SMALL MAMMAL COMMUNITIES AND FUNCTIONAL CONNECTIVITY IN THE LOWER RIO GRANDE VALLEY: A LANDSCAPE PERSPECTIVE

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GRANDE VALLEY: A LANDSCAPE PERSPECTIVE

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Abstract:

Habitat loss and fragmentation are major threats to global biodiversity, negatively affecting all major taxonomic groups. To mitigate these effects, the United States Fish and Wildlife Service manages three refuges in the Lower Rio Grande Valley (LRGV) of southern Texas with 1 goal of serving as a wildlife corridor connecting the Gulf coast with Falcon Reservoir. Since its creation in 1979, the LRGV National Wildlife Refuge (LRGVNWR) has grown to include 146 individual tracts, totaling about 44,500 ha primarily along the Rio Grande. The refuge offers the ability to conduct research in an increasingly common landscape pattern, a mosaic composed of native/restored habitat fragmented by agricultural and urbanized land use.

My study first examined how aspects of the habitat and landscape influenced small mammal diversity in LRGV refuge tracts. I live-trapped small mammals in 14 refuge tracts and calculated standard diversity indices from the resulting captures. Of 5,115 total captures, 49.7% were white-footed mice (*Peromyscus leucopus*) and hispid cotton rats (*Sigmodon hispidus*), representing 2 of 4 species statistically shown to prefer edge habitat. Although this demonstrated refuge lands were dominated by edge-adapted species, comparison to previous studies from within the refuge revealed a decrease in magnitude of their domination. Canonical redundancy analysis identified the amount of habitat available within 500 m of capture sites and average vegetation density within 150 m as important landscape features contributing to occurrence of small mammal species. These results demonstrated that the refuges in the LRGV are achieving their main goals to restore and maintain habitat.

Secondly, I examined effects of agricultural and urban fragmentation on genetic diversity and structure in populations of *P. leucopus* from 5 refuge tracts in the LRGV. Low nucleotide diversity combined with high haplotype diversity indicated a time of low effective population size of white-footed mice followed by recent population expansion. Localized population structuring suggested that *P. leucopus* was unable to effectively disperse through areas dominated by urbanization, while agricultural matrix offered no resistance. These results highlight the importance of preferentially acquiring and restoring land in areas dominated by an agricultural matrix to protect small mammal species from future urban encroachment.

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CHAPTER I

SMALL MAMMAL COMMUNITIES IN THE LOWER RIO GRANDE VALLEY: A LANDSCAPE PERSPECTIVE

Abstract

Habitat loss and fragmentation are major threats to global biodiversity, negatively affecting all major taxonomic groups. To mitigate these effects, the United States Fish and Wildlife Service manages 3 refuges in the Lower Rio Grande Valley (LRGV) of southern Texas, in part to establish a wildlife corridor connecting the Gulf Coast with Falcon Reservoir. Since its creation in 1979, the LRGV National Wildlife Refuge (LRGVNWR) has grown to about 44,500 ha of land primarily along the Rio Grande. Some areas have been restored from existing farm land to semi-native habitat by planting a mixture of native species found within climax habits. My study examined which aspects of the habitat and landscape influence small mammal diversity. To do this, I live-trapped small mammals in 14 tracts of the LRGVNWR and Santa Ana National Wildlife Refuge (SANWR) and calculated standard diversity indices from the resulting captures. I also used ordination to determine what habitat and landscape components were

associated with species occurrence. Of 5,115 total captures, 49.7% were white-footed mice (*Peromyscus leucopus*) and hispid cotton rats (*Sigmodon hispidus*), representing 2 of 4 species statistically shown to prefer edge habitat. Although this demonstrated refuge lands were dominated by edge-adapted species, comparison to previous studies from within the refuge revealed a decrease in magnitude of their domination. Results of canonical redundancy analysis identified the amount of suitable habitat within a 500-m buffer of capture sites and vegetation density within a 150-m buffer as important landscape features contributing to the occurrence of small mammal species. These results demonstrated that the refuges are achieving their main goals to restore and maintain habitat in the Lower Rio Grande Valley.

Introduction

Habitat loss and fragmentation

Habitat loss and fragmentation are major themes in conservation biology research (Haila 2002; Fazey et al. 2005), and they are considered severe threats to global biodiversity (Foley et al. 2005) that can negatively affect all taxonomic groups including birds and mammals (Andrén 1994; Recher 1999), reptiles (Gibbons et al. 2000), amphibians (Stuart et al. 2004), invertebrates (Didham et al. 1996), and plants (Hobbs and Yates 2003). With widespread expansion of agriculture and urbanization, significant parts of natural habitats have been lost or fragmented on every continent except Antarctica (Fazey et al. 2005). Habitat loss and fragmentation can reduce trophic chain length (Komonen et al. 2000), alter species interactions (Taylor and Merriam 1995), and reduce the number of specialist species (Gibbs and Stanton 2001). Habitat loss also

negatively affects breeding success (Kurki et al. 2000), dispersal success (With and Crist 1995; Pither and Taylor 1998; With and King 1999; B´elisle et al. 2001), predation rate (Hartley and Hunter 1998), and aspects of animal behavior that affect foraging success rate (Mahan and Yahner 1999).

Fragmentation, the spatial separation of habitat units, is a secondary consequence of loss of native habitats (Fahrig 2003). A number of processes threaten species persistence after habitat fragmentation: habitat loss and degradation, habitat isolation and subdivision, disruption of species interactions (including gene flow), disruption of species biology, and stochastic events (Kurki et al. 2000; Foley et al. 2005). Habitat fragmentation affects different species in different ways. Some species experience a sharp decline in population size or are extirpated from an area all together, others remain in comparable densities as before the disruption, and still others experience local population size increases (Dewalt et al. 2003). In general, species occupying higher trophic levels, with lower mobility, greater ecological specialization, and greater taxonomic age respond more quickly and negatively than species without these characteristics (Holt 1997). With this in mind, management agencies try to maintain connected native habitats or reconnect them during land acquisition, but this is not always possible because of the uncertain nature of land acquisition policy and funding.

Importance of patch size and edge effects

If a wildlife refuge consists of multiple, distinct patches of habitat, it is crucial to consider not only patch size but also the impact that the amount of suitable habitat (result of habitat loss) and edge effects (result of fragmentation) has on the diversity of flora and fuana. Research on the effects of patch size and edge effects was initially an adaptation

of island biogeography theory (IBT; MacArthur and Wilson 1967). Like the oceanic islands on which the theory was developed, it was thought that terrestrial habitat patches acted as distinct units whose species richness potential was a product of overall area (Harris 1984). While IBT has proven to correctly predict species richness in several cases (reviewed by Fahrig 2013), some do not (Hanski 2015). The assumption of IBT that space between neighboring islands (matrix) is inhospitable and subject only to stochastic dispersal events has been shown to be largely incorrect when used for terrestrial environments (Lomolino 2000). The matrix between terrestrial habitat patches can vary significantly in its resistance to dispersal and even seasonal and daily movements (e.g., Baguette et al. 2000; Broome 2001; Fraser and Stutchbury 2004; Petranka and Holbrook 2006; Roe et al. 2009). This is a primary reason why patterns of species richness often deviate from the predictions of IBT in continental areas (Fahrig and Palohemo 1988), which can confound the use of patch size as a reliable tool for predicting species richness (Fahrig 1998). Because movement and dispersal among habitat patches occurs at much higher frequencies than among oceanic islands, suitable habitat within a biologically meaningful area outside the patch should be included. Therefore, it is not appropriate to measure only the amount of habitat within a single patch. Instead, species richness is commonly measured in the total area of suitable habitat within a biologically relevant range away from a focal origin (Fahrig 1998).

Species composition in a fragmented habitat is also influenced by the habitat matrix and anthropogenic disturbance (i.e., fences, walls, and roads) close to the edge (Ranney et al. 1981; Harris 1984; Lovejoy et al. 1986). These edge effects often give rise to a community different from either adjacent habitats because some species increase in

abundance close to the edge and others decrease (Noss 1987; Yahner 1988). This type of edge effect can pose difficulty for managers attempting to maintain communities found on either side of the edge. Some small habitat patches may primarily consist of edge-modified habitat (Kapos 1989), causing species that are found in forest interior to be lost (Ranney et al. 1981). Edge effects may also extend far into a patch and, in a landscape containing large amounts of edge, lead to ecosystem modifications on a landscape level (Ranney et al. 1981; Noss 1983; Kapos 1989). Edge effects also have important theoretical ramifications. Attempts to apply IBT to fragmented terrestrial landscapes have been confounded by edge effects; smaller patches have more perimeter relative to area, on average, and have an environment that differs from that of larger patches. One conservation concern in landscapes with this configuration is that conditions created at the interface (edge) of agricultural lands are likely to alter wildlife communities within natural areas, favoring generalists at the expense of specialists (Laurance and Yensen 1991; Laurance 2000).

Lower Rio Grande Valley and its refuges

The Lower Rio Grande Valley (LRGV) is located in the 4 southernmost counties (Hidalgo, Starr, Cameron, and Willacy) in Texas. The LRGV is not geographically a valley, but more a delta that gently slopes upward and away from the Rio Grande (Lonard and Judd 1988). More than 600 vertebrate and 170 woody plant species occur in the LRGV, 84 of which are historically or currently listed as threatened, rare, or endangered by federal and state agencies (D. M. Leslie, Jr. pers. commun.). It is estimated that >95% of native habitat in LRGV has been converted to agricultural or urban areas in the last century (USFWS 1980, Parvin 1988a, Parvin 1988b). In 1979, an effort to preserve

remaining habitat resulted in the implementation of the United States Fish and Wildlife Service (USFWS) Land Protection Plan, calling for a 53,420-ha corridor linking tracts of native and restored vegetation along the Rio Grande and the establishment of the LRGV National Wildlife Refuge (LRGVNWR). Optimally, the corridor would be about 240 km in length, extending from the mouth of the Rio Grande west to Falcon Dam in Starr County, but the recent construction of the border wall along the Rio Grande by U.S. Homeland Security may alter land acquisition strategies in the future. Currently, the LRGVNWR is comprised of 146 tracts totaling about 44,500 ha.

From its inception, the LRGVNWR has primarily incorporated land previously used for agriculture. If used or managed, such land underwent secondary succession; the rate at which this process occurred was strongly dependent on the ability of mid and late successional plant species to disperse and compete with species already present (Sternberg and Judd 2006). Revegetation practices at LRGVNWR have followed the Facilitation Model (Connell and Slatyer 1977), which attempts to accelerate succession by planting climax species in previously altered areas.

Limited research has been conducted on how vertebrates are affected by restoration, connectedness, and fragmentation on LRGVNWR lands. Howe et al. (1986) conducted a pilot study in which tracts of various sizes were sampled for small mammals, reptiles, amphibians, and birds to assess effects of habitat fragmentation; few effects were documented. Two more recent studies examined the efficacy of revegetation projects in the LRGV and found that replanted tracts were more similar in composition to mature native brushland than tracts not replanted (Judd et al. 2002, Sternberg 2003). Sternberg and Judd (2006) found that replanted tracts of LRGV habitat supported higher diversities

of small mammals. These studies provide important insights into the relative success of the USFWS Land Protection Plan in the LRGV, but for long-term maintenance and restoration of biodiversity to be achieved, it is necessary to understand how refuge tracts compare to each other and how the refuge fits into the broad landscape around it.

