SOIL AND VEGETATIVE ASSOCIATIONS OF HETEROMYID RODENTS IN CENTRAL AND SOUTH TEXAS WITH COMMENTS ON TRAPPING TECHNIQUES

by

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TABLE OF CONTENTS

Page

LIST OF TABLES

Table **Page**

LIST OF FIGURES

Figure **Page**

ABSTRACT

Heteromyid rodents occur in arid and semiarid lands in western North America, and are primarily granivorous. Heteromyids often form guilds because of a shared food source. These guilds often are found in habitats with sandy soils and vegetation that offers both open areas and dense shrub cover. In this study, I investigated soil and vegetative associations for heteromyid communities at the landscape and microhabitat scales in Central and South Texas. I utilized captures as a proxy for abundance. As a minor objective, I investigated the capture success of *Dipodomys compactus*, the most trap-shy heteromyid species included in this study, for one season of trapping. I placed traps in each representative treatment (a combination of both land cover and soil type) on consecutive nights for three seasons on two study sites (Guadalupe County and Jim Hogg County). I assessed microhabitat parameters, including herbaceous cover of grasses and forbs, bare ground, leaf litter, and densiometer readings within each treatment for all seasons on both sites. For the landscape level analyses, I conducted a chi-square goodness of fit test to determine if captures of *Chaetodipus hispidus*, *Dipodomys compactus*, and *Perognathus merriami* differed per treatment. I conducted a simple linear regression model for each microhabitat parameter per species per site. Overall capture success for the Guadalupe County study site for all heteromyids within all seasons for 2,816 trap nights was 2.06% and overall capture success for the Jim Hogg study site for all heteromyids within all seasons for 2,646 trap nights was 19.16%. For the landscape level analyses, capture was significantly different per treatment for each

species on both study sites. For the microhabitat analyses on the Jim Hogg County study site, herbaceous cover and bare ground were significant predictors of occurrence of *C. hispidus* with a positive trend observed for herbaceous cover (β = 0.1259, R^2 = 0.1516, P = 0.0276), and a negative trend observed for bare ground (β = -0.2156, R^2 = 0.2477, P = 0.0038). No other microhabitat parameters were deemed significant for the other species on either site. For the paired trap study, extra-large (10.16x11.43x38.1 cm) folding H.B. Sherman traps had the highest probability of capture success for *D. compactus*. I determined that selection for or avoidance of certain land cover and soil types on the landscape scale could suggest potential habitat partitioning by heteromyid species. If a treatment was neither selected for nor avoided, then that indicates that a heteromyid species occurred as expected within that treatment, based on the overall availability of the particular land cover category and soil type. Microhabitat parameters were not important predictors of occurrence on the Guadalupe County study site, perhaps because of a homogeneous landscape, when compared with the Jim Hogg County study site, which offers more heterogeneity for heteromyid species.

I. INTRODUCTION

The family Heteromyidae within Rodentia includes the genera *Dipodomys* (kangaroo rats), *Microdipodops* (kangaroo mice), *Chaetodipus* and *Perognathus* (pocket mice), and *Heteromys* and *Liomys* (spiny pocket mice) (Wahlert 1993). Heteromyids occur in arid and semiarid lands in western North America, and are primarily granivorous (Brown and Harney 1993). Heteromyids affect arid ecosystems by physically modifying the environment by moving soil (e.g., burrowing, caching), consuming and dispersing seeds, and facilitating the germination of seeds through the propagation of plants from caches (Lemen and Rosenzweig 1978, Price and Jenkins 1986, Brown and Harney 1993, Reichman and Price 1993, Price et al. 2000, Longland et al. 2001, Geluso 2005). Heteromyids may be instrumental in maintaining plant community structure in desert ecosystems, especially for large-seeded annual plants (Brown et al. 1986). These rodents often form guilds because of a shared food source, and these guilds often are found in habitats with sandy soils and vegetation that offers both open areas and dense shrub cover (Brown and Harney 1993).

The Gulf Coast kangaroo rat (*Dipodomys compactus*), hispid pocket mouse (*Chaetodipus hispidus*), and Merriam's pocket mouse (*Perognathus merriami*) are present in central Texas (Paulson 1988, Baumgardner 1991, Best and Skupski 1994, Schmidly 2004). These species, along with Ord's kangaroo rat (*Dipodomys ordii*) and Mexican spiny pocket mouse (*Liomys irroratus*) are present in South Texas, with *L. irroratus* occupying habitats of the Rio Grande Valley in extreme South Texas (Dowler and Genoways 1978, Garrison and Best 1990, Schmidly 2004).

Each species within the genus *Chaetodipus* overlaps in range with another species within the genus. In addition, *C. hispidus* is the most widely distributed species within its genus (Schmidly et al., 1993). Similarly, *D. ordii* has the broadest distribution of any heteromyid (Schmidly et al., 1993). The distribution of *L. irroratus* is also extensive compared to its congeners (Schmidly et al., 1993). Because *C. hispidus, D. ordii*, and *L. irroratus* have large geographic ranges, they might be able to tolerate a wide range of environmental conditions, maintain high population densities in many habitats, and coexist with many other species. Other species with a more restricted geographic range, such as *P. merriami*, and *D. compactus*, may have limited tolerance of environmental conditions, and also coexist with fewer species (Brown and Harney, 1993; Schmidly, 2004).

Within arid and semiarid habitats of western North America, species richness can be high, with some rodent assemblages including over fifteen different species (Brown and Harney 1993). These rodent assemblages can include granivores other than heteromyids, i.e., *Baiomys*, *Peromyscus*, and *Reithrodontomys*, and omnivores on occasion, i.e., *Onychomys* (Brown and Harney 1993, Stapp 1997). However, heteromyids are the dominant guild, with cricetids comprising less than 50% of the individuals in most assemblages (Brown and Harney 1993).

Functional groups based on locomotion (i.e., bipedal heteromyids [*Dipodomys, Microdipodops*], quadrupedal heteromyids [*Chaetodipus, Heteromys, Liomys, Perognathus*], quadrupedal cricetids [*Baiomys, Peromyscus*, and *Reithrodontomys*]) have also been examined in rodent assemblages. Brown and Kurzius (1987) found that it is more likely for members of different functional groups (i.e., bipedal and quadrupedal heteromyids, and quadrupedal heteromyid and cricetids) to occur together than to occur with members of their same functional group. However, they also found that bipedal heteromyids are more likely to occur with quadrupedal heteromyids than quadrupedal cricetids, suggesting that quadrupedal heteromyids outcompete quadrupedal cricetids (Brown and Kurzius 1987). Habitats with sandy soils and vegetation that includes both open patches and dense cover have the highest species diversity of each functional group (Rosenzweig and Winakur 1969, Brown 1975, Brown and Harney 1993). When ranges overlap, bipedal heteromyids are typically associated with open areas (sparseness of vegetation), while quadrupedal heteromyids are associated with denser vegetation (herbaceous or shrub cover) (Rosenzweig and Winakur 1969, Rosenzweig 1973, Lemen and Rosenzweig 1978).

