pyriglena leucoptera</i>	MG	26.5	1.30	Duca et al. (2006)
<i>Myrmeciza disjuncta</i>	VE	15.0	1.77	Zimmer (1999)
<i>Thryothorus rufalbus</i>	MA	25.0	1.56	Martinez et al. (2008)
<i>Phaenostictus mcleannani</i>	LS	55.0	53.00	Chavez-Campos (2008)
<i>Hylophilax naevioides</i>	BCI	18.0	4.70	Willis (1972)
<i>Myrmeciza exsul</i>	BCI	27.4	2.50	Willis and Oniki (1972)
<i>M. exsul</i>	LCL	29.5	1.85	This study
<i>M. exsul</i>	BOL	29.5	1.20	This study

CHAPTER 4

Effects of the agricultural matrix on presence and movements of *Myrmeciza exsul*, a forest specialist bird, in two fragmented Costa Rican landscape

Sergio Losada-Prado¹ & Bryan Finegan¹

¹Department of Natural Resources and Environment, CATIE

ABSTRACT

Tropical forest fragments have long been considered as islands in fragmented landscapes and several studies find agricultural fields and cattle pastures a near absolute barrier to the movement of tropical forest birds. We tested the effects of several habitat types such as shaded coffee, sun-grown coffee, secondary growth vegetation, and cattle pastures on movements of Chestnut-backed Antbird (*Myrmeciza exsul*), a terrestrial forest insectivore. Using different methods (color-banded, radio-marked individuals, and song playbacks) and experiments, we showed *M. exsul*'s movements in shaded coffee crops and cattle pastures. Additionally, our observations support the idea that <1 ha forest fragments could be “stepping-stones” because they facilitate movements across the agricultural landscape, and we support the notion *M. exsul* may be a better disperser than other terrestrial insectivorous birds. Finally, we concluded that LCL is less restrictive to *M. exsul*'s movements than BOL and that shaded coffee plantations and secondary-growth vegetation contribute significantly to the dispersal of individuals.

Key words: Chestnut-backed Antbird, movements, terrestrial insectivorous, agricultural landscape, shaded coffee crop.

INTRODUCTION

Studies on animal movement patterns in relation to landscape composition are being considered owing to their impact on ecological processes (e.g., dispersal, pollination, and predation) that affect species in fragmented landscapes (Wiens 1995, Kattan 2002, Castellon and Sieving 2006, Harvey and Saenz 2008). In fragmented landscapes the matrix directly influences bird assemblages and movements. Occasionally, this matrix is defined as unsuitable and hostile habitat; however this same habitat may not necessarily be a complete barrier to dispersal (Renjifo

2001, Castellón and Sieving 2006, Sigel et al. 2006). Each animal species responds differently both to the matrix and secondary habitats, although little quantitative evidence regarding dispersal ability is available (Terborgh and Weske 1969, Castellón and Sieving 2006, Taylor et al. 2006, Moore et al. 2008, Young et al. 2008). Following Stouffer and Bierregaard (1995), important questions for conservation are how far birds will move through different cover types in the matrix, including second growth, and whether their use of agricultural habitats, second growth and fragments implies that they can maintain populations in those areas without colonization from larger adjacent areas of forest. This means that evaluating and understanding movements of birds with supposedly limited dispersal abilities in agricultural landscapes are essential to the design of conservation strategies at the landscape scale.

In addition, observations of successful movements by naturally dispersing animals in fragmented landscapes can demonstrate the conservation value of both corridors and agricultural matrices if actual travel routes can be identified (Beier and Noss 1998, Bennet 2004). Thus, the functional connectivity of landscape matrices must be considered and included in conservation planning in order to understand how habitat structure in the matrix influences permeability to animal movements (Vandermeer and Carvajal 2001, Hannon and Schmiegelow 2002, Castellón and Sieving 2006, Van Houtan et al. 2007, Lindenmayer et al. 2008, Moore et al. 2008, Young et al. 2008).

Forest-specialist birds, including terrestrial insectivores, perceive isolated fragments, <1-10 ha without surrounding secondary growth, as true islands with some trapped individuals, rare colonization events, and no more than one or two pairs in these fragments (Willis 1979, Terborgh et al. 1990, Bierregaard and Stouffer 1997, Moore et al. 2008). In addition, a distance of only 70-100 m from continuous forest may be sufficient to isolate species within a fragment;

however, for poor colonizers, the forest fragments with somewhat of forest cover is an important factor for species that are unwilling to cross open areas (Terborgh and Weske 1969, Stouffer and Bierregaard 1995).

Few studies have demonstrated movements of understory insectivorous birds in fragmented landscapes. In the lowland rain forest of central Amazonia, small unpaved roads (<40 m wide) can cause a major alteration in the distribution and abundance of many understory forest-specialist birds whereas edge/gap specialists increase in abundance near these individual roads (Laurance and Vasoncelos 2004). Castellón and Sieving (2006) demonstrated how *Scelorchilus rubecola* appeared reluctant to cross gaps ≥ 60 m in a pasture matrix, but wooded corridors and shrubby vegetation functioned similarly as movement habitat for dispersing individuals of Chucao (*S. rubecola*), a terrestrial insectivorous bird of South American temperate rainforest. Martinez (2008) documented movements of *Thryothorus rufalbus* and *Chiroxiphia linearis* through shrubby vegetation in a fragmented landscape in Nicaragua. Moore et al. (2008) showed the inabilities of some forest-specialist birds to fly even short distances (<100 m) over open-water gaps. However, no studies have demonstrated bird movements in agricultural matrices dominated by shaded coffee, sun-grown coffee, or pastures.

M. exsul is a terrestrial insectivore with low mobility found in lowland forest, forest edges, and older secondary forest (Willis and Oniki 1972, Skutch 1969, Sieving and Karr 1997, Zimmer and Isler 2003). It is among the most sensitive birds to fragmentation because of its limited dispersal abilities (Willis 1974, Karr 1990, Sieving and Karr 1997). In this study we evaluated the contribution of the agricultural habitats to *M. exsul* movements among forest fragments in two agricultural landscapes in southwestern Costa Rica. Our hypothesis was that shaded coffee crops and secondary growth vegetation facilitate movements to *M. exsul* more than

pastures and sun-grown coffee. For this hypothesis we made three experiments, in the first experiment we evaluated *M. exsul*'s occurrence frequencies in <10 ha forest fragments surrounded by agricultural habitats; in the second experiment we registered the *M. exsul* movements from the forest into agricultural habitats; and in the third experiment we evaluated the *M. exsul* habitat use in coffee and pastures adjacent to forest fragments.

MATERIALS AND METHODS

Study sites

This study was carried out in two fragmented landscapes in southwest Costa Rica, the Los Cusingos Landscape (LCL), located in the Alexander Skutch Biological Corridor and the Boruca Landscape (BOL) located in the proposed AMISTOSA Biological Corridor. The study area included the least disturbed area of Los Cusingos Natural Reserve in the Alexander Skutch Biological Corridor and Boruca Indigenous Reserve at AMISTOSA Biological Corridor (Losada-Prado et al. [Chapter 3]).

Experiment 1

In this experiment we tested the hypothesis that the occurrence frequencies (number of individuals) of *M. exsul* in forest fragments surrounded by agricultural habitats were equal to zero by gathering presence/absence data and estimating the number of individuals in each forest fragment. At LCL we chose five forest fragments surrounded by agricultural habitats (shaded coffee, sun-grown coffee, and secondary-growth vegetation) and at BOL we chose four forest fragments surrounded by pastures. All forest fragments were selected by using the following

criteria: (1) degree isolation from other forest fragments or continuous forest on all sides (minimum distance of 100 m), (2) fragments completely surrounded by agricultural habitat, (3) fragments with a closed canopy, and (4) the fragments cover a range of size classes (Table 1). The difference in fragment numbers and their characteristics were because each landscape has different agricultural matrices which made it difficult to choose forest fragments with the same conditions.