My objectives were to: 1) determine strength of edge effects within refuge tracts relative to small mammal communities, 2) determine effects of tract size, amount of suitable habitat, and density of vegetation on species richness of small mammals, and 3) identify potential trends in diversity of small mammals within the LRGV by comparing my findings to previous research done in the LRGV. To meet these objectives, I chose to study small mammals that lend themselves to assessment of habitat fragmentation because they occur in relatively small patches of habitat, are commonly found in high densities, and demonstrate varied and substantial responses to fragmentation (reviewed by Watling and Donnelly 2006).

Methods

Study area

My study was conducted in the LRGVNWR and SANWR in southern Texas. Sampling focused on 14 refuge tracts located in the Rio Grande Delta physiographic zone (Hathcock et al. 2012). These tracts were picked because "patches on a west-to-east gradient located between La Joya and Brownsville, Texas, are under the greatest threat of urban encroachment, and therefore constitute the areas of greatest concern*"* (B. R. Winton, Refuge Manager, LRGVNWR, pers. commun.). Within that biogeographical area, 14 tracts were sampled in 5 size classifications: 3 small tracts, 6−20 ha; 2 medium

tracts, 20−43 ha; 3 medium–large tracts, 90−121 ha; 3 large tracts, 174−225 ha; and 3 reference tracts, >800 ha (Fig. 1.1). Additional criteria were used to sample refuge tracts of highest concern: ≤ 2 km of Rio Grande River, >50% non-grass cover, and not physically connected to any other tract in the LRGVNWR or SANWR.

Sampling

In each sampled refuge tract, habitat was divided into edge and interior areas. Edge habitat included land within 100 m of the physical edge of the tract (Stevens and Husband 1998). Interior habitat included all land found within the 100-m edge area. Two locations were sampled in each tract, 1 in interior habitat and 1 in edge. Small mammals were trapped in a 5-by-5 square grid, with 10 m between traps and representing a total grid size of 0.25 ha (Lancia et al. 1996). At each grid point, 1 Sherman live trap was set and baited with rolled oats. Small mammals were collected using standard live trapping methods (Lancia et al. 1996; Hopkins and Kennedy 2004; Leis et al. 2008). Initial placement and baiting of traps were performed in the evening of the first trap night. Each location was sampled for 3 consecutive nights in December 2012, May 2013, August 2013, and January 2014. Traps were checked and captures processed before 0900 h to minimize heat stress. Traps were left closed during daytime hours and reopened the following evening. Capture and handling protocols followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and Oklahoma State University Institutional Animal Care and Use Committee Guidelines (ACUP AG-11-24). Data including sex, weight, length, identification to species, reproductive state, and general appearance (e.g., healthy or ill) were recorded for each capture.

Community indices

Small mammal communities were characterized from each grid location and by tract (edge and interior) using species richness, species diversity, and evenness. Species richness (n_s) was the number of species captured. Species diversity (H′) and evenness (J′) were calculated using the Shannon diversity index $\log_{10}$ (Brower et al. 1998; Krebs 1999). Linear regression was used to determine if species richness, diversity, and evenness were correlated with amount of available habitat (tract size). Effects of seasonal sampling period and edge/interior habitat on species richness, species diversity, evenness, and species abundance were assessed using repeated-measures ANOVA with Greenhouse-Geissor correction in SPSS 22 statistical software (IBM Corp. 2013).

Ordination

Ordination was used to identify associations among structure of small mammal communities and environmental variables. Values for 9 independent landscape and habitat variables were calculated using ARC GIS 10.2.2 (Environmental Systems Research Institute 2002): tract size in hectares (Tract_Si), perimeter-to-area ratio (Perim_Ar), nearest neighbor distance (Near_Nei), amount of habitat available within 3 concentric buffer areas (150_Area, 500_Area, and 1000_Are), and average density of vegetation within each buffer (150_NDVI, 500_NDVI, and 1000_NDVI). Buffers were created by first locating the geographical point located halfway between each tract's 2 sample grids. From this point, buffers of 150-m, 500-m, and 1,000-m radii were created, which was necessary because analyses were performed using small mammal capture data from both grid points in each tract together. Placing the center of the buffer areas between the 2 grid points captured habitat from both grids evenly, to minimize bias.

Amount of habitat available within each tract's 3 buffers was measured as tract area (m^2) within each respective buffer. Density of vegetation within each tract's 3 buffer was described using the Normalized Difference Vegetation Index (NDVI) a tool commonly used to characterize productivity or greenness of vegetation through the measurement of green light reflectance from the earth's surface by a satellite sensor (Shank 2008). One dataset from the time period within each of 4 sample periods was obtained from the National Aeronautics and Space Administration (NASA) web database (MODIS). NDVI values for each pixel were averaged for each tract across sampling periods to mediate seasonal bias. Detrended correspondence analysis of the species' data indicated that linear rather than unimodal ordination methods were most appropriate; therefore, redundancy analysis (RDA) was used (Hill and Gauch 1980). Responses of small mammal species to the 9 independent variables were examined with RDA using CANOCO 5.0 (Microcomputer Power 2014). Stepwise assessment and removal of variables were performed to optimize overall model performance. A Monte Carlo global permutation test gave the significance of the canonical axes, and the significance of the independent variable axis relationships was determined using a Monte Carlo permutation test under a reduced model (Tajovsky et al. 2012).

Results

Sampling

A total of 8,251 trap-nights resulted in 5,115 individual captures of small mammals. Capture success rates per tract over all sampling periods ranged from 55.0% in Vela Woods (medium–large size) to 67.5% in Monterrey Banco (medium size), with

an overall average of 62.0% throughout the study. Average capture success by season was lowest during summer at 44.6% (August 2012) and highest during spring 77.6% (May 2012). Average capture success was higher in edge habitat (68.4%) than interior habitat (56.6%). Of 9 small mammal species captured, *Peromyscus leucopus* (white-footed mouse), *Liomys irroratus* (Mexican spiny pocket mouse), and *Sigmodon hispidus* (hispid cotton rat) represented nearly three-quarters (n = 3,646; 71.3%) of total captures (Table 1.1). *Neotoma micropus* (southern plains rat; n = 26) and the exotic *Rattus rattus* (roof rat; n = 5) were least abundant species (0.6%). Six of 9 species preferred either edge or interior habitat (Fig. 1.2). Two species, *Oryzomys couesi* (Coues' rice rat) and *Liomys irroratus* (Mexican spiny pocket mouse), showed significant preference for interior habitat (F = 9.1, df = 1, P = 0.023 and F = 2.9, df = 1, P = 0.010, respectively). Of the 4 species with edge preference, 3 were native, known to prefer grassy habitat and preferentially occupy edge habitat (*P. leucopus*, F = 13.03, df = 1 P = 0.001; *S. hispidus*, F = 6.14, df = 1, P = 0.002; and *R. fulvescens*, F = 8.24, df = 1, P = 0.009), and 1 was nonnative (*R. rattus,* F = 25.0, df = 1, P = 0.038).

Community indices

Species richness (n_s) was lower in edge ($\bar{x}$ = 4.32, n_s = 2–6) than interior grids ($\bar{x}$ = 4.48, n_s = 3–7). Species richness of tracts ranged from 3 in Vaqueteria Banco East (small size) to 8 in SANWR (reference). Positive correlations existed between richness and tract size (R^2 = 0.373, P = 0.020). Analysis of variance identified an effect of season (F = 10.46, df = 2.4, P < 0.001) on species richness. Lowest average richness (n_s = 3.86) occurred in August 2012, and highest (n_s = 4.82) occurred in January 2013.

Shannon diversity was generally lower in edge grids ($\bar{x}$ = 0.511, H′ = 0.246–0.699) than interior grids ($\bar{x}$ = 0.531, H′ = 0.313–0.767). Diversity of tracts ranged from H′ = 0.449 in Vaqueteria Banco (medium size) to 0.764 in Santa Maria (large size). Analysis of variance identified an effect of season (F = 8.23, df = 2.57, P < 0.001) on species diversity. Overall diversity was H′ = 0.755 for all tracts and all collecting periods. Shannon evenness was lower in edge grids ($\bar{x}$ = 0.819, J′ = 0.516–0.996) than interior grids ($\bar{x}$ = 0.832, J′ = 0.657–0.995); it ranged from J′ = 0.704 in Santa Maria (large size) to J′ = 0.991 in Vaqueteria Banco East (small size).

Ordination

The RDA biplot showed species associations to 7 of 9 original environmental variables (Fig. 1.3). The first canonical axis explained 35.1% of the total variation and represents increasing amount of habitat available to small mammals as you move right on the axis. Six species (*O. couesi, B. taylori, L. irroratus, N. micropus, R. rattus, and O. leucogaster*) show positive association with axis 1 to varying degrees, while 3 species (*P. leucopus*, *S. hispidus*, and *R. fulvesencens*) show negative association. Axis 2 explained 25.7% of total variation and represents increasing distance to nearest refuge tract neighbor from top to bottom. Although overall associations tended to be weak with this axis, *R. fulvescens* showed positive association and *L. irroratus* showed very strong negative association. *Oryzomys leucogaster* and *R. rattus* associated with area of habitat within a 500-m buffer (500_AREA), which was the variable explaining most of the variation (24%, P = 0.0026; Table 1.2). *Baomys taylori*, *O. couesi*, and *N. micropus* associated with higher vegetation density within a 150-m buffer (150_NDVI, 11.2% variation, P = 0.066).

Discussion

The LRGV landscape is fragmented by urban zones and agricultural fields, and despite attempts to restore habitat to accommodate species once commonly found in the interior (Judd et al. 2002; Sternberg 2003; Sternberg and Judd 2006), my study found evidence of strong edge effects. Small mammal diversity was lowest in edge habitat, being dominated by only 2 species, *P. leucopus* and *S. hispidus*. These species along with *R. fulvescens* and *R. rattus* showed a statistically significant preference for edge habitat. *P. leucopus* and *S. hispidus* are known edge specialists (Pergrams and Lacy 2007) and were 2 of the 3 most frequently captured species throughout the study. RDA results suggested that presence of these 2 species was associated with the perimeter-to-area ratio, an edge-to-interior habitat proportion measurement. It may be difficult to increase biodiversity in a refuge dominated by edge specialists, which are usually also generalists, because they can decrease species richness by outcompeting interior species. Wilson et al. (2010) found that small mammal species present in habitat matrix with large amounts of edge, outcompeted specialists occurring only in interior forest habitat in South African fragmented landscapes. An overwhelming presence of edge specialists also has been shown to stall the small mammal community from moving toward a climax stage (Duncan and Duncan 2000; Cook et al. 2005), a struggle the LRGVNWR and SANWR face when restoring habitat to a nonfragmented climax community.