Differences in heteromyid body size and means of locomotion may influence foraging strategies (Thompson 1982). Seed size selection may be positively correlated with body size (Brown and Lieberman 1973, Brown and Harney 1993), and seed-caching behavior (scatterhoarding and larderhoarding) can also promote coexistence for heteromyids (Price et al. 2000). Coexistence within the functional group of bipedal heteromyids can also be driven by habitat selection, with one species avoiding competition by selecting a habitat that is not preferred by other species (Schroder and Rosenzweig 1975, Schroder 1987, Baumgardner and Schmidly 1985). Community structure and species composition can also be attributed to predation of heteromyids by vertebrate predators, including squamate predators (e.g., snakes), avian predators (e.g., owls, hawks), and mammalian carnivores (Brown and Harney 1993). There is further evidence that microhabitat use by heteromyids can be altered by actual and perceived predation risk (see Brown and Harney 1993).

Recently published literature is limited for heteromyids occupying arid lands of South Texas, and the accounts that are available focus on the taxonomic history for species groups (Baumgardner and Schmidly 1981, Coyner et al. 2010, Andersen and Light 2012). Detailed habitat requirements for South Texas heteromyids are only reported for the genus *Dipodomys*. Recent studies depict soil and vegetative requirements, along with microhabitat use, at the northern extent of the range for *D. compactus* in Central Texas, i.e., Guadalupe County (Oakley 2012, Phillips 2012). Oakley (2012) found that active *D. compactus* burrows were associated with sparse tree canopy cover, low percent cover of leaf litter, high percent cover of bare substrate, and high percent cover of forbs. Active burrows were present in areas with fine sand (Patilo and Arenosa soils [PaD] and Arenosa fine sand [ArD]), but were not present in areas with clayey or loamy soils (Nebgen-Judd Complex [NcF], Windthorst fine sandy loam [WdC3], and Demona loamy fine sand [DmC]) (Oakley, 2012). Baumgardner and Schmidly (1981, 1985) described soil and vegetation associations of *D. compactus* and *D. ordii* in an area of sympatry in South Texas (i.e., Jim Hogg and Zapata Counties). Suitable soil for *D. compactus* consisted of loose surface soil in contrast with more compacted soil suitable for *D. ordii* (Baumgardner and Schmidly 1985). Suitable habitat for *D. compactus* consisted of sparse vegetation (*Opuntia* sp., *Prosopis* sp., *Acacia* sp., and scattered weeds and grasses), approximately a meter or less in height, spaced at three to four meter intervals (low and open) (Baumgardner and Schmidly 1985). Suitable habitat for *D. ordii* consisted of closely spaced vegetation (woody and herbaceous, including the same species above), approximately two meters in height, spaced at one to two meter intervals (mature) (Baumgardner and Schmidly 1985). Similar habitat investigations have not been conducted for the other heteromyids occupying South Texas.

Microhabitat data are important to make inferences about species' occurrence in particular habitats (Inger and Wilson 1996). These data may also explain requirements of one species when associated with a second species (Brown and Harney 1993). Knowledge of microhabitat requirements for a species or group of species benefits conservation and management decisions (Inger and Wilson 1996).

Community assemblage data are important, especially if one species within that assemblage is rare (relative to detectability), or elusive to capture (McDonald 2004). Capture success in previous trapping efforts for *D. compactus* did not exceed 5%. Phillips (2012) recorded 2-3% capture success in the northern part of the species' range and Baumgardner and Schmidly (1985) had a 4% capture success in the southern extent of the species' range. Similarly, Rissel (2011) obtained 5% capture success for *D. compactus* on the barrier islands of Texas. Much greater trap success has been recorded for other species of *Dipodomys* (5-15%) (Chew and Butterworth 1964, Reichman and Van De Graaff 1973, Daly et al. 1980, O'Farrell and Uptain 1987, Monasmith et al. 2010, Vasquez and Alvarez-Castaneda 2014). Capture success for *C. hispidus* in Nebraska was at approximately 16% (Geluso and Wright 2010), and trap success for *Perognathus* species (i.e., *P. amplus*, *P. baileyi*, *P. intermedius*, *P. longimembris*, *P. penicillatus*) ranged from approximately 6% to 38%, with an average of those values comparable to the capture success of *C. hispidus* above (Reichman and Van De Graaff 1973, Rosenzweig 1973).

In this study I investigated the soil and vegetative associations for heteromyid species at landscape and microhabitat scales in Central and South Texas. Previous research has been conducted on the Central Texas site in Guadalupe County (Oakley 2012, Phillips 2012). Although previous research has not been conducted on the South Texas site in Jim Hogg County, Baumgardner and Schmidly (1981, 1985) have produced publications based upon their extensive trapping efforts within Jim Hogg County and neighboring counties of South Texas. As a secondary objective, I investigated the capture success of *Dipodomys compactus*, the most trap-shy (xenophobic) heteromyid species included in this study, on both sites during one season of trapping (spring).

II. STUDY AREA

Guadalupe County

For the Central Texas study site, I conducted my research on Diamond Half Ranch (ca. 2,303 ha), located approximately 12 km south of Seguin, and directly east of State Highway 123 (29.428875°N, 97.950468°W; WGS 84), within Guadalupe County, Texas. This site is actively managed for grazing cattle and hunting. Diamond Half Ranch falls within the Post Oak Savannah Ecoregion of Texas (Gould et al. 1960) on the Carrizo Sands (McBryde 1933), and is dominated by deciduous forest (ca. 1,263 ha), shrub/scrub (ca. 591 ha), pasture/hay (ca. 364 ha), and grassland/herbaceous (ca. 57 ha) upland cover types, with small open water (ca. 0.5 ha) ponds scattered throughout (Fig. 1, Fry et al. 2011). Black-jack oak (*Quercus marilandica*) and post-oak (*Quercus stellata*) are the dominant canopy species within the deciduous forest habitat, with American beautyberry (*Callicarpa americana*) and little bluestem (*Schizachyrium scoparium*) present within the understory. The shrub/scrub habitat type is composed of forbs [hogwort (*Croton capitatus*) and plains snakecotton (*Froelichia floridana*)], grasses [thin paspalum (*Paspalum setaceum*), rosette grass/panicgrass (*Dichanthelium* sp.), and little bluestem], and sedges (*Carex* sp.) scattered throughout. The shrub/scrub habitat also includes scattered cactus (*Opuntia* sp.) and Texas Queen's delight (*Stillingia texana*) in areas that are not managed for cattle. Introduced Bermuda grass (*Cynodon dactylon*) dominates the pasture/hay habitat, along with thin paspalum, rosette grass/panicgrass, little bluestem, and sandbur (*Cenchrus incertus*). The grassland/herbaceous land cover type is dominated by plains snakecotton, and various grasses including little bluestem, thin paspalum, Bermuda grass, and sandbur, with sedges (*Carex* sp.) scattered throughout.