Forest fragments at LCL were sampled from May 2008 to April 2009 and forest fragments at BOL were sampled from September 2008 to April 2009. Each forest fragment was monitored each month for 30 minutes to register the number of individuals in the fragment. Mist-nets were installed to band *M. exsul* individuals with color-leg bands for facilitating identification of individuals. We carefully searched for new individuals in each forest fragment by using binoculars and song playbacks. When a new individual without color-leg bands was registered we installed mist-nets to capture and mark that new individual. With this method we ensured that all individuals entering and leaving the forest fragments we accounted for. Individuals without color bands were not included in the analysis.

Experiment 2

In this second experiment we tested the hypothesis that the number of times *M. exsul* moved from the forest into agricultural habitats was equal to zero. The habitat types used were shaded coffee, sun-grown coffee, pastures, and secondary-growth vegetation. We used song playbacks where test animals held territories (Falls 1981, McGregor 1992, Sieving et al. 1996, Antongiovanni and Metzger 2005) near edges of forest fragments to simulate a potential territory invasion and to obtain a defensive behavior by target birds (Falls 1981, Sieving et al. 1996).

Playback experiments were conducted in the morning (06:00-10:00 h) at each habitat type using an Accurian Universal MP3 Folding Speaker and a Sony ICD-B500 Handheld Digital Voice Recorder to project aggressive call notes. The playback system was set ~20 m from the forest edge in a specific vegetation type. When an individual left the forest, it was considered a successful movement outside of the forest. No individual was evaluated for more than two consecutive mornings to avoid a learned behavior by the target individuals to help assure an aggressive response from target individuals. We repeated the sampling in different places with the habitat types to avoid pseudoreplication, so it provided independent replicates (McGregor 1992). The target individuals were located from each other to distance > 100 m in different territories. Thus, we worked with 36 *M. exsul* individuals in 36 different places (9 in each agricultural habitat: shaded coffee, sun-grown coffee, secondary- growth vegetation, and pastures). Songs were played varying amounts of time (5-10 minutes) depending upon the behavior of subjects. We registered the number of times that an individual left the forest to enter the adjacent vegetation type. Also, we registered aggressive responses when the number of songs per minute from each individual was >10 songs.

Experiment 3

We tested the hypothesis that *M. exsul* does not utilize coffee and pasture habitats adjacent to forest fragments. We selected three forest fragments surrounded by coffee in LCL and three forest fragments surrounded by pastures in BOL. Each forest fragment was occupied by radio-marked *M. exsul* individuals that were followed for three weeks (Bibby et al. 1992, Buckland 2006, Stouffer 2007) to estimate their occurrence frequency within coffee and pastures

(Table 1). Both radio telemetry and mapping methods of radio-marked individuals followed Losada-Prado et al. [Chapter 1].

Vegetation variables in agricultural habitats

We gathered data on the horizontal structure of agricultural habitats surrounding each forest fragment through temporary sampling-plots following Finegan et al. (2004). For this, we established four 20 × 20 m sampling plots around each forest fragment. The variables that quantified the woody vegetation structure were number of shade trees, canopy cover (%), basal area (m² / plot), diameter at breast height ≥10 cm (dbh), number of coffee plants, weed cover (%), and average height of coffee plants (cm) when present.

Two shade species were registered in coffee crops (Poro: *Erythrina poeppigiana* and Guaba: *Inga* sp.) with more Poro than Guaba individuals. A maximum of 15 shade trees was observed in the plots with a shade cover percentage up to 24% (Table 2). We registered an average of 205 coffee plants / plot with an average height of 184 cm / plant. The weed cover was between 25.19 and 88.38 % / plot. We did not evaluate pastures because this habitat did not have trees.

Statistical analyses

Experiment 1 and 3 were analyzed through chi-square to determine differences in the occurrence frequencies of *M. exsul* in the forest fragments. Also, these experiments were analyzed with Cochran Mantel-Haenszel test which included forest-fragment size as a factor that could affect both the movements and occurrence frequencies of *M. exsul* in forest fragments. This is because possibly in small forest fragments *M. exsul* could use agricultural habitat for

foraging in comparison with large forest fragments. Experiment 2 was not analyzed with statistical tests because *M. exsul* movements from the forest into matrix habitats were dependent of secondary growth vegetation. We used InfoStat version 2009 for the analyses (Di Rienzo et al. 2009).

RESULTS

Experiment 1

We registered a significant association between occurrence frequency of *M. exsul* and forest fragments surrounded by agricultural matrices, the mean occurrence frequencies in forest fragments were greater than zero both at LCL ($X^2 = 33.02$, $p < 0.0001$) and BOL ($X^2 = 11.18$, $p = 0.0108$). In addition, the occurrence frequencies in fragments were not significantly different between landscapes ($X^2 = 0.21$, $p = 0.6473$). Additionally, the Cochran-Mantel-Haenszel test suggested non-significant relationship between forest-fragment size ($p > 0.9999$) and *M. exsul* occurrence frequencies in both landscapes.

A qualitative analysis of *M. exsul*'s movements was registered for each forest fragment (Appendix 1). Thus, LCL-FF2, LCL-FF3, LCL-FF4, and LCL-FF5 were more dynamic than LCL-FF1 regarding movements of individuals from the agricultural matrix into forest fragments and from forest fragments into agricultural matrix. We registered 18 individuals moving into fragments from the matrix and 17 individuals moving out of fragments into the matrix. In addition, a new individual was hatched in LCL-FF4 between May and June 2008 and left the fragment between July and August 2008. Of the individuals moving into fragments from the matrix only five had juvenile plumage and incomplete skull ossification. Likewise, these

individuals plus LCL-FF4's juvenile left the forest fragments and were not registered again in any fragment.

With this method and sampling design we were unable to recapture individuals moving between forest fragments. However, we did recapture individuals (e.g., netted or seen) in the same fragments where these were originally banded, permitting us to confirm the presence of stable territories in the fragments. Thus, we registered males and females, for instance, a pair in LCL-FF1 were settled from May/08 to Mar/09; a pair in LCL-FF3 were established from Jun/08 to Apr/09, a pair in LCL-FF4 were established from May/08 to Apr/09 and a pair from Nov/08 to Apr/09, a pair in LCL-FF5 were established from May/08 to Apr/09. Thus, adult pairs settle territories in forest fragments for several months.

At BOL where forest fragments are surrounded by pastures, movement dynamics were fewer in number than at LCL (Appendix 1), although we only have registers from Sep/08 to Apr/09. However, numbers of *M. exsul* individuals both entering and leaving the forest fragments were not associated with the landscape ($X^2 = 2.00$, $p = 0.1573$). Movements into fragments from the matrix were registered for a pair at BOL-FF1, a pair at BOL-FF2, and a pair at BOL-FF3. A juvenile was registered in LCL-FF1 in Dec/08, but we did not register this one in Jan/09. Thus, this one was the unique register of movements out of fragment into the matrix, although it may have died in the site or evaded detection. In addition, we registered six individuals moving into fragments from the matrix.

Experiment 2

In all cases the target birds answered to the playback and we registered a song average of 11.5 ± 1.79 songs / minute ($n = 90$ observations). Thus, we interpreted this behavior as response

to the potential invasion. However, no individual entered shaded coffee (0 of 18), sun-grown coffee (0 of 18), or pastures (0 of 18); for these habitats target birds stopped at the forest edge after investigating the source of the invasion. On the other hand, all individuals entered secondary-growth vegetation \pm 5-7 m height (18 of 18). In the forest the individuals responded strongly to playbacks during preliminary trials; the male displayed aggressive behavior to the speaker while the female made slow approaches to the speaker. Both in the forest and secondary-growth vegetation the individuals (males and females) approached the speakers to within \sim 1 m, so that distances moved into second-growth vegetation were \sim 20 m.