Refuge managers should be aware of the difference in using tract size and some measurement of amount of suitable habitat when considering biodiversity of new land acquisitions. My study showed tract size was positively correlated with small mammal species richness; however, this pattern was not well supported by the results of the RDA.

Instead, RDA indicated that the amount of suitable habitat within a 500-m buffer was more important in determining small mammal species presence and abundance than tract size. These conflicting results highlight a well-known and well-studied discrepancy between tract size metrics and those that measure amounts of suitable habitats within a biologically meaningful buffer (Fahrig 1997; Bender et al. 2002; Tischendorf et al. 2002). For example, a 500-m buffer zone potentially contains 78.5 ha of suitable habitat. Vaqueteria Banco is small (20 ha) in size, and the entire tract falls within a 500-m buffer zone. Diversity estimates in this small tract would be low if one only used tract size; however, it is adjacent to Vaqueteria Banco East (14.4 ha). Biodiversity estimates for either of these tracts would include data from the adjacent tract if amount of suitable habitat within a 500-m buffer is considered. Conversely, Garza-Cavazos is medium–large (121 ha) in size but rectangular in shape. Although tract size exceeds the total buffer area, the circular buffer only overlaps the rectangular tract, including 27.3 ha of suitable habitat. In this situation, diversity values for this tract using tract size would be inflated compared with diversity values estimated with amount of suitable habitat in a 500-m buffer. It is evident that both metrics have value in estimating habitat restoration potential, but when evaluating potential land acquisitions, it is important to consider tract shape and amount of adjacent refuge land within 500-m.

Although the distinction between tract size and amount of habitat within a biologically meaningful buffer is of importance to land conservation and management in the LRGV, combined they represent significant components of the RDA axis 1. Together with axis 2, a distance measure of patch isolation, it appears that my study is one of relatively few to find that IBT's 2 primary predictors of species richness and relative

abundance among oceanic islands were the strongest predictors in the LRGV's fragmented terrestrial landscape (reviewed in Laurance 2008). A meta-analysis performed by Prugh et al. (2008) compiled data from more than 100 studies collected from bird, mammal, reptile, amphibian, and invertebrate species from 6 continents and found patch/habitat area and isolation are surprisingly poor predictors of occupancy for most species. The study proposed the following 4 explanations for the low predictive power of patch/habitat area and isolation: 1) patches studied were of an inappropriate scale, such that areas and distances were not matched to focal species' body sizes and dispersal abilities; 2) particular taxonomic groups or species with certain life history traits were less sensitive than others; 3) most of the species were able to tolerate disturbance and not be threatened with extinction; or 4) the habitat island paradigm is not adequate in fragmented terrestrial systems because of strong effects of the matrix surrounding patches. With these ideas in mind, an examination of my study's design and the life history of each species captured may reveal areas in need of additional attention and constitute motivations for future research.

Density of vegetation within a 150-m buffer of a sample site also appears to play an important role in determining small mammal species presence and abundance in the LRGVNWR and SANWR. The presence of *N. micropus*, *O. couesi*, and *B. taylori* increased as NDVI values increased; however, only *N. micropus* is known to occur in dense vegetation (Schmidly 2004). The other 2 species, *O. couesi* and *B. taylori*, inhabit grassy areas more frequently than dense woody areas (Schmidly 2004). Although previously used as an effective measurement of vegetation density (Andela et al. 2013), these results highlight the potential weakness of its use without some additional physical

description of vegetation. Without predominant species identified, or at the least vegetation type (e.g. grass, shrubs, and trees), it is not possible to make conclusions about why the presence of these species was affected by vegetation.

My results were compared with Sternberg and Judd (2006) who collected small mammal community data in 2000 from native woodland, replanted fields, and unaided secondary successional sites to assess efficacy of revegetation efforts in the LRGVNWR. I compared my results from 2011–2013 to their data to identify trends in small mammal community structure. Sternberg and Judd (2006) reported total small mammal biomass estimates from the LRGVNWR for the first time with values from 3.2 to 12.1 kg/ha, which were 7.1–13.4 times higher than similar studies conducted in central and western Texas (Grant et al. 1985; Henke and Bryant 1999). I planned to include estimations of small mammal density and biomass, but failure to recapture any of 800 individuals marked using passive integrated transponders during the first sampling period resulted in abandonment of the mark-recapture aspect of my study. Despite not having density and biomass estimates, I compared capture rates between the 2 studies, and recorded slightly higher overall capture rates (62.0%) than Sternberg and Judd (2006; 56.6%). Therefore, small mammal biomass in 2011–2013 was likely equal to or higher than biomass estimates in Sternberg and Judd (2006). Together, these findings show that the subtropical habitat of the LRGV is capable of supporting high densities of small mammals.

In Sternberg and Judd (2006) and my study, 3 species (*P. leucopus, L. irroratus,* and *S. hisipidus*) accounted for the majority of captures: 88% in Sternberg and Judd (2006) and 71.3% in my study. Although it is not possible to know if I captured

relatively fewer of these 3 species because of a reduction in their population sizes or an increase in prevalence of more rare species. Higher species diversity and evenness in 2011–2013 compared to 2000 data ($H' = 0.246–0.727$ vs. $H' = 0.2–0.65$, and $J' = 0.574–0.996$ vs. $J' = 0.21–0.95$) suggest the latter. As mentioned above, it is possible that the 2 generalist species, *P. leucopus* and *S. hispidus*, outcompete interior specialists, and there are some data to suggest that refuge tracts have enhanced small mammal community restoration in the last 10–12 years, because the proportion of interior species has increased. Sternberg and Judd (2006) reported *S. hispidus* as most prevalent (51.7%) species followed by the *P. leucopus* (22.5%) and *L. irroratus* (14.7%). In contrast, my study found *P. leucpous* to be most prevalent (32.5%) with interior-preferring *L. irroratus* ($P = 0.010$; 21.6%) and *S. hispidus* the least prevalent (17.2%).

Although my study revealed that small mammal communities in the LRGVNWR and SANWR were dominated by species specializing in edge habitat, comparison with previous research suggested a positive trend toward species preferring interior habitat. With this encouraging trend, it is clear that the LRGVNWR is achieving its goal to restore and maintain habitat within the LRGV. My study identifies the importance of considering not only size and shape of potential land acquisitions but also their distance from neighboring refuge lands. With this knowledge, the LRGVNWR could choose to purchase small additions closer to existing refuge land instead of ones that would be functionally isolated from the majority of the refuge.

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Table 1.1 Capture data of small mammals by refuge tract in edge (left) and interior (right) habitat in 4 sampling periods between December 2011 and January 2013. Tracts are arranged by size category from smallest to largest (small, 6−20 ha; medium, 20−43 ha; medium–large, 90−121 ha; large, 174−225 ha; and reference, >800 ha). Species are listed horizontally from most to least captured: *P.l.*, white-footed mouse (*Peromyscus leucopus*); *L.i.*, Mexican spiny pocket mouse (*Liomys irroratus*); *S.h.*, hispid cotton rat (*Sigmodon hispidus*); *R.f.*, fulvous harvest mouse (*Reithrodontomys fulvescens*); *B.t.*, northern pygmy mouse (*Baomys taylori*); *O.c.*, Coues' rice rat (*Oryzomys couesi*); *N.m.,* southern plains woodrat (*Neotoma micropus*); *O.l.*, northern grasshopper mouse (*Onychomys leucogaster*); and *R.r.*, roof rat (*Rattus rattus*).

			Species								
Tract	Size	Class	*P.l.*	*L.i.*	*S.h.*	*R.f.*	*B.t.*	*O.c.*	*N.m.*	*O.l.*	*R.r.*
Vaqueteria Banco East	14.4	Sm.	66/64	40/66	118/26						
Villitas Banco	20	Sm.	83/71	19/45	79/31	7/3	14/6				
Vaqueteria Banco	20	Sm.	127/0	57/0	74/0	67/0					
Culebron Banco	34	Med.	67/47	35/53	33/17	60/28					
Monterrey Banco	40	Med.	64/43	17/48	63/44	46/20	33/27				
Vela Woods	90	Med-Lg.	72/27	8/34	62/37	15/7	31/22	0/10			
Abrams West	96	Med-Lg.	55/33	70/100	9/5		52/30				
Garza-Cavazos	121	Med-Lg.	106/84	2/14	31/48	52/18					
Marinoff	174	Lg.	82/29	40/79	40/11	37/6	27/17		2/0	0/2	
La Parida Banco	179.5	Lg.	77/49	9/28	18/2	41/21	54/16			24/20	
Santa Maria	225	Lg.	29/4	9/43	17/4	70/7	37/23	0/117	13/2		
La Joya	825	Ref.	88/67	41/65	29/15	13/14				20/6	2/0
Santa Ana	844	Ref.	72/20	20/49	31/15		19/30	5/122	5/4	0/5	3/0
Ranchito	1557	Ref.	86/51	42/71	14/6	17/5	17/5	8/60		7/3	
TOTAL			1074/589	409/695	623/256	485/69	284/184	13/309	20/6	51/36	5/0
GRAND TOTAL			1663	1104	879	554	468	322	26	87	5

Table 1.2 Results of canonical redundancy analysis based on 5,115 small mammal captures in 14 tracts of the Lower Rio Grande Valley National Wildlife Refuge and Santa Ana National Wildlife Refuge. Independent variables are listed in order from greatest to least amount of total variation explained. Tract size in hectares (Tract_Si), core area index (Perim_Ar), nearest neighbor distance (Near_Nei), available habitat within 3 buffer sizes (150_Area, 500_Area, and 1000_Are), and vegetation density within a 150-m buffer (150_NDVI).