Dominant soils within the uplands include Patilo and Arenosa (PaD, ca. 1,921 ha) and Arenosa fine sand (ArD, ca. 275 ha) soil types, moderately well-drained or somewhat excessively-drained soils, respectively, with depth to the water table at least 1.2 m (1.2-1.8 m for PaD, and over 2 m with ArD), and depth to the restrictive feature over 2 m (Fig. 2, USDA/NRCS 1995). Lithic bedrock is the only restrictive feature in association with the soils on the property, a component present at 0.1 to 0.4 m in the Nebgen-Judd Complex (NcF, ca. 67 ha).

Jim Hogg County

My South Texas study site was the Palangana Ranch (ca. 3,294 ha), located in Jim Hogg County, Texas, approximately 28 km south of Hebbronville, and five km west of Farm to Market Road 1017 (29.055316°N, 98.658282°W; WGS 84). The site falls within the South Texas Plains Ecoregion on the South Texas sand sheet (Gould et al. 1960), and is dominated by grassland/herbaceous (ca. 2,944 ha) and shrub/scrub (ca. 252 ha) upland cover types (Fig. 3, Fry et al. 2011). The grassland/herbaceous land cover type is dominated by forbs including prairie tea (*Croton monanthogynus*), widow's tears (*Commelina erecta*), hoary milkpea (*Galactia canescens*), partridge pea (*Chamaecrista fasiculata*), woolly croton (*Croton capitatus* var. *lindheimeri*), and amaranth (*Amaranthus* sp.). Grasses include sandbur, rosette grass or panicgrass, lovegrass, buffel grass (*Pennisetum ciliare*), and windmill grass (*Chloris* sp.), along with flatsedge. The shrub/scrub habitat type is composed of forbs including prairie tea, scarlet pea

(*Indigofera mineata*), slender dwarf morning-glory (*Evolvulus alsinoides* var. *angustifolius*), Texas vervain (*Verbena halei*), hoary milkpea, and widow's tears, with weedy species of ragweed (*Ambrosia* sp.), and amaranth present. Grasses include sandbur, thin paspalum, tanglehead (*Heteropogon contortus*), lovegrass (*Eragrostis* sp.), and buffel grass, along with flatsedge (*Cyperus* sp.).

Soils within the uplands include Delmita soils (Dl, ca. 1,380 ha), Nueces-Sarita association (Ns, ca. 1,319 ha), Brennan fine sandy loam (Br, ca. 323 ha), Delmita Association (Dn, ca. 194 ha), and Randado-Delmita association (Rd, ca. 87 ha), all moderately well-drained or well-drained soil types, with depth to the water table over 2 m, and depth to the restrictive feature at least 0.5 m (0.5-1 m to petrocalcic for Dl and Dn, and over 2 m for Ns and Br) (Fig. 4, USDA/NRCS 1995). The Cuevitas-Randado association (Cu), an excavated area of Comitas soil (Cm), and a caliche pit (CLP), comprise a minor component of the site (ca. 11 ha).