Experiment 3

We registered 973 locations in the forest fragments for four radio-marked individuals (Appendix 2) and none in coffee in LCL. There was a significant association between *M. exsul* locations and forest habitat ($X^2 = 12.00$, $p = 0.0213$). According to Cochran-Mantel-Haenszel's test there was no effect of fragment size ($p > 0.9994$) on occurrence frequency of *M. exsul* in LCL's forest fragments. Two individuals moved from LCL-FF2 to LCL-FF6, this pair spent five days in LCL-FF2 and they abandoned this forest fragment to move to LCL-FF6 located to \pm 1058 m. LCL-FF6 is a secondary forest fragment with pastures both to the north and to the south, riparian forest to the west, and primary forest toward the northeastern. There are shaded coffee, secondary-growth vegetation, and riparian forest between LCL-FF2 and LCL-FF6. The distance between these fragments is \sim 1000 m. However, we were unable to detect these birds in coffee. When we came back to LCL-FF2 on the sixth day, this pair was not there and we radiotracked them around this forest fragment, finding them located at LCL-FF6 at noon. We never monitored

LCL-FF6 because it is not surrounded by coffee crops and the movement of this pair was unexpected for us.

We registered 966 locations in the forest fragments with the four radio-marked individuals in BOL (Appendix 2). We only registered two locations (0.21 %) outside forest fragments, both in secondary-growth vegetation (a small strip ~2m wide connected to forest fragment) for one individual at ~30-40 m from the edge forest fragment. No locations were made in pasture and there was significant association between *M. exsul* locations and forest habitat ($X^2 = 12$, $p = 0.0213$). According to Cochran-Mantel-Haenszel's test there was no effect of fragment size ($p > 0.9994$) on occurrence frequency of *M. exsul* in BOL's forest fragments.

DISCUSSION

A significant occurrence frequency of *M. exsul* in forest fragments (<10 ha) surrounded by agricultural matrix was somewhat surprising because we did not expect *M. exsul* might move through this matrix types. Although, individuals moving out of fragments into the agricultural matrix are indirect evidence, we cannot confirm these movements because the absence of individuals in forest fragments could be due to predation, natural mortality or dispersal. In addition, we did not register color-marked individuals moving through coffee between different forest fragments. Likewise, in Amazonia, Stouffer and Borges (2001) did not register movements of banded individuals between fragments surrounded either by *Cecropia* or by *Vismia*. In reference to terrestrial insectivores Stouffer and Bierregaard (1995) showed movements through tall *Cecropia*-dominated second growth (~six year old) and they did not find an effect of fragment size on recolonization of these, being this variable a poor predictor when some birds had recolonized. We observed a similar behavior where fragment sizes were not

significant regarding occurrences of *M. exsul* in fragments. Van Houtan et al. (2007) estimated that a small fraction of understory insectivores near Manaus, Brazil, disperse beyond five kilometers (e.g., *Myrmotherula axillaris*, *Percnostola rufifrons*, *Hylophylax poecilinota*, *Pithys albifrons*, *Gymnopithys rufigula*, and *Myrmornis torquata*). Antongiovanni and Metzger (2005) found significant differences in the frequencies of occurrences of seven understory birds between primary forest and two types of secondary growth forest depending of matrix type. In our study, we considered that *M. exsul*'s movements across shaded coffee are not accidental and this crop is permeable to this species. Therefore, we could confirm the results of long-distance movements of birds (Grinnell 1922, Van Houtan et al. 2007) because *M. exsul* moved between fragments separated 1058 m each other.

Regarding forest fragment dynamics, Stouffer and Borges (2001) demonstrated that ant-following birds were nearly absent in small fragments (1-10 ha), but were more common in second growth. We found *M. exsul* in all of the fragments studied and our observations demonstrated regular movement of individuals into fragments from the agricultural matrix for forest fragments surrounded by shaded coffee at LCL. In contrast, forest fragments surrounded by pastures at BOL only registered immigrations; although the frequency of occurrence between landscapes did not differ and the matrix type did not affect the frequencies. In addition, *M. exsul*'s movement through secondary growth vegetation (~5 m height) in response to playback suggested that this habitat type can be considered permeable to its movements. In addition, Losada-Prado et al. [Chapter 1] registered some locations (0.74%) of *M. exsul* in secondary growth in territories both at LCL and BOL. With other species Sieving et al. (1996) demonstrated that scattered cover was a “soft” barrier for movements of Chucao (*Scelorchilus rubecola*), a terrestrial insectivore, and open pastures were a “hard” barrier to these individuals.

Similarly, Castellon and Sieving (2006) identified shrubby vegetation as corridor habitat for dispersing Chucaos.

Willis (1979) and Karr (1982) suggested that for understory insectivores, isolated fragments without surrounding secondary growth are analogous to true islands, with some individuals trapped by this isolation, and new individuals only rarely colonizing. Our study strongly suggests that for *M. exsul* fragments surrounded by shade coffee and secondary-growth vegetation may in fact be connected, but that the identity of the surrounding landuse is critical. Regarding other species, we did not register understory insectivores (e.g., *Gymnopithys leucaspis*, *Gymnocichla nudiceps*, and *Formicarius analis*) in the forest fragments with the exception of *F. analis* at LCL-FF3 and LCL-FF4 which occurred in 0.33 and 0.41 of our surveys (unpublished data).

According to Stouffer and Bierregaard (1995) canopy cover is the most important feature in secondary growth which facilitates movements across this habitat type; thus, the 14-23% cover found in shade coffee may contribute to these movements. In addition, another important factor could be the height of coffee plants, which is between 178 and 199 cm; this value is above the normal height of *M. exsul*'s vertical movements in the forest where this species moves under ~150 cm (Losada-Prado et al. [Chapter 1]). Although coffee plant height was not evaluated as a hypothesis test for movements, this variable could be an important factor regarding *M. exsul*'s movements among forest fragments surrounded by coffee crops, which should be evaluated for different terrestrial insectivorous birds.

The presence of *M. exsul* pairs in forest fragments over periods of several months could indicate a suitable habitat in these places. However, a detailed study would be necessary to estimate prey availability in fragments and continuous forest, even though insect abundance and

diversity in secondary areas may be a little bit reduced (Janzen 1973). In addition, the brief presence of *M. exsul* individuals for some days in the 0.16 ha fragment in LCL suggest that *M. exsul* needs forest fragments of at least 1 ha for developing normal activities according to Losada-Prado et al. [Chapter 1]'s home-range data. It may be that <1 ha forest fragments could serve as “stepping-stones” in fragmented landscapes, but are not suitable long-term habitat. Such movements have been suggested in other studies where small patches are used for transitory movements in the landscape and species preferentially disperse from smaller to larger fragments likely selecting the latter (Prevett 1991, Strong and Bancroft 1994, Russell et al. 1994, Van Houtan et al. 2007).

Finally, our results indicate how shaded coffee and second-growth vegetation contribute to the movements of *M. exsul* in agricultural landscapes. In addition, *M. exsul* could be increasing dispersal distances after isolation in the same way as *M. axillaris* who frequent primary forest, secondary forest, edges and some gaps (Cohn-Haft et al. 1997, Van Houtan et al. 2007). Likewise, *M. exsul*'s responses in this study may be useful to many species with limited dispersal especially terrestrial insectivores (Castellon and Sieving 2006) regarding conservation planning in agricultural landscapes. Therefore, conservation actions could prioritize to maximize the number of ≥ 1 ha forest fragments in the farms.