Code	Variation Explained %	*F*-value	*P*-value
500_Area	24.0	3.8	0.0026
150_NDVI	11.2	1.9	0.08639
Near_Nei	10.7	2.0	0.07679
150_Area	8.7	1.7	0.15128
1000_Are	8.4	1.8	0.13349
Tract_Si	5.3	1.2	0.35636
Perim_Ar	6.7	1.6	0.21448

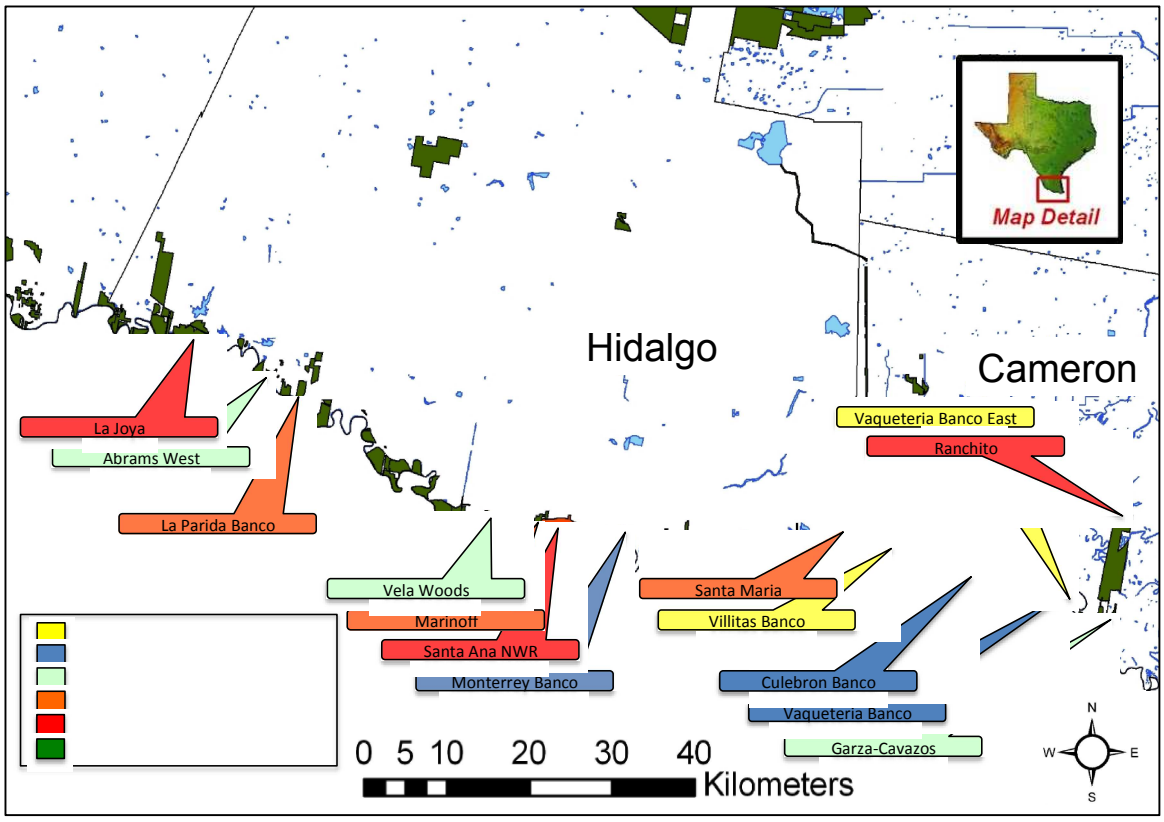

Figure 1.1 Lower Rio Grande Valley highlighting 14 tracts sampled from the Lower Rio Grande Valley National Wildlife Refuge and Santa Ana National Wildlife Refuge. Colored text boxes indicate size classification.

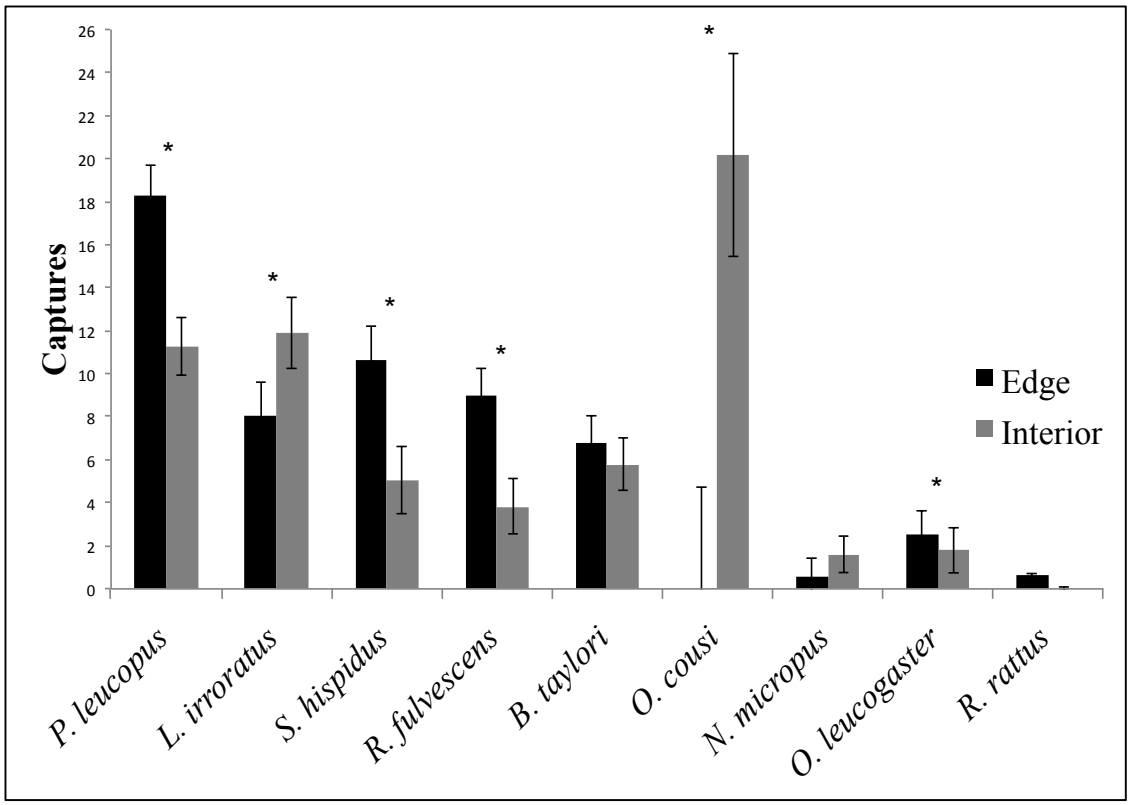

Figure 1.2 Repeated-measures ANOVA of capture rates (average number of captures/tract/trip) of small mammals in edge and interior habitat with significance ($P < 0.05$) noted by asterisk (*).

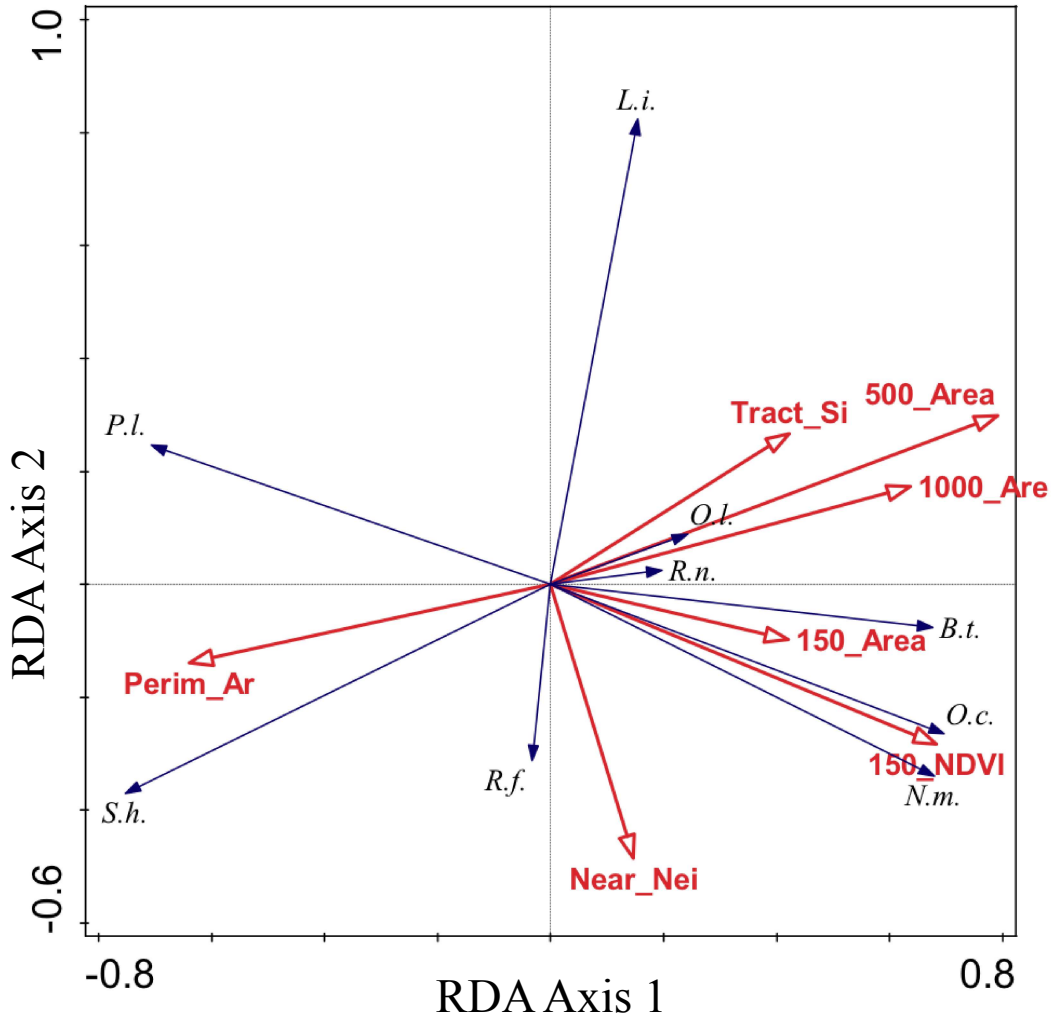

Figure 1.3 Biplot results of canonical redundancy analysis based on 5,115 small mammal captures in 14 tracts of the Lower Rio Grande Valley National Wildlife Refuge and Santa Ana National Wildlife Refuge. Independent variables are: tract size in hectares (Tract_Si), core area index (Perim_Ar), nearest neighbor distance (Near_Nei), available habitat within 3 buffer sizes (150_Area, 500_Area, and 1000_Are), and vegetation density within a 150-m buffer (150_NDVI). Species names are abbreviated as: *P.l.*, white-footed mouse (*Peromyscus leucopus*); *L.i.*, Mexican spiny pocket mouse (*Liomys irroratus*); *S.h.*, hispid cotton rat (*Sigmodon hispidus*); *R.f.*, fulvous harvest mouse

(*Reithrodontomys fulvescens*); *B.t.*, northern pygmy mouse (*Baomys taylori*); *O.c.*, Coues' rice rat (*Oryzomys couesi*); *N.m.*, southern plains woodrat (*Neotoma micropus*); *O.l.*, northern grasshopper mouse (*Onychomys leucogaster*); and *R.r.*, roof rat (*Rattus rattus*). Species arrow length corresponds to strength of correlation to variables. Independent variable arrow length corresponds to proportion of total variation explained.