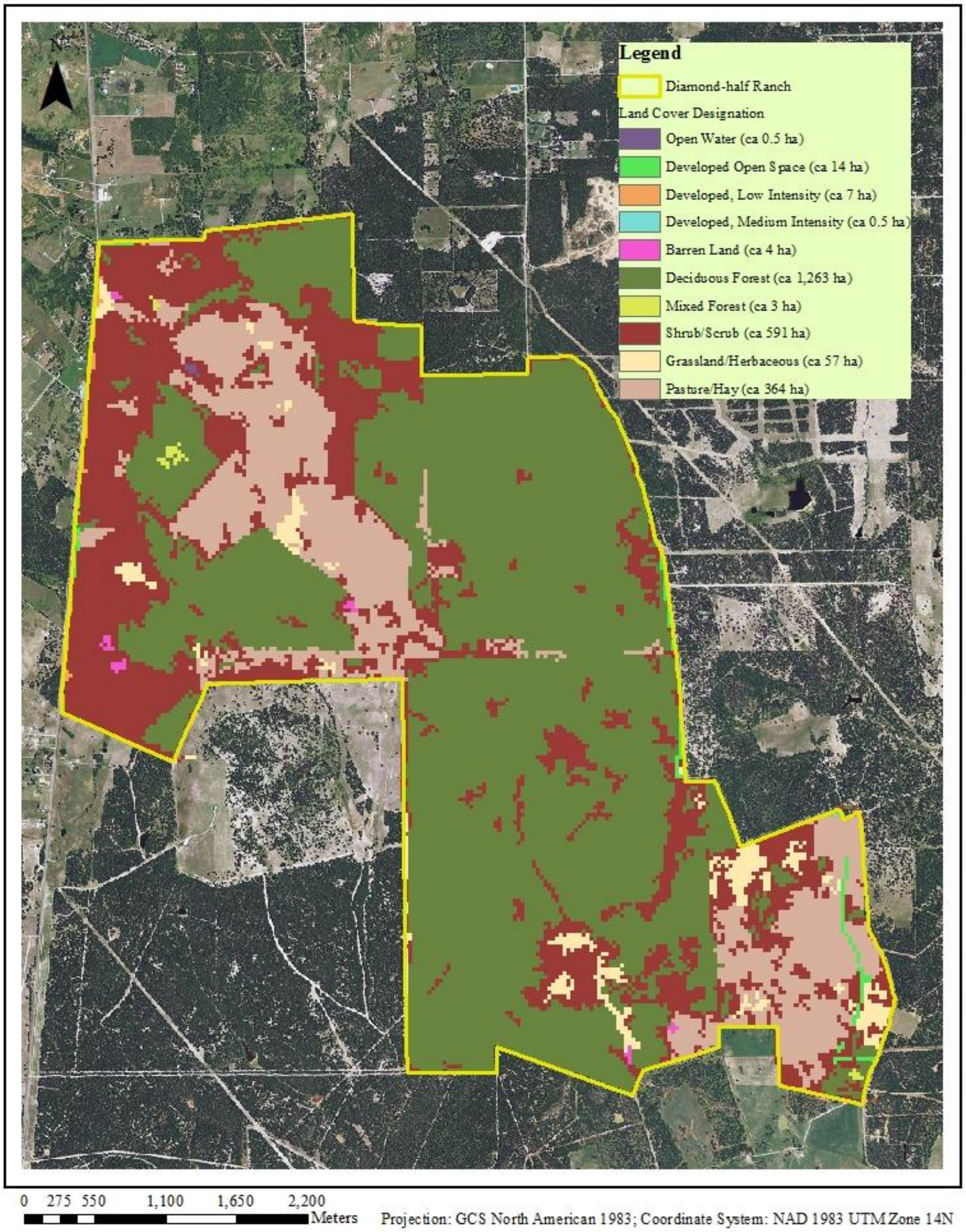

Figure 1: Land cover map of Diamond Half Ranch in Guadalupe County, Texas.

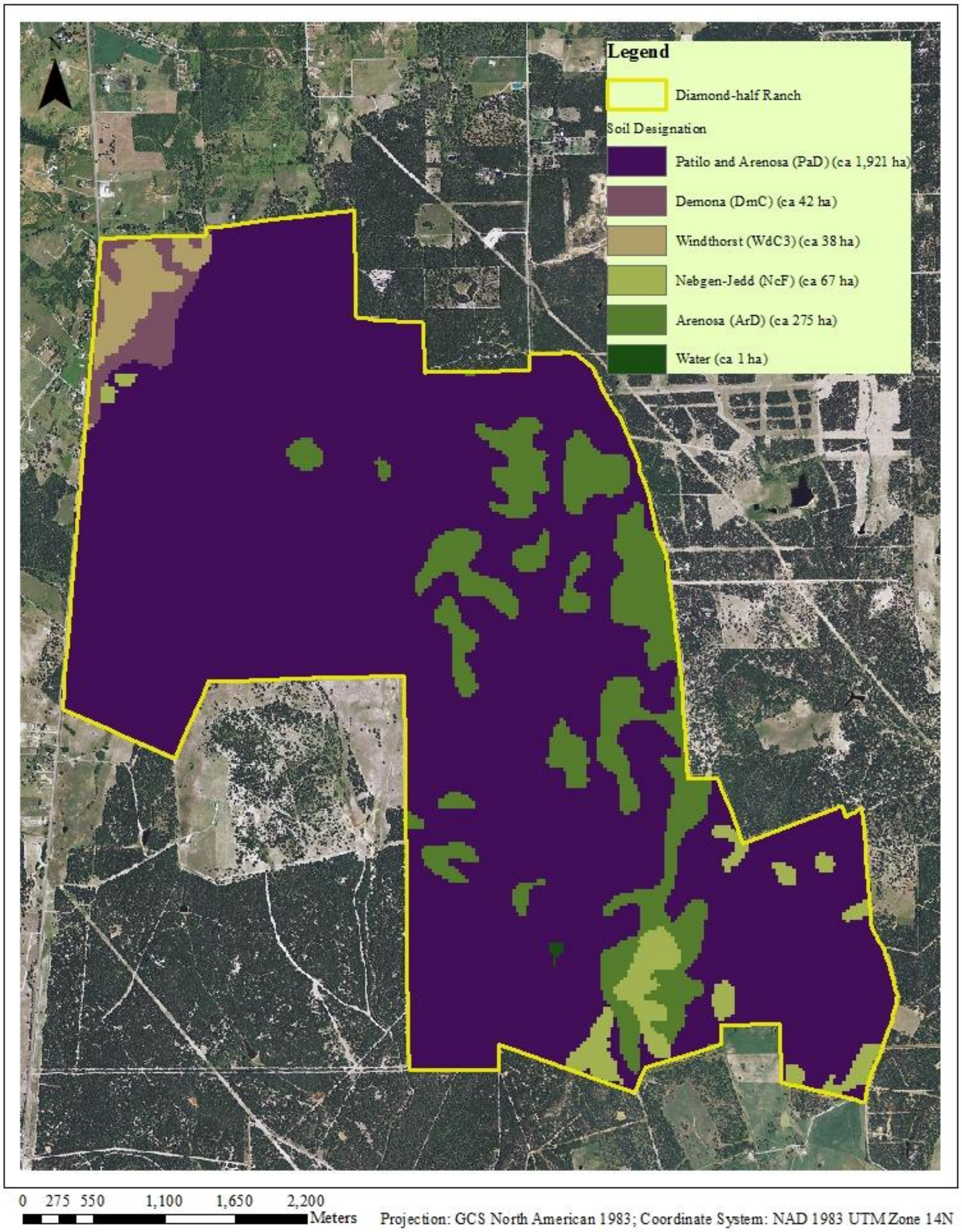

Figure 2: Soil map of Diamond Half Ranch in Guadalupe County, Texas.