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TABLE 1. Forest fragment descriptions at LCL and BOL in southwestern Costa Rica (2008-2009). Source: Losada-Prado et al. [Chapter 1].

Fragment code	Area (ha)	Description
LCL-FF1	1.5	It is surrounded by shaded coffee toward all directions. The shade tree is Poro (<i>Erythrina poeppigiana</i>). According with the landowners this forest fragment was isolated ~20 years ago.
LCL-FF2:	0.16	It is surrounded by shaded coffee toward all directions. The shade trees are Poro (<i>Erythrina poeppigiana</i>) and Guaba (<i>Inga</i> sp.). Two trees (~30 cm dbh) were extracted during our study time.
LCL-FF3	3.0	It is surrounded by shaded coffee to north, west, and east, and by sugar cane toward southeast. The shade trees are Poro (<i>Erythrina poeppigiana</i>) and Guaba (<i>Inga</i> sp.). This forest fragment is crossed for a small stream and there is shrub vegetation to at each side of this water body.
LCL-FF4	10	It is surrounded by shaded coffee with Poro and Guaba and is crossed by a small stream.
LCL-FF5	2.5	It is surrounded by shaded coffee to southeastern, pastures to western, and shrub vegetation to southwestern.
BOL-FF1	2.0	It is surrounded by pastures to cattle. We registered cattle in Sep/08 inside and around of this fragment, but in Oct/08 the cattle were in other pasture land.
BOL-FF2	2.5	It is surrounded by pastures.
BOL-FF3	5.0	It is surrounded by pastures
BOL-FF4	10	It is surrounded by pastures.

TABLE 2. Structural variables in vegetation plots in coffee crops at LCL. Four vegetation plots (20 x 20 m) were located around each forest fragment. Data are reported as mean \pm SD. SGC: Sun grown coffee, SV: second-growth vegetation, *: trees with dbh \geq 10 cm.

Site ID	Shade trees (#)	Shade species Richness	Basal area (m ²)	Shade cover (%)	Coffee plants (#)	Mean coffee height (cm)	Weed cover (%)
LCL-	15.00 \pm	1.75 \pm 0.50	0.38 \pm	23.25 \pm	198.25 \pm	179.43 \pm	40.19 \pm
FF1	1.41		0.07	9.21	8.50	20.97	31.18
LCL-	11.25 \pm	1.0 \pm 0.0	0.56 \pm	14.69 \pm	221.50 \pm	198.80 \pm	25.19 \pm
FF2	0.96		0.11	3.16	6.03	27.57	8.60
LCL-	6.50 \pm 1.0	2.0 \pm 0.0	0.16 \pm	21.45 \pm	198.25 \pm	177.85 \pm	88.38 \pm
FF3			0.04	5.84	2.36	17.17	6.02
SGC-1					209.44 \pm	190.78 \pm	
					4.85	5.29	
SV-1	14.25 \pm	8.13 \pm	0.76 \pm	80.09 \pm			
	2.55*	2.75*	0.29	2.29			

APPENDIX 2. Number of sightings (locations) of *M. exsul*'s radio-marked individuals at LCL and at BOL both inside and outside of the forest fragments.

Forest Fragment	Individual ID	Sightings in Forest Fragments	Sightings outside Forest Fragments
LCL-FF2	14M	243	0
LCL-FF2	14F	244	0
LCL-FF3	12M	249	0
LCL-FF4	13M	237	0
BOL-FF1	09M	235	0
BOL-FF1	09F	246	0
BOL-FF2	08M	246	2
BOL-FF3	15M	239	0

CHAPTER 5

Density and apparent survival of *Myrmeciza exsul* in landscapes with agricultural matrices

Sergio Losada-Prado¹ & Bryan Finegan¹

¹Departement of Natural Resources and Environment, CATIE

ABSTRACT

Habitat fragmentation has negative effects on the demographic parameters (e.g., density and apparent survival rate) and body condition index of wildlife populations. These variables can be influenced by either habitat degradation or functional connectivity in the landscape. We evaluated density and apparent survival rate of Chestnut-backed Antbird (*Myrmeciza exsul*) in two regions in southwestern Costa Rica and compared the body condition index of *M. exsul* individuals from Los Cusingos Landscape (LCL) and Boruca Landscape (BOL) with individuals in fragmented regions in the Costa Rican lowlands in the Atlantic slope. We sampled forest fragments of varying sizes (0.16-10 ha) and continuous forest (> 100-ha) in both LCL and BOL. Density was estimated by using Distance Program and apparent survival rate through mark-recapture analyses. We did not find significant differences in density values between regions and our average density was similar to that recorded in the primary forest of Barro Colorado Island (Panama). Apparent survival rate was influenced by time and sex in Los Cusingos Landscape (LCL), whereas in Boruca Landscape (BOL) apparent survival was not affected by these variables. Body condition index indicated *M. exsul* populations from LCL and BOL were not different to other populations in fragmented landscapes in Atlantic slope in Costa Rica. We considered that the stability of *M. exsul* populations is maintained by strategies such as territoriality and parental care during the post-fledging period. These aspects of the species' biology are also potential factors influencing the evolution of small clutches in tropical birds.

Key words: Chestnut-backed Antbird, *Myrmeciza exsul*, density, apparent survival rate, body condition index, agricultural landscape.

INTRODUCTION

Population size, density, and survival are key variables in population biology for predicting population variations with regards to environmental factors (Williams et al. 2002, Bayne and Hobson 2002, Melbourne et al. 2004, Reed 2004, Ruiz-Gutiérrez et al. 2008). In tropical birds, an understanding of population dynamics requires an examination of habitat requirements and patterns of habitat use by species (Stiles 1983, Stiles 1994, Terborgh 1990). However, these patterns can be changed by habitat fragmentation (Restrepo et al. 1997, Bierregaard and Stouffer 1997) with some bird populations increasing in fragments while often remain unaffected, decline or disappear (Warburton 1997). In addition, reductions or alterations of habitats may result in consequent variations in population size (Stouffer and Bierregaard 1995, Goosem 1997, Stouffer 2007), reproductive success (Donovan et al. 1997, Lloyd et al. 2005, Tewksbury et al. 2006, Young et al. 2008), and survival of species of conservation concern (Horak and Lebreton 1998, Matthysen 1999, Ruiz-Gutiérrez 2008).

Some terrestrial birds in tropical regions that have low fecundity, low reproductive success, and are thought to be long-lived could alter their population growth and individual lifetime reproductive success by fragmentation (Ricklefs 1976, Wikelski et al. 2003, Martin 2004, Knutson et al. 2006). Currently there is a lack of evidence regarding population density, apparent survival, and habitat variables of *M. exsul* or other understory insectivorous birds in agricultural landscapes. We are aware of only three studies all of which evaluated *M. exsul*'s activities on Barro Colorado Island (BCI), Panama. In the first, Willis and Oniki (1972) evaluated *M. exsul*'s habitat requirements and estimated a density of 0.6 ind / ha. In the second, Stutchbury et al. (2005) evaluated vocalizations and movements of *M. exsul*, while in the third Moore et al. (2008) evaluated *M. exsul*'s ability to cross open waters in Panama Canal. However,

there is no information about how this species survives, forages, reproduces and disperse in agricultural landscapes.

For these reasons, it is necessary to know about *M. exsul*'s demographic parameters in agricultural matrices in order to predict responses of this species at the landscape scale in regions with a different fragmentation type to those that impacted BCI. In this study we evaluated the population density and apparent survival rate of *M. exsul* in two fragmented landscapes with different agricultural matrices (LCL with a shaded coffee matrix and BOL with a pasture matrix) and compared body condition index of *M. exsul* populations from LCL and BOL with regions of lowlands in the Costa Rican Atlantic slope.