CHAPTER II

FUNCTIONAL CONNECTIVITY OF THE WHITE-FOOTED MOUSE (*PEROMYSCUS LEUCOPUS)* IN THE HIGHLY FRAGMENTED LOWER RIO GRANDE VALLEY OF SOUTHERN TEXAS

Abstract

Fragmentation of natural habitats is a major challenge to conservation efforts and is 1 of the top threats to biodiversity. The Lower Rio Grande Valley National Wildlife Refuge (LRGVNWR) in southern Texas provides an example of urban and agricultural fragmentation in an area with high biodiversity and provides an opportunity to examine how the impact of fragmentation on genetic diversity of 1 habitat generalist species can be used to make conclusions about potential effects of fragmentation on a ecosystem. I examined genetic diversity and population structure of *Peromyscus leucopus* (white-footed mice) from 5 locations in LRGVNWR to determine their response to fragmentation. Low nucleotide diversity combined with high haplotype diversity indicated a time of low effective population size of white-footed mice followed by recent population expansion. This can be explained by fragmentation and conversion of the habitat to an agricultural and urban matrix in the 1920s followed by restoration to

semi-natural habitat of more than 12,000 ha beginning in 1979 (creation of the LRGVNWR). Small but measurable amounts of localized population structuring caused by an urban matrix suggest *P. leucopus* is unable to effectively disperse through areas dominated by urbanization. Agricultural matrix showed no resistance to gene flow. My study highlighted the importance of preferentially acquiring and maintaining native habitat in areas dominated by agricultural matrix to protect small mammal species from future urban encroachment.

Introduction

Fragmentation of natural habitats is a major challenge to conservation efforts and 1 of the top threats to regional and global biodiversity (Hanski 1999; Fahrig 2003; Henle et al. 2004). Alteration of natural habitat, which causes spatial separation of previously connected habitat units can decrease overall habitat availability, change spatial configuration, and reduce habitat quality (Fahrig 2003; Ezard and Travis 2006). Theoretical and empirical studies demonstrate that habitat fragmentation can erode neutral and adaptive genetic diversity of populations by decreasing effective population size and inter-population connectivity (Johansson et al. 2007). Subsequent to fragmentation, isolated smaller populations may experience greater effects of genetic drift, increased risk of inbreeding, and potentially extirpation or extinction (Avise et al. 1987; Reed and Frankham 2003). Gene flow among these populations mitigates negative effects but often requires connectivity of suitable habitat. Fragmentation in areas of high biodiversity can affect multiple species, and studying these affects on multiple species is not often feasible due to limited resources; however, an assessment of genetic diversity of

a single generalist species in a fragmented landscape can be used as an indicator of how more specialist species in the community may be affected by habitat fragmentation.

The Lower Rio Grande Valley (LRGV) in southern Texas provides an example of fragmentation in an area with high biodiversity and provides as an opportunity to examine how genetic diversity of 1 species can be used to make conclusions about the potential effects of fragmentation on a community. The LRGV is located in the 4 southernmost counties (Hidalgo, Starr, Cameron, and Willacy) in Texas and is within the Matamoran Biogeographic District of the Tamaulipan Biotic Province (Blair 1950). More than 600 vertebrate and 170 woody plant species occur in the LRGV, 84 of which are historically or currently listed as threatened, rare, or endangered by federal and state agencies (D. M. Leslie, Jr. pers. commun.). It is estimated that >95% of native habitat in the LRGV has been converted for agricultural or urban purposes in the last century (USFWS 1980; Parvin 1988a; Parvin 1988b). In 1979, an effort by United States Fish and Wildlife Service to preserve remaining habitat resulted in the implementation of the Land Protection Plan, calling for a 53,420-ha corridor linking tracts of native and restored vegetation along the Rio Grande and the establishment of the Lower Rio Grande Valley National Wildlife Refuge (LRGVNWR). Optimally, the corridor will be more than 240 km, extending from the mouth of the Rio Grande west to Falcon Dam in Starr County, Texas. Now, the LRGVNWR consisted of 146 tracts, totaling about 44,500 ha (Sternberg and Judd 2006).

Limited research has been conducted on vertebrate communities on LRGVNWR land, relative to restoration, connectiveness, and fragmentation. Howe et al. (1986) conducted a pilot study in which tracts of various sizes were sampled for small mammals,

reptiles, amphibians, and birds to assess effects of habitat fragmentation; few effects were documented. Two recent studies examined the efficacy of revegetation projects in the LRGVNWR and found that replanted tracts were closer in species similarity and diversity to mature native tracts than those not replanted (Judd et al. 2002; Sternberg 2003), and replanted tracts supported higher diversity of small mammals (Sternberg and Judd 2006).

To properly address effects of habitat connectivity on the LRGVNWR, it is important to consider 2 components of landscape connectivity. Structural connectivity involves physical relationships among patches, such as corridors and inter-patch distance (Taylor et al. 2006), while functional connectivity describes the potential for organismal movement or flow through patches in the landscape. Distinguishing between these is necessary because having a structural corridor between areas of suitable habitat does not necessarily mean that species of interest use it (Kadoya 2009). The relationship between structural and functional connectivity for a given species is determined by many interacting factors including feeding ecology, social organization, predation risk, reproduction, vagility, and corridor use (Bennett 1999). Population genetic approaches provide a direct method of determining functional connectivity for a given species at the landscape scale because the degree of genetic similarity among populations is determined largely by gene flow, which in turn reflects success in both dispersal among habitat fragments, and subsequent breeding (Frakham et al. 2002). Therefore, I examined genetic diversity and population structure of *Peromyscus leucopus* (white-footed mouse) in the LRGVNWR to determine if it has been affected by fragmentation.

Small mammals are useful in habitat fragmentation studies because they are capable of occurring in relatively small patches of habitat, are commonly found in high

densities, and demonstrate substantial response variation as a result of fragmentation (Watling et al. 2011). They also offer a link between primary producers and multiple higher tropic levels (Swanson et al. 2011). *P. leucopus* has been studied extensively in fragmented landscapes and occurs in all sampling sites in the LRGVNWR (Gaines et al. 1997; Krohne and Hoch 1999; Wilder and Meikle 2005; Keyghobadi 2007; Rytwinski and Fahrig 2007; Anderson and Meikle 2010; Mushi-South and Kharchenko 2010). Anderson et al. (2003) found higher densities of *P. leucopus* in small patches (59 ha) than in large patches (110–150 ha), which they attributed to disproportionately high population densities in edge habitat of small patches. The generalist behavior of *P. leucopus* would suggest it is resistant to negative effects of habitat fragmentation; therefore, I predicted that large and small tracts would have similar genetic diversity and no evidence of population structuring. Alternatively, evidence of reduced genetic diversity in smaller more isolated tracts, or population structuring, suggests they were negatively affected by fragmentation and habitat specialists may be suffering even greater negative effects in the LRGV.

Methods

Study Area

As part of a larger study that assessed small mammals in 14 tracts in the LRGV (Chapter 1), I trapped *P. leucopus* in 5 tracts within the LRGVNWR between December 2011 and January 2013. Tracts were sampled in 5 size classifications (1 tract from each, 5 total): small, 6−20 ha; medium, 20−43 ha; medium–large, 90−121 ha; large, 174−225 ha; and reference (>800 ha) to serve as contiguous natural habitat. Tracts sampled

adhered to the following criteria: ≤ 2 km away from Rio Grande River, >50% non-grass cover, and not physically connected to any other tract managed by the LRGVNWR (Fig. 2.1).

Trapping design and genetic sampling

Tracts were divided into edge and interior areas because diversity of small mammal species has been shown to differ significantly when sampled near edges versus interior habitat (Harris 1998, Saunders et al. 1991). Edge habitat was classified as areas beyond 100 m of the physical edge of the tract. Interior habitat was classified as all habitat found within the 100-m edge portion. Small mammals were trapped using 5-by-5 square shaped grids, 1 central and 1 edge (Lancia et al. 1996). Grid points were located 10 m from each other, representing a total grid size of 0.25 ha. At each point, 1 Sherman live trap was set and baited with oats. Initial placement and baiting of traps were performed in the evening before the first trap night. Traps were checked the next morning, and captures were processed before 0900 h to minimize heat stress. Sampling periods were 3 nights per tract.

Sex, weight, length, identification to species, reproductive state, and general appearance (e.g., healthy or ill) were recorded for each capture. All captured individuals were identified to species, and a third of the right ear was taken from each *P. leucopus*. Samples were stored in lysis buffer while in the field. To avoid infection, antibiotic ointment was applied to the ear clip sight, and tools were flame sterilized and cleaned with ethanol between sample collections. Capture and handling protocols followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and Oklahoma

State University Institutional Animal Care and Use Committee Guidelines (ACUP AG-11-24).

Laboratory methods

Whole genomic DNA was isolated from ear tissue using a DNeasy kit (Qiagen) following manufacturer's protocols. Approximately 400 base pairs of the mtDNA control region were amplified using primers MDF and 12S1 (Morzunov et al. 1998). Polymerase chain reactions (PCR) were carried out in 30-µL reactions containing 200–500 ng of DNA, 2 mM $MgCl_2$, 0.14 mM of each deoxynucleoside triphosphate, 0.15 µM of each primer, 0.8 mg/mL bovine serum albumin, 6 µl of 5X buffer, 1 unit Go*Taq* polymerase (Promega), and ddH_2O to volume. The thermal profile comprised an initial denaturation step of 95°C for 10 min, followed by 35 cycles of 95°C for 1 min, 55°C for 1 min, and 72°C for 1 min. The Wizard SV Gel PCR Prep DNA Purification System (Promega) was used to purify PCR products that were subsequently sequenced using Big Dye chain terminators (following manufacturer's suggested protocol) on an ABI 3130 Genetic Analyzer (Applied Biosystems Inc. Grand Island, New York). Manual verification and alignment of sequences was performed using Geneious v. 5.5.6 (Biomatters Ltd., Auckland, New Zealand).

Genetic analyses

The program TCS v.1.21 (Clement et al. 2000) was used to characterize and generate a network of unique haplotypes and illustrate genetic divergence at an intraspecific level. Ordinary least square regression was performed using the program SYSTAT v 1.0 (Wilkinson 2010) to identify bias caused by uneven sample size. After finding no association between sample size and haplotype diversity, all subsequent

analyses were performed using uncorrected haplotype frequencies. Ordinary least square regression was performed between fragment area and within-tract indices of genetic diversity to test for the possible effects of tract size on genetic diversity (Dixo et al. 2009). The program Arlequin v. 3.5 (Excoffier and Lischer 2010) was used to calculate the following population indices of genetic diversity: number of haplotypes, nucleotide diversity, and haplotype diversity. Arlequin v. 3.5 (Excoffier et al. 2005) was also used to estimate pairwise F_{ST}. Critical significance levels for multiple F_{ST} comparisons were corrected following the sequential Bonferroni procedure (Rice 1989). Analysis of molecular variance (AMOVA) was used to identify population sub-structuring with significance being assessed via 10,000 randomized replicates.

Spatial analyses

The program IBDWS v. 3.23 (Jensen et al. 2005) was used to test for a pattern of isolation by distance (IBD) across sites by correlating a matrix of pairwise genetic distances ($F_{ST}/1 + F_{ST}$) among sites with linear geographic distance using a Mantel correspondence test. Significance of the association was measured using 1,000 permutations. The program Alleles in Space (AIS; Miller 2005) was used to test for barriers to gene flow by iteratively identifying sets of contiguous, large genetic distances along a connectivity network. The analysis consisted of the following steps: (1) connecting adjacent geographical locations of individuals using Delaunay triangulation (Brassel and Reif 1979), resulting in a network of connectivity; (2) calculating genetic distances between neighboring samples and associating distances with each edge of the network, and (3) identify boundaries using Monmonier's maximum difference algorithm (Monmonier 1973; Manel et al. 2003).