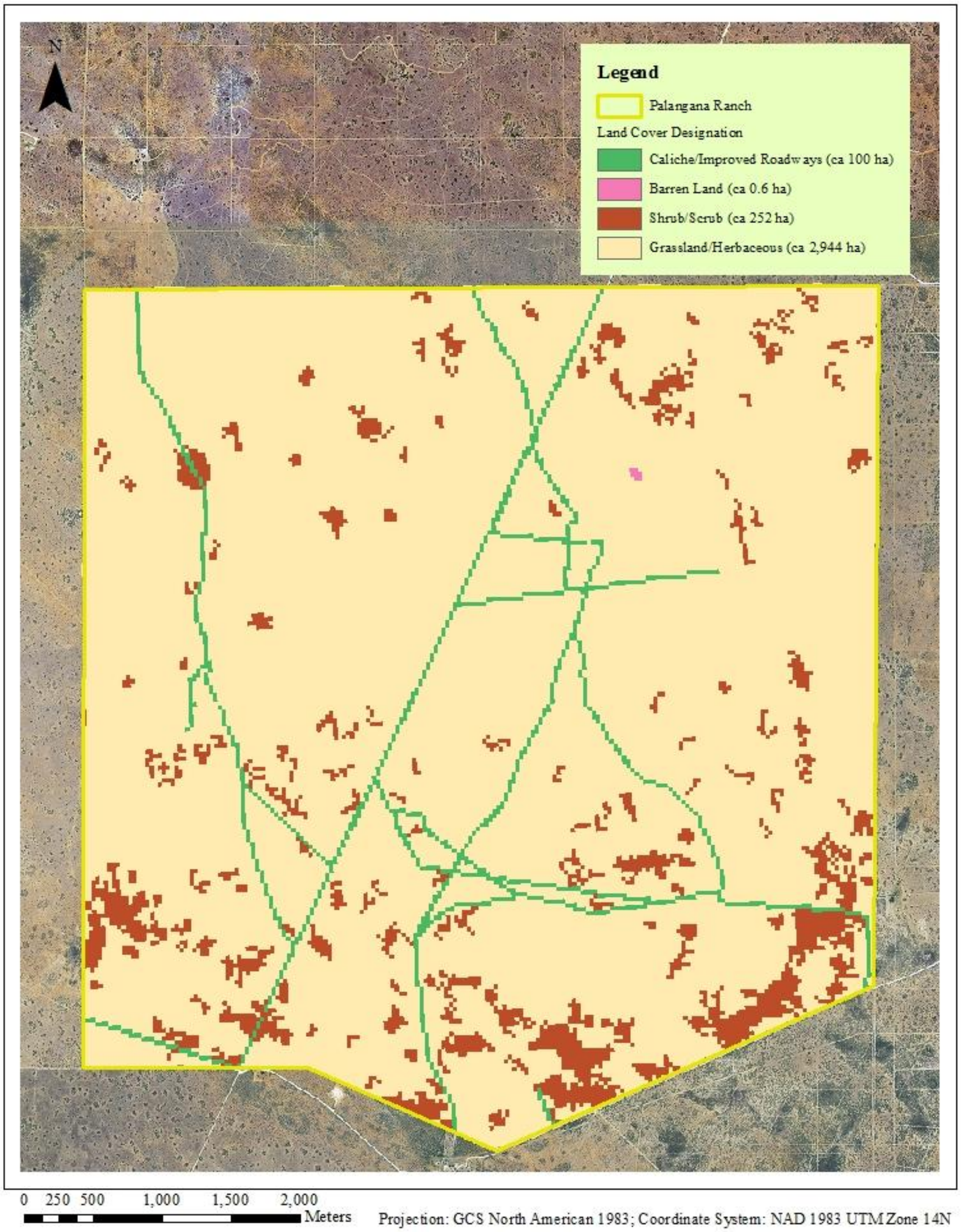

Figure 3: Land cover map of the Palangana Ranch in Jim Hogg County, Texas.

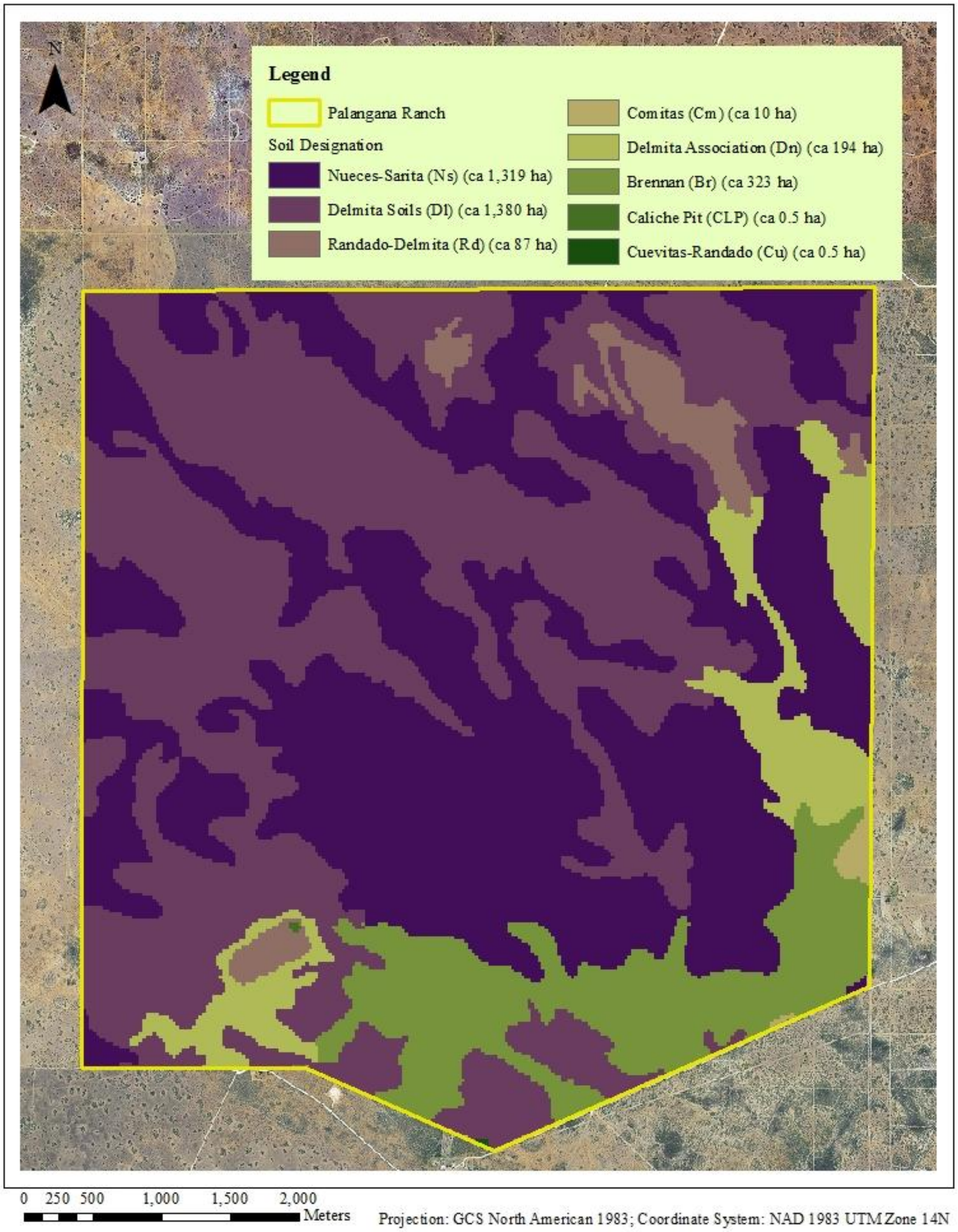

Figure 4: Soil map of the Palangana Ranch in Jim Hogg County, Texas.