MATERIALS AND METHODS

Study sites

This study was carried out in two fragmented landscapes in southwestern Costa Rica. The Los Cusingos Landscape was located in the Alexander Skutch Biological Corridor with three sites: Los Cusingos Natural Reserve (LCUL), La Escondida (ESCL), and Chober (CHOL). The Boruca Landscape was located in the proposed AMISTOSA Biological Corridor with three sites: Kantan Reserve (KANL), San Joaquin (SANL), and Changuina (CHAL). The study area included the least disturbed area of Los Cusingos Natural Reserve and Boruca Indigenous Reserve in the AMISTOSA Biological Corridor (Losada-Prado et al. [Chapter 1]).

Density

We estimated *M. exsul* population density establishing 16 point-counts located 150 m from each other, covering ~20 ha in forest areas (Buckland 2006, Roberts 2007); each point-count was a ~50 m radius circle. We chose three forest sites (>100 ha) separated one kilometer from each other in each landscape. With a portable external speaker we projected aggressive call notes for two minutes at each point-count and we waited ~2-3 minutes after that for detecting individual responses. Individuals seen or heard were assumed as a responding individual. Each site was visited three times from December 2008 to March 2009. A total of 48 points by site and 144 points by landscape were analyzed. We noted azimuth direction and distance of each individual and the data were analyzed with Distance Program 5.0 Release 2 following Buckland et al. (2004) and Thomas et al. (2006) to estimate population density.

Capture methods for survival analysis

We sampled birds by using mist nets (2 x 12m, four shelf, 36-mm mesh) in <10 ha forest fragments surrounded by agricultural matrix and >100 ha forest sites (Losada-Prado and Finegan [Chapter 1 and 2]). All birds were banded with color bands, and sex and age were determined on the basis of plumage and skull. Since some *M. exsul* individuals learn about the presence of the net from the first time they were netted, we used tape playback for resighting banded individuals. New individuals were easily netted in the net places. LCL was sampled each month from April 2008 to March 2009 and BOL was sampled from September 2008 to April 2009.

Physical condition of *M. exsul* individuals

We developed a single body condition index from collected data of each *M. exsul* individual. Most condition indices are based on body mass adjusted for structural body size, calculated as simple ratios or residuals from regressions because unadjusted body mass can mask variation in condition among individuals (Heusner 1982, Schamber et al. 2009). Thus, we estimated corrected body mass following Roberts (2007), using a regression of body mass against tarsus length and wing chord for each bird by gender and used as the corrected measure of body condition. We estimated differences regarding corrected body condition index among landscapes such as LCL, BOL, La Selva Biological Station, Rio Frio (a fragmented landscape close to La Selva), and Tortuguero National Park (Table 1). Data from LCL and BOL were obtained from March 2008 to April 2009. La Selva Biological Station and Tortuguero National Park are located on Atlantic coast slope with lowland primary forests. Rio Frio fragmented landscape (Atlantic coast slope) is dominated by pastures, crops, and scattered lowland forest fragments of different sizes.

Vegetation plots

We analyzed habitat variables through temporary sampling-plots at each site by landscape following Finegan et al. (2004) for estimating horizontal and vertical structure of the habitat. We established two 110 m transects with at least 50 m distance from each other. Each transect had four sampling-plots of 20 x 20 m for a total of 8 sampling-plots by site. Horizontal structure was measured through variables such as density (# / ha), basal area ($G = m^2 / ha$), diameter at breast height ≥ 10 cm (dbh), and canopy cover. Transects were located at the same

area where Losada-Prado and Finegan [Chapter 1] captured *M. exsul* individuals, thus we assured *M. exsul*'s presence in the sites.

We quantified the vertical structure of the forest according to Thiollay (1992) by estimating the average foliage cover within each of the 5 layers from understory to canopy (0-2 m, 2-9 m, 10-20 m, 20-30 m, and >30 m). For this we established imaginary plots of 10 x 10 m within 20 x 20 m-plots and by using a simplified scale of 0-3 if the percentage of foliage cover is 0, 1-33, 34-66, and 67-100% respectively. The mean of the indices in all strata was used as an index of vertical heterogeneity for each vegetation plot.

Statistical analyses

Bird density data were obtained through the Distance Program 5.0 Release 2 for wildlife population assessment (Thomas et al. 2006). Conventional distance sampling analysis refers to analysis of distance sampling data using methods where the probability of detection is modeled as a function of observed distances from the line or point by using robust semi-parametric methods (Thomas et al. 2006). Thus, the detection function is the central part of this analysis and twelve models are obtained from key functions [4] and series expansion [3], where the best model is selected by using Akaike's Information Criterion (Thomas et al. 2006).

We estimated apparent survival rate and recapture probabilities by using Cormack-Jolly-Seber (CJS) capture-mark-recapture analyses in the MARK Program for open populations to fit a set of models varying in their assumptions of apparent survival and recapture probabilities (Ruiz-Gutiérrez 2008). Tropical species are long-lived and have year-around territories and adult individuals with high survivorship shows low emigration rates (Karr et al. 1990, Sandercock et al. 2000, Jones et al. 2004, Gill and Stutchbury 2006). As survival and recapture probabilities

can vary with time for various reasons, including unequal sampling effort, we included time-dependent models (t) for these probabilities. Also, we included sex-dependent, sex*time-dependent, and constant models. Apparent survival and recapture probabilities were estimated by selecting Akaike's Information Criterion from the MARK Program (White and Burnham 1999). The parameter estimates from each model were weighted by Akaike weights of that model, which represent how well the data support a model, relative to all the other models to test. Additionally, probabilities from each model come with standard errors and confidence intervals to 95%. Our analysis included capture histories by sex for improving the estimates and estimating differences in survival between sex groups (Nichols et al. 2004), even though *M. exsul*'s males and females did not differ in their movement patterns (Losada-Prado and Finegan [Chapter 1 and 2]).

Regarding body condition index, for *M. exsul* males, body mass was best correlated with tarsus length through equation: predicted body mass = (tarsus length \times 0.07) + 27.53, (F = 0.51, $r^2 = 0.02$, $p > 0.05$, n = 30). For *M. exsul* females, body mass was best correlated with wing chord and the determined equation was: predicted body mass = (wing chord \times 0.28) + 11.15 (F = 2.04, $r^2 = 0.11$, $p > 0.05$, n = 19). Mean standardized residuals from the regression analysis for each sex were used to compare mean differences in body condition between landscapes by using a *t*-test.

Principal Component Analyses (PCA) were developed to determine the behavior of each vegetation variable within each landscape and these variables together with population density were analyzed to determine differences among landscapes through one-way ANOVA. Vegetation variables were analyzed through Student's *t* and Mann-Whitney tests between landscapes and one-way ANOVA among sites within each landscape. Non-parametric analysis

through Kruskal Wallis test was realized for some variables. An alpha of 0.05 was used in all tests and data were reported as mean \pm SD.

RESULTS

Density

There were no significant differences between landscapes ($t = -0.34$, $p = 0.7489$), with densities being 0.69 ± 0.39 ind / ha in LCL and 0.61 ± 0.12 ind/ ha in BOL (Table 2). At LCL there were significant differences among sites according to a Kruskal-Wallis test ($H = 6.49$, $p = 0.0107$) and LCUL registered the highest density with 1.14 ind / ha and ESCL and CHOL registered lower values. At BOL there were no significant differences among sites ($F = 0.90$, $p = 0.4540$).