AIS was then used to generate a 3-dimensional surface plot of genetic distances across the range of tracts sampled, known as a "genetic landscape shape" (Miller 2005). Unlike Monmonier's algorithm, this method provides a visual representation of genetic divergence across the landscape as opposed to genetic barriers or breaks. The following general steps were conducted: 1) construction of a connectivity network of sampled individuals and assignment of calculated genetic distances to landscape coordinates at midpoints of connectivity edges; 2) interpolate genetic distances at locations on a uniformly spaced grid overlaid on the sample landscape; and 3) generate a 3-dimensional surface plot where *X* and *Y* coordinates correspond to geographical locations on a rectangular grid and surface plot heights (*Z*) reflect genetic distance (Miller 2005). To better visualize results of this analysis, ArcGIS 9.3 (ESRI Corporation, Redlands, CA) was used to interpolate the 3-dimensional surface plot into a 2-dimensional heat map overlaid on the study area. I could then associate landscape features with increased or decreased inter-individual genetic distance, suggesting that they either facilitate or restrict gene flow.

Results

Genetic analyses

I collected ear samples from 121 *P. leucopus* and obtained control region sequences from 114 individuals. The final alignment was 383 base pairs in length and contained 12 distinct haplotypes. All 12 haplotypes were grouped into 1 network with 95% confidence (Fig. 2.2). Haplotype C was identified as ancestral and found in the 3 western most tracts (Vela Woods, Marinoff, and Monterey Banco). Haplotype A was

recovered from all 5 tracts sampled. Three of 5 haplotypes found in the reference tract were unique (G, H, and K; Fig. 2.3; Table 2.1). Seven of 11 haplotype transitions involve only a single base pair change (Fig. 2.2). Haplotype diversity (*h*) by tract ranged from 0.684 in Vaqueteria Banco (small tract) to 0.767 in Ranchito (reference tract; Table 2.1). Nucleotide diversity by site (π) was 0.00371 in Monterey Banco (medium tract) and 0.00711 in Ranchito (reference tract; Table 2.1). The absolute number of haplotypes per tract ranged from 4 to 6 (Table 2.1). Least square regression found no significant correlation between tract diversity indices and geographical area (*h,* $P = 0.255$; π, $P = 0.140$; A, $P = 0.966$). Pairwise F_{ST} values ranged from 0.004 to 0.226, and 2 of 10 comparisons revealed significant genetic differentiation after sequential Bonferroni correction (Rice 1989). These comparisons were between Monterrey Banco and tracts to the east (Vaqueteria and Ranchito Table 2.2). Analysis of molecular variance found significant evidence of population sub-structuring ($F_{ST} = 0.1301$; $P < 0.001$; Table 2.3). Evidence for hierarchical grouping of tracts was not supported for an east and west grouping ($F_{CT} = 0.0716$; $P = 0.209$) or reference vs. remaining tracts ($F_{CT} = 0.0012$; $P = 0.801$; Table 2.3). There is significant structuring within (not between) each of the 2 groupings, east and west ($F_{SC} = 0.0903$; $P < 0.001$), and reference vs. remaining tracts ($F_{SC} = 0.1306$; $P < 0.001$; Table 2.3).

Spatial analyses

The Mantel test found no evidence of isolation by distance ($r = 0.1345$, $P = 0.5250$). Monmonier's maximum difference algorithm identified a single, strong barrier to gene flow located between Ranchito and Vaqueteria Banco sample tracts. The genetic landscape generated in AIS revealed areas corresponding to low and high inter-individual

genetic distance (Fig. 2.4). Highest inter-individual genetic distances were in the 4.3 km separating Vaqueteria Banco and Ranchito tracts, which is the location of the town of Encantado-Ranchito (6.63 km^2). A second area of high inter-individual genetic distance was identified between Vela Woods and Marinoff sample tracts, which corresponded to the location of Pharr-Reynosa International Bridge. Genetic distances were lowest directly east of Santa Ana NWR between Marinoff and Monterey Banco, an area dominated by agriculture (Fig. 2.4).

Discussion

The population of *P. leucopus* in central LRGVNWR is characterized by low nucleotide diversity and high haplotype diversity. Nucleotide diversity values were low (0.003–0.007) compared with those reported from other rodent species such as *Neotoma fuscipes* (dusky-footed woodrat; 0.010–0.039, Matocq 2002) and *Lemmus sibiricus* (Siberian brown lemming; 0.018–0.028, Ehrich and Stenseth 2001). In contrast, haplotype diversity values were high (0.684–0.767), similar to those reported from populations of *L. sibiricus* (0.69–0.80, Ehrich and Stenseth 2001). This pattern suggests that the population of *P. leucopus* comprised a high number of closely related haplotypes. Statistical parsimony corroborated this by identifying 7 of 12 haplotypes that were separated by a single mutational step, with the remaining 5 haplotypes separated by < 3 steps (Fig. 2.2). Conclusions from Grant and Bowen (1998) provide a potential explanation for these results, hypothesizing that low nucleotide diversity in conjunction with high haplotype diversity results when a species with low effective population size undergoes significant range expansion.

Initial fragmentation and conversion of the majority of LRGV native habitat to an agricultural and urban matrix occurred in the early 1920s as a result of increasing agriculture practices and urbanization (Jahrsdoerfer and Leslie 1988). It is likely that populations of *P. leucopus* were reduced in size and confined to small patches of remaining native habitat. In 1948, Santa Ana National Wildlife Refuge (SANWR) was created and represented one of the largest additions of native/restored habitat until the creation of the LRGVNWR in 1979. Since then, more than 30,000 ha of habitat have been restored. This increase in suitable habitat gave *P. leucopus* the opportunity to rapidly expand in population density and distribute itself throughout the LRGV. Although habitat reclamation has occurred in a highly fragmented manner, results in the AIS genetic landscape map demonstrate *P. leucopus* has the ability to successfully disperse through an agricultural matrix in the LRGV. Other studies have documented *P. leucopus* dispersing through agricultural matrices (Krohne and Hoch 1999; Anderson and Meikle 2010), up to 14.7 km (Maier 2002; Jung et al. 2005).

Some rodent species do not disperse through fragmented habitat and therefore suffer genetic structuring and a loss of genetic variation. An examination of 5 case studies using either allozyme or mitochondrial data from small mammals in fragmented landscapes reported both of these responses to fragmentation (Gaines et al. 1997). A survey conducted by Keyghobadi (2007) of 32 studies found increased genetic structuring (69%) and decrease of genetic variation (58%) in the majority of cases. Within those 32 studies, 5 small mammals species were examined for population structure, and 3 of those species had populations that became genetically differentiated. Of the 6 small mammal species examined for genetic diversity, 3 species lost significant

genetic diversity in at least 1 marker type analyzed. Since Keyghobadi (2007), multiple studies have reported population structuring and loss of genetic diversity for small mammals in fragmented landscapes (White and Searle 2007; Biedrzycka and Radwan 2008; Macqueen et al. 2008; Booth et al. 2009; Kozakiewicz et al. 2009; Lampila et al. 2009; Vignieri 2010).

Genetic structuring and loss of genetic variation resulting from habitat loss and fragmentation highlights the importance of maintaining population connectivity and gene flow among geographically isolated habitat patches (Frankham et al. 2002). It appears that populations of *P. leucopus* in my study area are demonstrating some early signs of population sub-structuring. Populations in the sampled refuge tracts do not follow an isolation by distance pattern, and an overall F_{ST} of 0.1301 ($P < 0.001$) falls into the moderate sub-structuring category as reported by Wright (1978). The specific substructure pattern could not be clearly identified because hierarchical AMOVA's and pairwise F_{ST} comparisons failed to clearly separate out Ranchito and Vela Woods tracts, which was hinted at within the map of haplotypes in each tract (Fig. 2.3). Caution should be used when relying on these methods to provide statistical significance for population structure. Using simulations, Fitzpatrick (2009) identified 6 sample populations as the least amount of populations that can be used to obtain significant F_{CT} values in a hierarchical AMOVA. With only 5 sampled populations in this study, a $P \geq 0.100$ is the lowest mathematically expected. Fitzpatrick (2009) suggests focusing on individual pairwise F_{ST} values to make biologically meaningful groupings; however, the lack of significant pairwise F_{ST} comparisons may be due to over conservativeness of Bonferroni's post hoc correction (Narum 2006). Considering that only early signs of population sub-

structuring were detected in my study, it is of interest that before performing the Bonferroni correction, 7 of 10 pairwise comparisons were significant ($P < 0.05$). In addition, Alleles in Space did identify both a strong barrier to gene flow caused by high inter-individual genetic distances between Ranchito and all 4 other tracts as well as a lesser barrier located between Vela Woods and other sample tracts. It appears the town of Enchantada-Ranchito may be responsible for reduced gene flow through the 4.3 km between Ranchito and the nearest suitable habitat to the east, Vaqueteria Banco (Fig. 2.4). This finding is contrary to previous research documenting *P. leucopus* as an urban adaptor that can occur at high population densities in human-disturbed habitats (Wilder and Meikle 2005; Rytinski and Fahrig 2007). Nevertheless, Mushi-South and Kharchenko (2010) examined the genetic structure of *P. leucopus* in small fragmented habitats within Queens and Bronx counties, New York, and found evidence that urbanization was responsible for rapid differentiation. They concluded that although *P. leucopus* is an urban adaptor known to take advantage of parkways, cemeteries, and other manicured vegetation, anthropogenic structures such as buildings, parking lots, and interactions with human commensals (i.e., *Rattus rattus*, roof rat) counteract any potential corridor effect.

The other area identified with high inter-individual genetic distances was between Vela Woods and Marinoff tracts, which are separated by the Pfarr-Reynosa International Bridge and Border Station (Fig. 2.4). The 4-lane, 4.9-km bridge accommodates about 400,000 freight trucks annually, which represents 93% of the annual truck crossings in the Rio Grande Valley (Rajbhandari et al. 2012). Other mammal species have shown avoidance behavior or population declines in proximity of transportation infrastructure

(Benitez-Lopez et al. 2010), although a positive correlation between population size and road frequency has been documented in *P. leucopus* (Rytwinski and Fahrig 2007). It is not completely clear if the AIS results in this area of the LRGVNWR can be explained only by the presence of the bridge.