III. METHODS

Guadalupe County

Presence Surveys.−I obtained baseline data regarding the presence or absence of heteromyids on the Diamond Half Ranch from 2011 and 2012 (Oakley 2012). In Oakley's (2012) study, 57 randomly distributed points (generated by ArcGIS software) were evaluated for the presence of *D. compactus* burrows by determining active burrow entrances within a 10 m radius of the center point. I duplicated this effort in June 2013 by re-evaluating 56 of the randomly distributed points to confirm the presence of heteromyid burrows prior to selecting trapping locations.

Trapping Locations.− Using ArcGIS software (ESRI 2011, ESRI 2013), I examined the U. S. Department of Agriculture, Natural Resource Conservation Service (USDA/NRCS 1995) soil types where heteromyid burrows were observed during the 2012 and 2013 surveys. Heteromyid burrows were found on the dominant soil types of Patilo and Arenosa (PaD) and Arenosa fine sand (ArD) soil types, and were not present on the minor soil types (<7% of the total area), specifically, Demona loamy fine sand (DmC), Nebgen-Jedd complex (NcF), Windthorst fine sandy loam (WdC3), which include some component of loam (loamy fine sand or fine sandy loam). Therefore, the PaD and ArD soil types were determined suitable for heteromyids and were included in the study. Again, using ArcGIS, I examined the National Land Cover Database (Fry et al. 2011) land cover classes where heteromyid burrows were present during the 2012 and 2013 surveys. I excluded the following classes: open water, developed land (developed, open space; developed, low intensity; developed, medium intensity), barren land, deciduous forest, and mixed forest, given that these cover types were either infrequently encountered at the study sites or were already known not to be habitat for heteromyids. I combined the pasture/hay and grassland/herbaceous land cover classes into one category, because the physical validation of habitat during the 2013 survey did not reveal a difference between the two classes. I combined soil types and the land cover classes to establish unique treatments that included soil and land cover data. I determined trapping locations within each representative soil and land cover treatment based upon the presence of burrows during the presence surveys conducted in 2012 and 2013, and I did not include a trap location associated within a soil and land cover treatment if burrows were absent during both the 2012 and 2013 surveys (i.e., I trapped only where heteromyids were known to exist as indicated by the presence of burrows). Because a few treatments did not have a randomly generated point within their boundary (from the 2012 survey), I surveyed these treatments for the presence of burrows. I incorporated one additional treatment area into the trapping plan (a randomly generated point from the 2012 survey was not associated with this treatment) due to the presence of burrows. I included the following treatments in this study: shrub/scrub land cover with Patilo and Arenosa soils (hereafter, Shrub-PaD), shrub/scrub land cover with Arenosa fine sand (hereafter, Shrub-ArD), pasture/hay/grassland/herbaceous land cover with Patilo/Arenosa soils (hereafter, Grassland-PaD), and pasture/hay/grassland/herbaceous land cover with Arenosa fine sand (hereafter, Grassland-ArD).

Trapping Effort.—I placed large (7.62x8.89x22.86 cm) folding H. B. Sherman small mammal live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida; hereafter, Sherman traps), baited with oats and mixed bird seed, in each representative soil and land cover treatment suitable for heteromyids. I placed Sherman traps in the general vicinity of each selected point (randomly generated from the 2012 surveys) within the treatments. I placed Sherman traps over 30 m from treatment boundaries to ensure that Sherman traps remained within the interior of each soil and land cover treatment, and not along the periphery. I placed traps approximately 10 m apart along a linear transect. At some points within a treatment, I placed multiple trap lines in a field or in natural areas on either side of an unimproved road, essentially forming a small grid. I trapped three to four consecutive nights in August 2013 (summer), December 2013 (winter), and March 2014 (spring) to obtain capture success per treatment. I used capture success as an indicator of abundance for each species within each treatment type to determine use of the various habitats by heteromyid species. I set 200 Sherman traps in the summer, 198 in the winter, and 408 in the spring. I placed traps in proportion to the treatment area (with approximately one trap per every five ha in the summer and winter, and approximately one trap per every 2.5 ha in the spring), with a minimum of six traps within the smallest treatment area in a given season (Table 1). I maintained consistency during each season by placing traps at the same points within the same soil and land cover treatments on the property. If an area associated with a point within a certain treatment type was managed (i.e., disked, fertilized, or altered for the grazing of cattle) prior to a trapping event, an alternate point associated with that treatment type was selected.

During spring trapping I evaluated capture success of four different live trap types: large (7.62x8.89x22.86 cm) folding H.B. Sherman traps (hereafter, and as above, Sherman traps), new unused large (7.62x8.89x22.86 cm) folding H.B. Sherman traps (hereafter, clean traps), wire mesh Fitch (1950) traps (hereafter, Fitch traps), and extra-large (10.166x11.43x38.1 cm) folding H.B. Sherman traps (hereafter, long traps). I also evaluated two different bait types: oats with mixed bird seed (hereafter, regular bait), and an oats, peanut butter, and vanilla extract mixture (hereafter, specialty bait). I used the large folding Sherman trap as my "standard" trap, and baited this trap with the regular bait. I paired the standard trap with regular bait with one of the following trap/bait combinations: clean trap with regular bait, Fitch trap with regular bait, long trap with regular bait, and Sherman trap with specialty bait.

Jim Hogg County

Presence Surveys.−Because baseline data regarding the presence of heteromyids on this property did not exist, I conducted road cruising and pedestrian surveys in July 2013 (summer) to determine areas where heteromyid burrows were present and concentrated. I placed a total of 110 Sherman traps in various locations across the landscape for one night to verify the presence of heteromyids on the Palangana Ranch.