Apparent survival

We analyzed 291 captures from 43 individuals from LCL and 124 captures from 24 individuals from BOL. At LCL the best-supported model included an effect of time (months) on apparent survival probability and sex on recapture probability (Tables 3 and 4). Model estimates for apparent survival probabilities ranged from 0.844 ± 0.064 SE to 1.000 ± 0.00 SE across months. Model estimates for recapture probabilities for males and females ranged from 0.991 ± 0.008 SE to $1.000 \pm 0.13E-08$ SE across months. At BOL the best-supported model did not include effects of either time or sex on apparent survival probabilities and recapture probabilities. Model estimates for apparent survival probability were 0.958 ± 0.018 SE across months with a recapture probability of 1.00 ± 0.00 SE across months.

Vegetation variables

LCL registered higher values than BOL for basal area, tree density, vertical structure, and mean diameter at breast height; whereas BOL registered the greater values than LCL for total canopy cover (Table 5). Likewise, there were significant differences between landscapes regarding basal area ($t = -5.81, p < 0.05$), vertical structure ($t = -8.00, p < 0.05$), tree density ($W = 387.50, p < 0.05$), canopy cover ($W = 812.50, p < 0.05$), but there was no significant difference regarding mean diameter at breast height ($W = 611, p > 0.05$).

Los Cusingos Landscape. There were significant differences among sites for tree density, canopy cover, and vertical structure, but there were no differences for basal area and dbh in Los Cusingos Landscape (Table 6). According to Principal Component Analysis the first component explained an 84% of variability, whereas the second component explained 16% of variability. The first component was related to basal area, vertical structure, canopy cover, and dbh, and second component was related with tree density. Additionally, the Chober site showed a linear relationship with canopy cover and dbh, while Los Cusingos site registered a linear relationship with the vertical structure, and the La Escondida site showed linear relationships with basal area and density (Figure 1).

Boruca Landscape. There were significant differences among sites for tree density, basal area, vertical structure, and mean dbh. Canopy cover did not register significant difference (Table 6). Principal Component Analysis explained a 54% of variability with the first component, while the second component explained a 46% of variability. The first component was related to basal area, tree density, and canopy cover; whereas the second component was related to vertical structure and dbh (Figure 2). Likewise, the Changuina site showed linear

relationships with vertical structure and dbh, Kantan site showed linear relationship with canopy cover and tree density, and in the San Joaquin site no one variable showed a linear relation.

Vegetation variables and *M. exsul* density. Through PCA, *M. exsul* density was negatively correlated with canopy cover and positively associated with the second component, while the first component was associated to basal area, vertical structure, and tree density (Figure 3). The first component explained 51.4% of variability while the second component explained 25.2% of variability.

Physical condition of *M. exsul* individuals

Both for males and females mean corrected residuals were not significantly different between landscapes (males: $t = -1.35$, $p > 0.05$, $df = 29$; females: $t = 0.54$, $p > 0.05$, $df = 17$). For males, the mean corrected residual was 0.23 ± 1.09 at LCL and -0.26 ± 0.85 at BOL, whereas for the females mean corrected residual was -0.13 ± 1.29 at LCL and 0.12 ± 0.70 at BOL.

Additionally, there was no significant difference between males and females at either LCL ($t = -1.05$, $p > 0.05$, $df = 23$) or at BOL ($t = 0.68$, $p > 0.05$, $df = 22$).

We used wing chord and weight of individuals from three important regions in the lowlands of Costa Rican Atlantic slope to compare body condition index among landscapes. The regions included two natural reserves (La Selva Biological Station and Tortuguero National Park) as well as one fragmented landscape (Rio Frio landscape). We estimated the mean corrected residuals from *observed body mass* – *predicted body mass* by using the equation: $\text{predicted body mass} = (\text{wing chord} \times 0.28) + 11.15$. With these data we found significant differences among regions ($F = 6.45$, $p < 0.01$, $df = 4$, $n = 176$), where LCL and BOL registered

higher mean corrected residuals than La Selva Biological Station, Rio Frio landscape, and Tortuguero National Park (Table 7).

DISCUSSION

Density and apparent survival

The average densities of *M. exsul* in both LCL (0.69 ind / ha) and BOL (0.61 ind / ha) were similar to values registered by Willis and Oniki (1972) on Barro Colorado Island (0.6 ind / ha). In other Neotropical regions with congeneric species, density values ranged from 0.14 to 0.36 ind / ha both in Manaus-Brasil and French Guiana respectively with *Myrmeciza ferruginea* (Stouffer 2007). For *M. fortis* a 0.1 ind / ha density was reported by Willson (2004) and 1.99 ind / ha for five obligate ant-followers in Amazonian Peru. *Hylophilax naevioides* registered 0.45 ind / ha on Barro Colorado Island by Willis (1972) and *Gymnopithys bicolor* registered 0.03 ind / ha (Willis 1974). Our values therefore fall well in the range for similar species. Additionally, density values reported by Stouffer (2007) for the terrestrial avian community were different than values found at LCL and BOL for *M. exsul* alone, for instance, 0.89 ind / ha in Manaus, 1.48 ind / ha in Panama, 1.38 ind / ha in Peru and 1.51 ind / ha in French Guiana. However, density data can vary across landscapes, for example, we reported values from 0.43 to 1.14 ind / ha among our study sites, being LCUL where we registered the highest value in the study.

Territoriality has been hypothesized as a driving proximate force in stabilization of population dynamics in tropical birds (Greenberg and Gradwohl 1986). Thus, for Neotropical birds that have stable populations, stable territorial boundaries often remain unchanged for years (Willis 1974, Munn and Terborgh 1979, Munn 1985, Greenberg and Gradwohl 1986, 1997,

Roper and Goldstein 1997, Jullien and Thiollay 1998, Robinson et al. 2000, Willson 2004, Styrsky 2005, Styrsky et al. 2005, Stutchbury and Morton 2008). For instance, *M. fortis*' population density remained stable over three years in Amazonian Peru (Willson 2004). Conversely, non-territorial antbirds showed significant population declines as *Phlegopsis nigromaculata*, *Rhegmatorhina melanosticta*, and *Gymnopithys salvini* (Willson 2004). Although LCL registered higher values than BOL regarding habitat variables, we did not find any relationships with *M. exsul*'s density; however, density was associated with the second component in this analysis which could support the idea that territoriality may stabilize *M. exsul*'s population dynamic in both of our landscapes in southwestern Costa Rica, allowing this species to maintain stable density values in agricultural landscapes.

On the other hand, Losada-Prado and Finegan [Chapter 2]'s observations agree with Willis and Oniki (1972) and Stiles (1983) in that adult males hold territories throughout the year and annually. This behavior was recorded for 17 individuals at LCL and 10 individuals at BOL. Additionally, we recorded females likewise holding territories during the year, a new observation for this species. We also observed a new female (14F) with the male 05M in January, 2009, indicating mate replacement perhaps due to predation. On Barro Colorado Island Willis and Oniki (1972) registered a similar observation.

Our estimates of the range of apparent survival probability, from 0.844 to 1.000, were higher than those recorded for other species of resident tropical birds (Karr et al. 1990, Brawn et al. 1995, Faaborg and Arendt 1995, Johnston et al. 1997, Blake and Loiselle 2002, Parker et al. 2006, Pearce-Higgins et al. 2007, Ruiz-Gutierrez et al. 2008). We believe that our data are consistent because the apparent survival probability did not change between two *M. exsul* populations in our fragmented landscapes. In addition, variations between *M. exsul*'s populations

across a broad geographic scale was not evident with our data, thus we disagree with Dhondt (2001) and Frederiksen et al. (2005) that survival varies geographically among populations of resident birds. However, we observed a change in the survival models because at LCL the apparent survival and recapture probabilities were influenced by time and sex, whereas at BOL these probabilities were constant without effects of these two variables.