My study represents a first look into genetic functional connectivity within the fragmented LRGV landscape. Its findings highlight a recent trend in the study of habitat fragmentation focused on the importance of landscape matrix (Rickett 2001). There are 2 types of matrix within the central riparian habitat of the LRGV. It appears the agricultural matrix does not restrict gene flow of a generalist species like *P. leucopus,* but even small zones of urbanization can act as genetic barriers. Regardless of the type of matrix (urban or agricultural), the chance of colonizing other areas of suitable habitat is decreased. My results showed that even a generalist species like *P. leucopus*, documented to readily adapt to fragmented landscapes and successfully disperse, is negatively affected by urbanization and suffers loss of functional connectivity in the LRGV. If this species shows signs of having reduced gene flow between proximate populations because of urbanization, I hypothesize other more specialized species like *Onychomys leucogaster* (northern grasshopper mouse) and state-listed endangered *Oryzomys couesi* (Coues' rice rat) are likely to be impacted to a greater degree. There may be less of their preferred habitat in the LRGVNWR, or patches of suitable habitat could be separated by urbanized areas. *Sigmidon hispidus* (hispid cotton rat) is also a habitat generalist shown to thrive in fragmented landscapes but may not respond well to urbanization and could react in a similar manner as *P. leucopus* (Lidicker 1999). Additional population genetics studies are necessary to examine the extent to which small

mammal species may have been impacted by either the agricultural or urban matrix in the LRGV.

With this perspective on how fragmentation of the LRGV landscape has impacted 1 of its prominent rodent species, modifications to the LRGVNWR's comprehensive conservation plan may be warranted. In 1996, the interim plan was adopted for the LRGVNWR and SANWR and is still currently used (but undergoing revision). The plan serves as a tool for refuge staff by providing planning perspectives and considerations, descriptions of the ecosystem and natural resources, legal guidelines, and management programs for both refuges. Results from this study could suggest that it is beneficial to protect tracts in the LRGVNWR that are known to currently sustain diverse small mammal communities (e.g. Santa Maria, Santa Ana, and Ranchito) because it is likely that human populations will continue to increase and urban areas will expand (Peña 2012).

My study provides insights for strategic acquisition of new lands. Adding new habitat to existing tracts and connecting adjacent tracts in the LRGVNWR are already priorities as defined in their conservation plan but trying to connect habitat near urban areas can be difficult. The acquired connected lands should add interior habitat to help mitigate impacts of urbanization on small mammals. Acquiring lands currently used for agriculture could also prevent urban areas from encroaching further into the LRGV and fragmenting the landscape with large urban barriers to gene flow.

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Table 2.1 Distribution of white-footed mouse (*Peromyscus leucopus*) mtDNA control region haplotypes (letters A–L) across sampled tracts. Number of samples collected from each tract (*n*), haplotype diversity (*h*), nucleotide diversity (π), total number of alleles (*A*), and number of private alleles (*P*) found within each sample tract. Collection localities are arranged from east to west.

Collection locality	A	B	C	D	E	F	G	H	I	J	K	L	*n*	*h*	π	*A*	*P*
Vela Woods	2	1	3	10	1	3							20	0.726 ± 0.09	0.006 ± 0.004	6	0
Marinoff	9	2	3						1	2			17	0.699 ± 0.10	0.004 ± 0.003	5	1
Monterey Banco	4	5	13	12									34	0.715 ± 0.04	0.004 ± 0.003	4	0
Vaqueteria Banco	11	6				3			1			1	22	0.684 ± 0.08	0.005 ± 0.004	5	1
Ranchito	3				9		4	3			2		21	0.767 ± 0.07	0.007 ± 0.004	5	3

Table 2.2 Pairwise F_{ST} comparison values (below diagonal) among sampled tracts of white-footed mice (*Peromyscus leucopus*) with associated Bonferroni significance comparisons indicated in bold (above diagonal). Collection localities are arranged geographically from east to west.

Sample Location	Vela Woods	Marinoff	Monterey Banco	Vaqueteria Banco	Ranchito
Vela Woods	–	0.009	0.045	0.009	0.009
Marinoff	0.165	–	0.009	0.378	0.09
Monterey Banco	0.052	0.176	–	**0.000**	**0.000**
Vaqueteria Banco	0.174	0.004	0.226	–	0.072
Ranchito	0.113	0.046	0.198	0.045	–

Table 2.3 Results of the hierarchical analyses of molecular variance (AMOVA) to identify maximally differentiated groupings. Variance components from each grouping are reported (F-values) with *P*-values and percent variation explained.

Grouping[a]	F-value	*P*-value	Variation
1 Group	F_{ST} = 0.1301	0.000	13.01
2 Groups (VB & R) vs. (VW, M & MB)	F_{CT} = 0.0716	0.209	7.16
Tracts within the 2 groups	F_{SC} = 0.0903	0.000	8.38
Among tracts regardless of grouping	F_{ST} = 0.1555	0.000	84.45
2 Groups (R) vs. (VB, VW, M and MB)	F_{CT} = 0.0012	0.801	0.12
Tracts within the 2 groups	F_{SC} = 0.1306	0.000	13.04
Among tracts regardless of grouping	F_{ST} = 0.1316	0.000	86.84

[a] VB = Vaqueteria Banco, R = Ranchito, MB = Monterey Banco, M = Marinoff, VW = Vella Woods.

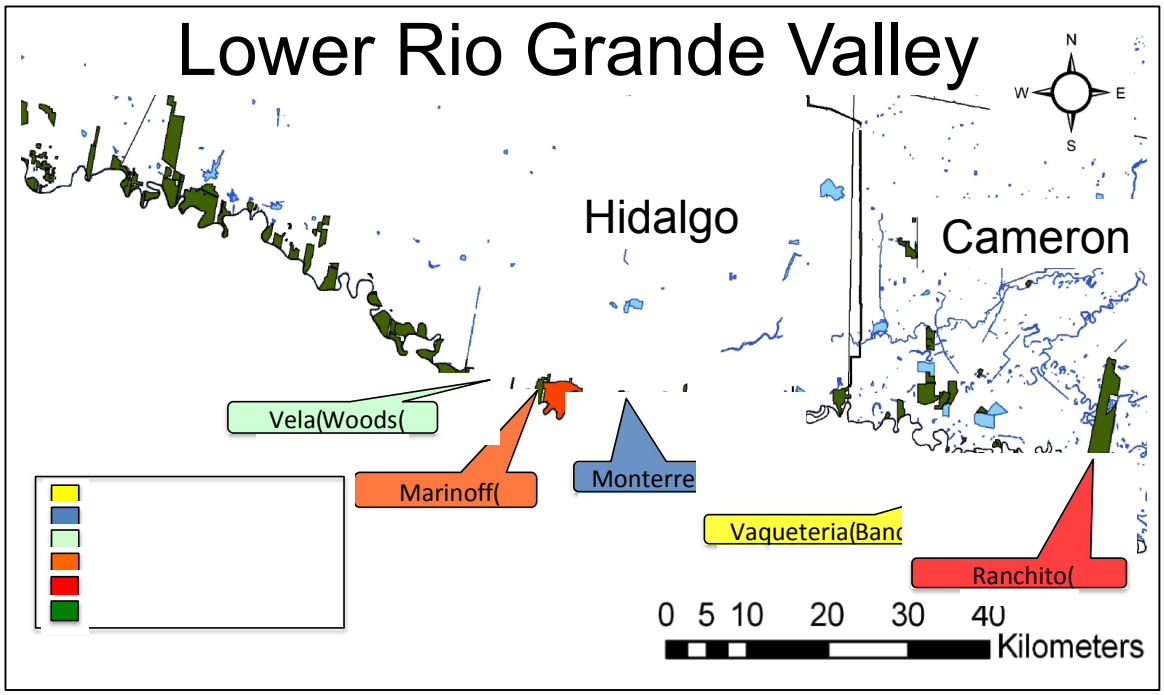

Figure 2.1 Lower Rio Grande Valley highlighting 5 tracts sampled from the Lower Rio Grande Valley National Wildlife Refuge. Colored text boxes indicate size classification.

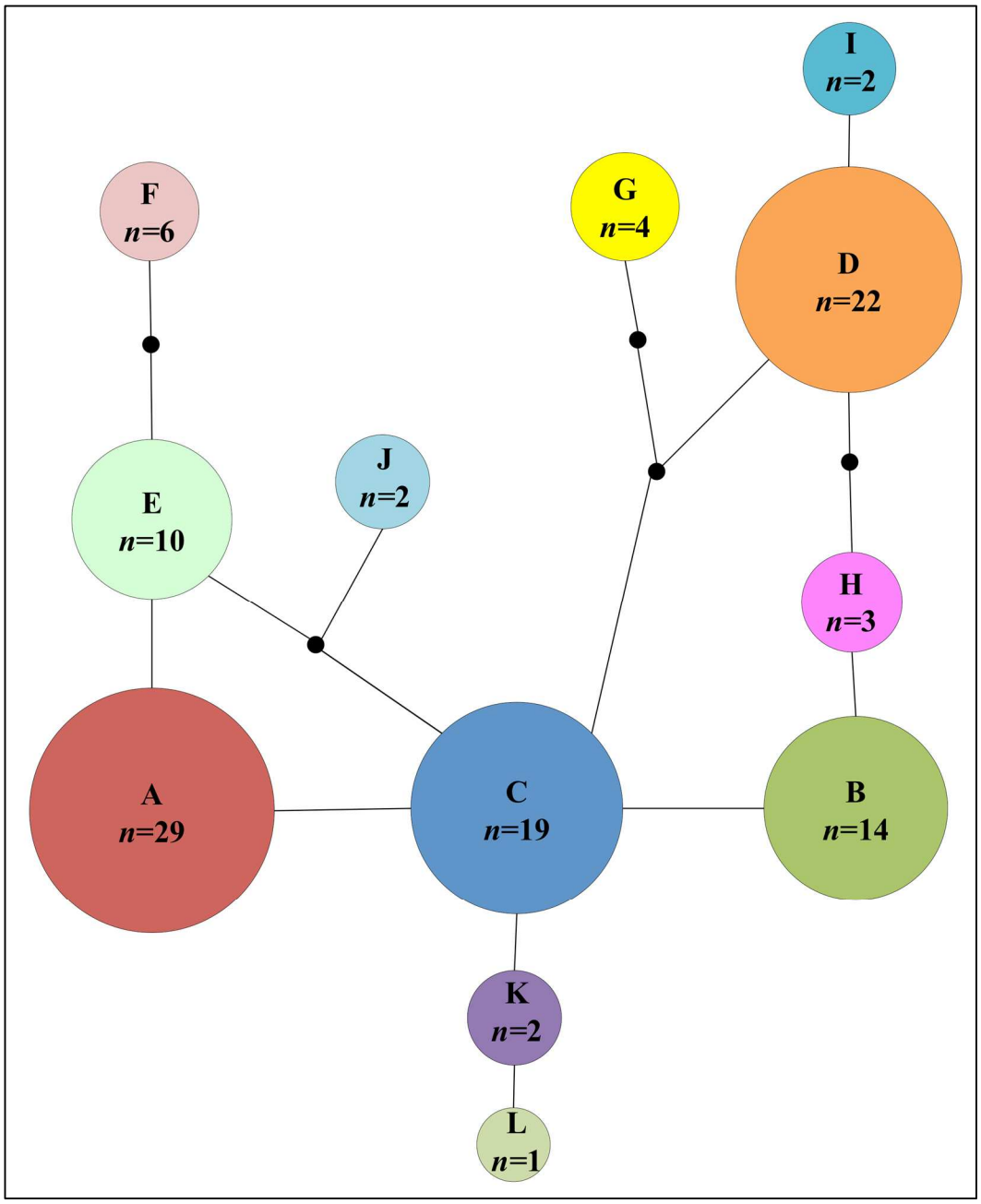

Figure 2.2 Haplotypic network based on 383 base pairs of mtDNA control region from 114 white-footed mice (*Peromyscus leucopus*). Lines uniting haplotypes indicate a single base pair difference; black circles represent unsampled haplotypes; and haplotypes designated with a letter and sample sizes are proportional to the relative size of circles.