Trapping Locations.−Following the presence survey, I conducted a desktop analysis of the soil types and land cover classes on the ranch comparable to those on the study site in Guadalupe County. I utilized soil (USDA/NRCS 1995) and land cover (Fry et al. 2011) information to determine trap locations. I included all soil types on the property except for a caliche pit (CLP), an excavated area (Cm), and soils with a depth to the restrictive feature beginning at 0.2 m (Rd and Cu). I included both land cover classes present on the property (shrub/scrub and grassland/herbaceous). I compared the representative soil and land cover treatments on the property to areas outside of the property boundary, but still within Jim Hogg County, with known capture records of *D. compactus* and *D. ordii* (Baumgardner and Schmidly 1985, Biodiversity Research and

Teaching Collection at Texas A&M University, accessed 3 May 2013) to ensure that the treatments on the study site were suitable trap locations for heteromyids. Using ArcGIS software, I generated 30 randomly distributed points (within the property boundary) to overlay onto the soil and land cover layers, and selected trap locations within each representative soil and land cover treatment based upon ease of access and distribution across the site, regardless of burrow presence or absence. Sherman traps were placed within each representative soil and land cover treatment, regardless of previous capture efforts for heteromyids on that soil type and/or land cover class. I included the following treatments in this study: grassland/herbaceous land cover with Delmita soils (hereafter, Grassland-Dl), grassland/herbaceous land cover with Nueces-Sarita association soils (hereafter, Grassland-Ns), grassland/herbaceous land cover with Brennan fine sandy loam soils (hereafter, Grassland-Br), and grassland/herbaceous land cover with Delmita Association soils (hereafter, Grassland-Dn), shrub/scrub land cover with Delmita soils (hereafter, Shrub-Dl), shrub/scrub land cover with Nueces-Sarita association soils (hereafter, Shrub-Ns), shrub/scrub land cover with Brennan fine sandy loam soils (hereafter, Shrub-Br), shrub/scrub land cover with Delmita Association soils (hereafter, Shrub-Dn).

Trapping Effort.−For the Palangana, I duplicated the trapping methodology used on the Diamond Half Ranch. I also trapped within each season (excluding the fall) during consecutive nights (three to four consecutive night periods) to obtain capture success per treatment. I used capture success as an indicator of abundance for each species within each treatment type to determine use of the various habitats by heteromyid species. I trapped in September 2013 (summer), January 2014 (winter), and May 2014 (spring). I set 170-230 Sherman traps in the summer (170 Sherman traps were set the initial trap night, and 230 Sherman traps were set on subsequent nights), 200 in the winter, and 354 in the spring. I placed traps in proportion to size of treatment areas (with approximately one trap per every 15 ha in the summer and winter, and one trap per every eight ha in the spring), with a minimum of eight traps within the smallest treatment area in a given season (Table 2). I maintained consistency during each season by placing traps within the same soil and land cover treatments on the property. In addition, I implemented a paired trap study in the spring, by duplicating the methodology used on the Guadalupe County study site.

Species Identification

One kangaroo rat species, *D. compactus*, has been documented on the Guadalupe County study site of Diamond Half Ranch in recent studies (Oakley 2012, Phillips 2012). Because *C. hispidus* and *P. merriami* are the only additional heteromyids with overlapping ranges on the site (Schmidly 2004), these are the only three species of heteromyid rodents expected to be present on the Guadalupe County study site.

Both *C. hispidus* and *P. merriami* are the only known species from their respective genera occupying habitats in South Texas (Paulson 1988, Best and Skupski 1994). Present in extreme South Texas, *L. irroratus* is outside of the range of the Jim Hogg County study site (Dowler and Genoways 1978). Both *D. compactus* and *D. ordii* have overlapping ranges on the South Texas mainland (Garrison and Best 1990, Baumgardner, 1991), and are morphologically similar (Desha 1967, Johnson and Selander 1971, Schmidly 1971, Stock 1974, Schmidly and Hendricks 1976, Kennedy and

Schnell 1978, Kennedy et al. 1980, Baumgardner and Schmidly 1981, Garrison and Best 1990, Baumgardner 1991, Baumgardner and Kennedy 1993). External measurements collected on live captured *Dipodomys* from the Jim Hogg County study site strongly suggests that only *D. compactus* was captured during this study. Therefore, all captures are recorded as *D. compactus* until genetic analyses to confirm species identity can be conducted.

For each captured individual, I collected the following data: site, date, location of capture (point within treatment), trap type, bait type, species, sex, and status of reproductive maturity (juvenile or adult). Additional notes were taken on reproductive condition (non-reproductive, scrotal, lactating, or pregnant) when appropriate. For *Dipodomys*, I collected additional morphological measurements, including weight, hind foot length, ear length, tail length, body length, and total length. I also collected a tissue sample (ear tissue) from captured *Dipodomys* to use for genetic analyses at a later date. I vouchered specimens representative of each taxa and cataloged them into research and teaching collections at Texas State University. The capture and handling of animals was approved by the Texas State University-San Marcos Intuitional Animal Care and Use Committee (IACUC) protocol number 1109-0817-09 and the Texas Parks and Wildlife Department (TPWD) Scientific Permit number SPR-0993-638.

Vegetative Surveys to Quantify Microhabitat

I determined vegetative composition on both study sites using the Daubenmire frame technique (Daubenmire 1959) recording percent cover of bare ground, leaf litter or woody debris, and herbaceous species (grasses and forbs). In addition, I used a spherical densiometer (Adler and Wilson 1987) at each Daubenmire frame to determine percent cover of shrub and canopy species. The vegetative analysis was conducted during every season of trapping at all locations in which Sherman traps were set.

Statistical Analyses

Landscape Level Analyses.−I conducted chi-square analyses to determine if captures differed per treatment (combination of soil and land cover designations) at the landscape scale. I analyzed each study site separately because soil treatments are not replicated between the two sites, a reflection of different soil origins (i.e., Carrizo Sands versus South Texas sand sheet). For each study site, I conducted a chi-square goodness-of-fit test to determine if captures for each heteromyid species differed per treatment for all seasons combined. I then used the chi-square test statistic to produce a value of determination based upon the number of treatments available for each heteromyid species (i.e., value of determination = χ^2 / number of treatments). The value of determination served as a benchmark to infer whether there was selection for or avoidance of a given land cover and soil type treatment. Treatments with an $((O_i-E_i)^2)/E_i$ value that is greater than the value of determination indicated selection for (if $O_i-E_i > 0$) or avoidance of (if $O_i-E_i < 0$) the treatment.

Microhabitat Analyses.−I conducted all microhabitat analyses in R v3.3.0 (R Core Team 2016). I used simple linear regression models to determine if each component of the landscape at the microhabitat level (i.e., herbaceous cover of forbs and grasses, bare ground, leaf litter, and densiometer readings representing shrub and canopy cover) were important predictors of capture success (representing abundance) for each species for each site. Data from the Daubenmire vegetation surveys allowed for a test of habitat associations at a finer spatial scale (i.e., microhabitat) than the previously described analyses of land cover and soil type treatments.