It is known that habitat fragmentation has a negative effect on survival (Horak and Lobregon 1998, Matthysen 1999, Ruiz-Gutierrez et al. 2008); however, our results demonstrated that *M. exsul* was not affected in its density or apparent survival among landscapes with different fragmentation degrees and landscapes dominated by agricultural uses. Additional studies of broader temporal scale (5-7 years) are recommended for evaluating apparent survival probability in agricultural landscapes. Additionally, strategies like territoriality and parental care during the post-fledging period (Styrsky et al. 2005) could be reducing fragmentation effects on *M. exsul*'s population dynamics, so these effects cannot be perceived at least in this study. According to Styrsky et al. (2005) parental care during the post-fledging period is a potential key factor influencing the evolution of small clutch sizes in tropical birds. We registered three mates with one juvenile each one during the breeding season and a nest with only one egg. Thus, these strategies (territoriality and parental care during post-fledging period) could influence the population dynamics of *M. exsul* in fragmented landscapes with agricultural matrices where the survivorship would be affected by anthropogenic effects, habitat degradation, and limited dispersal between habitat fragments.

Physical condition of *M. exsul*

The presence of significant differences between landscapes indicated that *M. exsul* had different body conditions in agricultural landscapes in southwestern Costa Rica. Likewise, *M. exsul* population's body condition in protected areas and fragmented landscapes, in the Atlantic slope, suggests that this species is unaffected by fragmentation with regards to its body condition. The single exception was the Tortuguero National Park population where body condition index was lower regarding other regions, indicating that Tortuguero individuals could be affected by habitat conditions differently from individuals in other regions.

Finally, our data suggest that *M. exsul* populations in southwestern Costa Rica are not affected and these populations would be maintaining somewhat different demographic parameters to stabilize the dynamic in the population in fragmented landscapes with agricultural matrices. However, we suggest evaluating these populations at broader temporal scales (e.g., inter-annual scale).

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TABLE 1. Costa Rican regions with morphometric data from *M. exsul*. TIBMP: Tortuguero Integrated Bird Monitoring Program.

Region	Slope	Convention	n	Years	Source
Los Cusingos	Pacific	LCR	25	2008- 2009	This study
Boruca	Pacific	BOR	24	2008- 2009	This study
La Selva Biological Station	Atlantic	LSER	124	2004- 2009	S. Woltmann (<i>unpublished data</i>)
Rio Frio's fragmented landscape	Atlantic	RFIR	35	2004- 2009	S. Woltmann (<i>unpublished data</i>)
Tortuguero National Park	Atlantic	TORR	118	1995- 2006	TIBMP

TABLE 2. Density (D) of *M. exsul* at Los Cusingos (LCL) and Boruca (BOL) Landscapes in southwestern Costa Rica. LCL: 95% Lower confidence limit, UCL: Upper confidence limit, AIC: Akaike Information Criterion. Models from Distance Program.

Landscapes	Sites	D	LCL	UCL	AIC	Model
LCL	Los Cusingos	1.137	0.369	3.500	97.12	Hazard rate cosine
LCL	La Escondida	0.430	0.297	0.623	69.47	Uniform simple polynomial
LCL	Chober	0.505	0.337	0.758	60.09	Uniform simple polynomial
BOL	Kantan	0.737	0.392	1.384	40.30	Uniform simple polynomial
BOL	San Joaquin	0.589	0.079	4.421	18.93	Half-normal simple polynomial
BOL	Changuina	0.505	0.337	0.758	60.09	Uniform simple polynomial

TABLE 3. Models used to generate apparent survival and recapture probabilities of *M. exsul* at LCL in southwest Costa Rica. Phi: apparent survival, p: recapture probabilities, t: time, (.): constant, K: number of parameters, AICc: Akaike's Information Criterion values.

Model	K	AICc	AICc Weights
Phi(t) p(sex)	13	156.189	0.518
Phi(.) p(.)	2	157.691	0.244
Phi(.) p(sex)	3	158.355	0.175
Phi(sex) p(sex)	4	160.418	0.063
Phi(t) p(t)	22	171.810	0.00021
Phi(sex*t) p(sex)	24	177.601	0.00001
Phi(sex*t) p(sex*t)	44	224.950	0

TABLE 4. Models used to generate apparent survival and recapture probabilities of *M. exsul* at BOL in southwest Costa Rica. Phi: apparent survival, p: recapture probabilities, t: time, (.): constant, K: number of parameters, AICc: Akaike's Information Criterion values.

Model	K	AICc	AICc Weights
Phi(.) p(.)	2	45.756	0.632
Phi(.) p(sex)	3	47.859	0.221
Phi(sex) p(sex)	4	49.277	0.109
Phi(t) p(sex)	9	51.397	0.037
Phi(t) p(t)	14	63.738	8.0E-05
Phi(sex*t) p(sex)	16	66.473	2.0E-05
Phi(sex*t) p(sex*t)	28	102.894	0.00

TABLE 5. Vegetation variables at Los Cusingos landscape (LCL) and Boruca landscape (BOL) in southwestern Costa Rica. Density = number of trees ≥ 10 dbh / ha; dbh= diameter at breast height. Mean and \pm SD.

Landscapes	Sites	Density (# / ha)	Basal area (m ² / ha)	Canopy cover (%)	Vertical Structure	Mean dbh
LCL		702.34 \pm 145.27	28.05 \pm 7.53	76.16 \pm 9.11	1.18 \pm 0.25	19.83 \pm 2.29
	Los Cusingos	670.31 \pm 109.25	28.32 \pm 9.26	70.62 \pm 4.76	1.26 \pm 0.26	19.64 \pm 2.83
	La Escondida	809.38 \pm 178.75	29.90 \pm 6.70	74.87 \pm 8.37	1.25 \pm 0.14	19.63 \pm 1.51
	Chober	659.38 \pm 135.58	25.67 \pm 3.47	88.53 \pm 1.45	0.93 \pm 0.10	20.42 \pm 1.81
BOL		404.17 \pm 224.42	15.19 \pm 9.01	81.13 \pm 4.72	0.63 \pm 0.25	19.02 \pm 3.83
	Kantan	640.63 \pm 220.77	19.79 \pm 8.54	83.95 \pm 6.97	0.53 \pm 0.18	17.91 \pm 1.78
	San Joaquin	215.63 \pm 74.33	6.85 \pm 4.87	79.34 \pm 2.39	0.50 \pm 0.19	16.86 \pm 3.75
	Changuina	356.25 \pm 63.74	18.92 \pm 7.13	80.09 \pm 2.21	0.88 \pm 0.21	22.30 \pm 3.48

TABLE 6. ANOVA results for vegetation variables by landscape. Degree freedom = 2. ^a: Data analyzed through Kruskal Wallis test.

Landscapes	Density	Basal area	Canopy cover (%)	Vertical structure	Mean dbh
LCL	F= 3.35, p= 0.0490	F= 0.64, p= 0.5358	H= 18.68, p= 0.0001 ^a	F= 7.85, p= 0.0019	F= 0.33, p= 0.7198
BOL	H= 19.11, p= 0.0001 ^a	F= 8.52, p= 0.0020	H= 2.42, p= 0.2967 ^a	F= 9.35, p= 0.0012	F= 6.82, p= 0.0052

TABLE 7. Mean standardized residuals (MSR) of body condition index by landscapes in Costa Rica. LCL: Los Cusingos Landscape, BOL: Boruca Landscape, LSER: La Selva Biological Station, RFIR: Rio Frio's fragmented landscape, TORR: Tortuguero National Park. Different letter means significant difference $p \leq 0.05$.