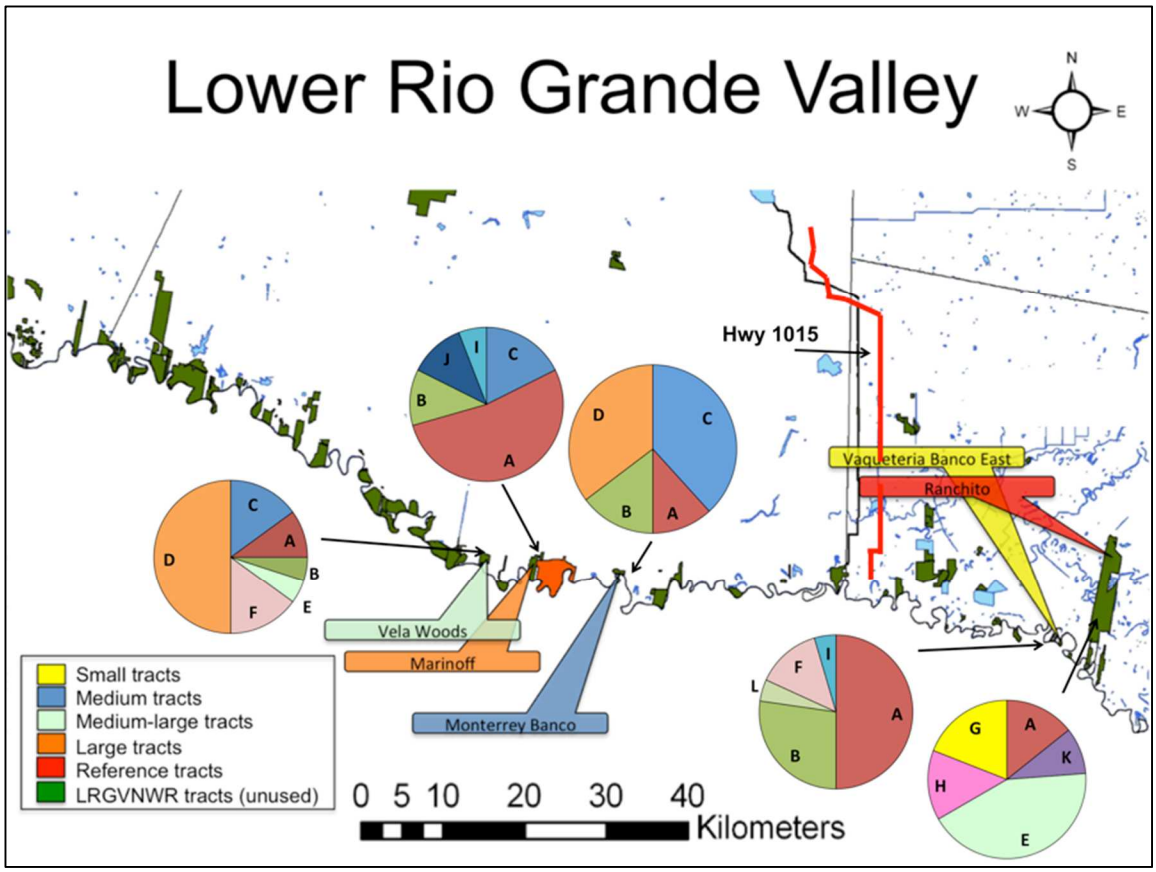

Figure 2.3 Map of Lower Rio Grande Valley with haplotype frequencies of each tract sampled.

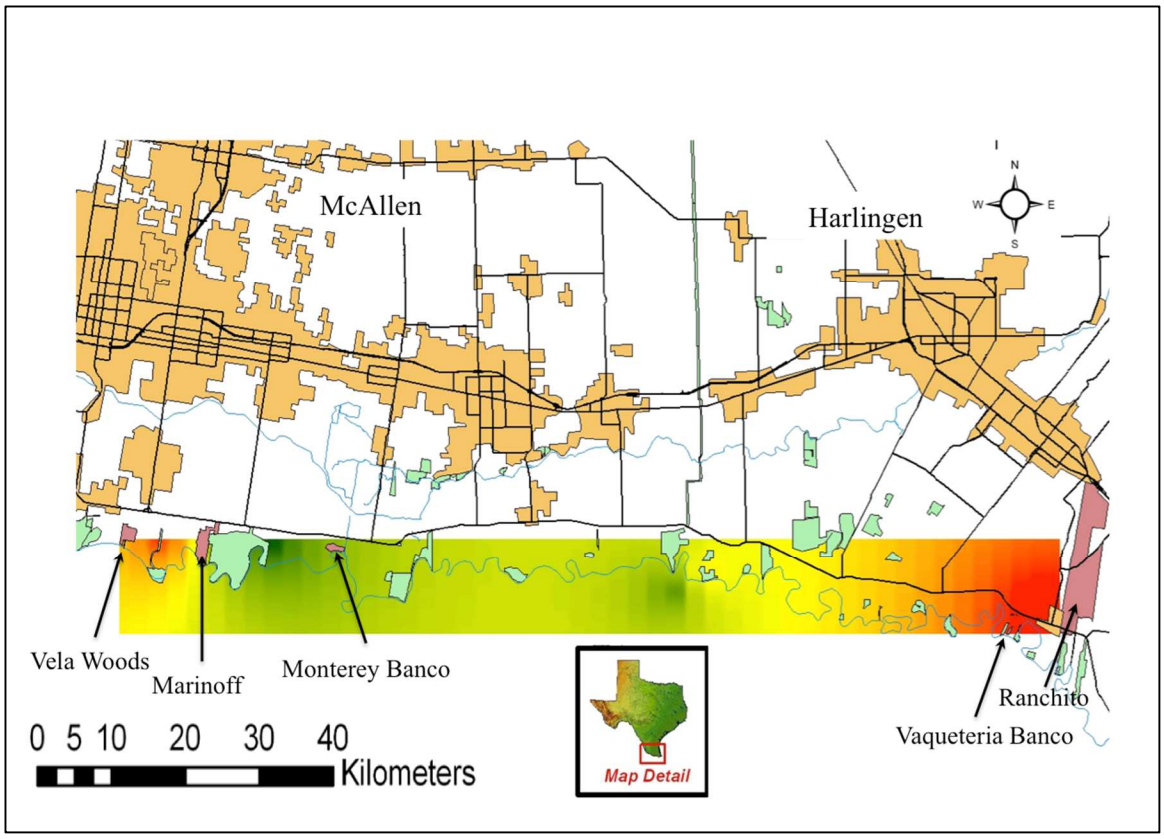

Figure 2.4 Map of Alleles in Space inter-individual genetic distance interpolation with Lower Rio Grande Valley (LRGV) reference. Inter-individual genetic distance ranges from low represented by green color to high represented by red. LRGV National Wildlife Refuge tracts colored in green and tracts sampled in pink. Black lines correspond to major highways. Areas with orange color indicate city/town zones.

APPENDIX

APPENDIX 1. Species capture and sex data by refuge tract with male (left), female (middle), and total (right and bold) from 4 sampling periods between December 2011 and January 2013. Tracts are arranged by size category from smallest to largest (small, 6−20 ha; medium, 20−43 ha; medium–large, 90−121 ha; large, 174−225 ha; and reference, >800 ha). Species are listed horizontally from most to least captured: *P.l.*, white-footed mouse (*Peromyscus leucopus*); *L.i.*, Mexican spiny pocket mouse (*Liomys irroratus*); *S.h.*, hispid cotton rat (*Sigmodon hispidus*); *R.f.*, fulvous harvest mouse (*Reithrodontomys fulvescens*); *B.t.*, northern pygmy mouse (*Baomys taylori*); *O.c.*, Coues' rice rat (*Oryzomys couesi*); *N.m.,* southern plains woodrat (*Neotoma micropus*); *O.l.*, northern grasshopper mouse (*Onychomys leucogaster*); and *R.r.*, roof rat (*Rattus rattus*).

			Species								
Tract	Size	Class	*P.l.*	*L.i.*	*S.h.*	*R.f.*	*B.t.*	*O.c.*	*N.m.*	*O.l.*	*R.r.*
Vaqueteria Banco East	14.4	Sm.	57/73/**130**	71/35/**106**	70/74/**144**						
Villitas Banco	20	Sm.	92/62/**154**	26/38/**64**	85/25/**110**	6/4/**10**	3/17/**20**				
Vaqueteria Banco	20	Sm.	62/65/**127**	44/13/**57**	22/52/**74**	26/41/**67**					
Culebron Banco	34	Med.	50/64/**114**	33/55/**88**	22/28/**50**	36/52/**88**					
Monterrey Banco	40	Med.	43/64/**107**	46/19/**65**	28/79/**107**	18/48/**66**	30/30/**60**				
Vela Woods	90	Med-Lg.	33/66/**99**	10/32/**42**	19/80/**99**	5/17/**22**	37/16/**53**	4/6/**10**			
Abrams West	96	Med-Lg.	39/49/**88**	117/53/**170**	4/10/**14**		40/42/**82**				
Garza-Cavazos	121	Med-Lg.	40/150/**190**	3/13/**16**	48/31/**79**	28/42/**70**					
Marinoff	174	Lg.	71/40/**111**	82/37/**119**	48/3/**51**	18/25/**43**	15/29/**44**		0/2/**2**	0/2/**2**	
La Parida Banco	179.5	Lg.	85/41/**126**	6/31/**37**	6/14/**20**	17/45/**62**	50/28/**78**		19/23/**44**		
Santa Maria	225	Lg.	15/18/**33**	40/12/**52**	3/18/**21**	33/44/**77**	30/30/**60**	99/18/**117**		9/6/**15**	
La Joya	825	Ref.	76/79/**155**	37/69/**106**	16/28/**44**	24/3/**27**					2/0/**2**
Santa Ana	844	Ref.	41/51/**92**	22/47/**69**	10/36/**46**		40/9/**49**	88/39/**127**	1/4/**5**	0/9/**9**	2/1/**3**
Ranchito	1557	Ref.	66/71/**137**	100/13/**113**	5/15/**20**	14/8/**22**	10/12/**22**	20/48/**68**	2/8/**10**		
TOTAL			770/893/**1663**	637/497/**1134**	194/790/**984**	225/356/**581**	255/213/**468**	211/109/**320**	61/73/**134**	9/17/**26**	4/1/**5**

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