Regions	n	MSR \pm SD	LSD Fisher
TORR	100	-0.31 \pm 1.02	A
RFIR	18	0.20 \pm 1.01	B
LSER	9	0.41 \pm 1.08	B
BOL	25	0.43 \pm 0.57	B
LCL	24	0.52 \pm 0.78	B

FIGURE 1. Principal Component Analysis (PCA) for vegetation variables at Los Cusingos landscape. G = basal area; dens = tree density; vest = vertical structure; caco = canopy cover; dap = diameter at breast height; escl = La Escondida; lcul = Los Cusingos; chol = Chober.

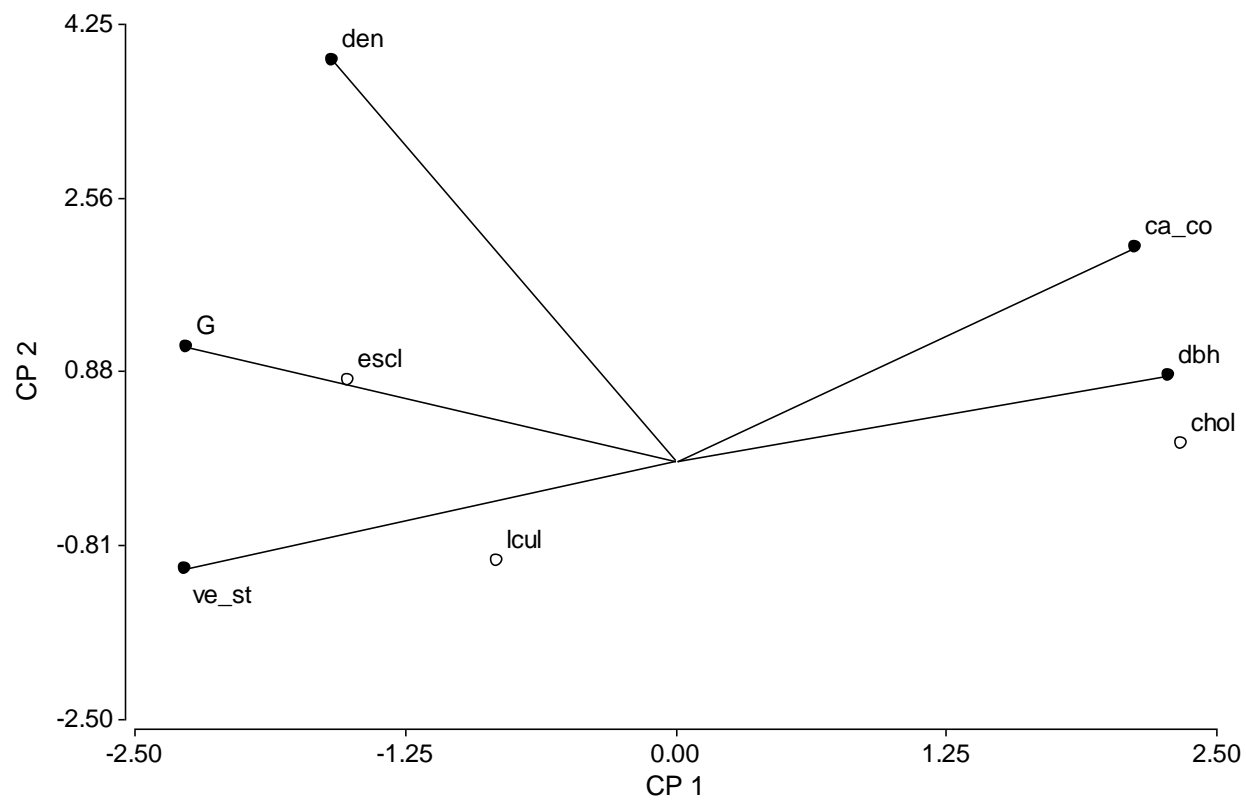


FIGURE 2. Principal Component Analysis (PCA) for vegetation variables at Boruca landscape.

ve_st = vertical structure; dbh = diameter at breast height; G = basal area; den = tree density;

ca_co = canopy cover; sanl = San Joaquin; chal = Changuina; kanl = Kantan.

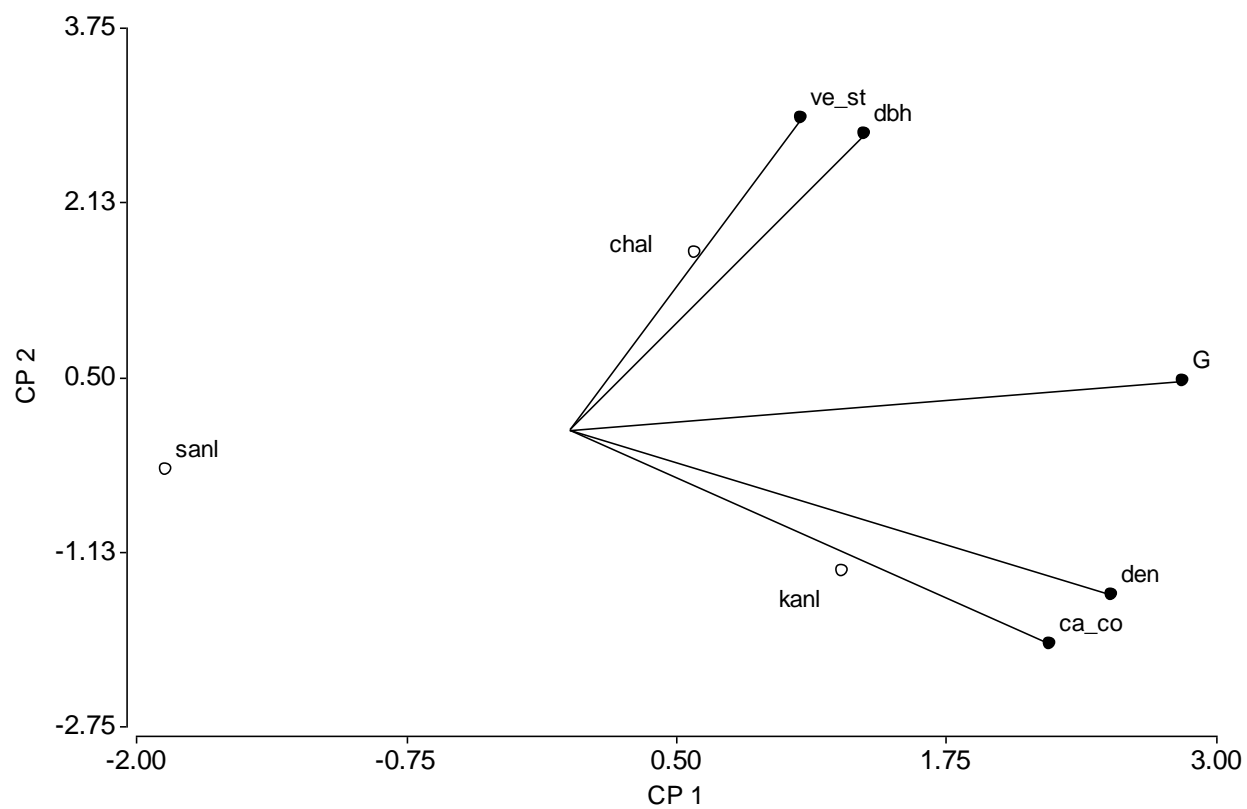


FIGURE 3. Principal Component Analysis (PCA) for vegetation variables and *M. exsul* density in southwestern Costa Rica. D_Mexs = *M. exsul* density; ve_st = vertical structure; dens = tree density; G = basal area; dbh = diameter at breast height; ca_co = canopy cover.