Paired Trap Analyses.− I conducted the paired trap analyses in R v2.15.1 (R Core Team 2012). I used a logistic regression, in combination with a likelihood ratio test (chi-square analysis), to identify significant parameters associated with the capture of *D. compactus*. Captures from every treatment for all seasons were included in the analyses. I used site and trap type as predictor variables. Site is a factor with two levels (the Guadalupe County study site and the Jim Hogg County study site), and trap type is a factor with five levels (Sherman trap with regular bait, clean trap with regular bait, Fitch trap with regular bait, long trap with regular bait, and a specialty bait used in the standard Sherman trap). Because the specialty bait was placed in standard Sherman traps only, it is also classified as a specific trap type. I coded the response variable, captures, as binary (0 or 1). I evaluated three logit models: a model with site as a predictor, a model with trap type as a predictor, and a model with both site and trap type as predictor variables. I then determined what factors were causing significance. By determining the factors significant for the capture of *D. compactus*, this suggested selection of one trap type over another (for the trap that has the highest probability of success) on which site (if applicable). I created a data frame to hold the factors that were not causing significance constant. I then used the "predict" function to obtain the fitted predictions for the regression coefficients (β_x), along with the estimated standard error (SE) for each regression coefficient. I used the fitted predictions and standard error for the regression coefficients to 1) determine predicted probabilities of capture success for *D. compactus* with capture probability = $\exp(\beta_x)/(1+\exp(\beta_x))$ where x = Sherman, clean, Fitch, long, and specialty bait trap types, and 2) approximate 95% confidence intervals with upper bound = $\exp(\beta_x+1.96*SE\beta_x)/(1+\exp(\beta_x+1.96*SE\beta_x))$ and lower bound = $\exp(\beta x-1.96*SE\beta_x)/(1+\exp(\beta x-1.96*SE\beta_x))$ for each trap type.

Table 1: Summary of the trapping locations and trapping effort for the Guadalupe County study site.

Season	Treatment	Point[1]	Coordinates[2]	Traps	Consecutive Nights	Trap Nights
Summer	Shrub-PaD	1	29.454420°N, 97.930700°W	48	4	192
		2	29.412082°N, 97.889839°W	48	4	192
	Shrub-ArD	3	29.435925°N, 97.920461°W	10	4	40
		4	29.417004°N, 97.900538°W	8	4	32
	Grassland-PaD	5	29.452325°N, 97.938395°W	38	4	152
		6	29.439264°N, 97.934012°W	36	4	144
	Grassland-ArD	7	29.443037°N, 97.931169°W	6	4	24
		8	29.402802°N, 97.905925°W	6	4	24
Winter	Shrub-PaD	1	29.454420°N, 97.930700°W	46	4	184
		2A	29.447570°N, 97.926968°W	48	4	192
	Shrub-ArD	3	29.435925°N, 97.920461°W	10	4	40
		4	29.417004°N, 97.900538°W	8	4	32
	Grassland-PaD	5A	29.442672°N, 97.933900°W	40	4	160
		6A	29.433450°N, 97.926441°W	34	4	136
	Grassland-ArD	7	29.443037°N, 97.931169°W	6	4	24
		8	29.402802°N, 97.905925°W	6	4	24
Spring	Shrub-PaD	1	29.454420°N, 97.930700°W	90	3	270
		2A	29.447570°N, 97.926968°W	90	3	270
	Shrub-ArD	3	29.435925°N, 97.920461°W	20	3	60
		4	29.417004°N, 97.900538°W	16	3	48
	Grassland-PaD	5A	29.442672°N, 97.933900°W	80	3	240
		6A	29.433450°N, 97.926441°W	80	3	240
	Grassland-ArD	7	29.443037°N, 97.931169°W	16	3	48
		8	29.402802°N, 97.905925°W	16	3	48

[1]Vegetative point associated with the Daubenmire survey.
[2]WGS84

Table 2: Summary of the trapping locations and trapping effort for the Jim Hogg County study site.

Season	Treatment	Point[1]	Coordinates[2]	Traps	Consecutive Nights	Trap Nights
Summer	Grassland-Dl	1	27.053423°N, 98.638432°W	30	3	90
		2	27.029083°N, 98.696280°W	30	2	60
	Grassland-Ns	3	27.014209°N, 98.646923°W	30	3	90
		4	27.048170°N, 98.696400°W	30	2	60
	Grassland-Br	5	27.015895°N, 98.644249°W	10	3	30
	Grassland-Dn	6	27.036453°N, 98.638602°W	20	3	60
	Shrub-Dl	7	27.052656°N, 98.647275°W	30	3	90
	Shrub-Ns	8	27.027403°N, 98.679950°W	30	3	90
	Shrub-Br	9	27.001636°N, 98.669896°W	10	3	30
	Shrub-Dn	10	27.009439°N, 98.686173°W	10	3	30
Winter	Grassland-Dl	1	27.053423°N, 98.638432°W	30	3	90
		2	27.029083°N, 98.696280°W	20	3	60
	Grassland-Ns	3	27.014209°N, 98.646923°W	10	3	30
		4	27.048170°N, 98.696400°W	20	3	60
		11	27.015324°N, 98.656454°W	20	3	60
	Grassland-Br	5	27.015895°N, 98.644249°W	10	3	30
	Grassland-Dn	6	27.036453°N, 98.638602°W	20	3	60
	Shrub-Dl	7	27.052656°N, 98.647275°W	20	3	60
	Shrub-Ns	8	27.027403°N, 98.679950°W	30	3	90
	Shrub-Br	9	27.001636°N, 98.669896°W	10	3	30
	Shrub-Dn	10	27.009439°N, 98.686173°W	10	3	30
Spring	Grassland-Dl	1	27.053423°N, 98.638432°W	52	4	208
		2	27.029083°N, 98.696280°W	36	4	144
	Grassland-Ns	3	27.014209°N, 98.646923°W	20	4	80
		4	27.048170°N, 98.696400°W	36	4	144
		11	27.015324°N, 98.656454°W	30	4	120
	Grassland-Br	5	27.015895°N, 98.644249°W	20	4	80
	Grassland-Dn	6	27.036453°N, 98.638602°W	36	4	144
	Shrub-Dl	7	27.052656°N, 98.647275°W	32	4	128
	Shrub-Ns	8	27.027403°N, 98.679950°W	52	4	208
	Shrub-Br	9	27.001636°N, 98.669896°W	20	4	80
	Shrub-Dn	10	27.009439°N, 98.686173°W	20	4	80

[1]Vegetative point associated with the Daubenmire survey.
[2]WGS84

IV. RESULTS

Capture Success

Overall capture success for the Guadalupe County study site for all heteromyids within all seasons for 2,816 trap nights was 2.06% (58 total captures, 2 captures/100 trap nights); for *C. hispidus*, 1.07% (30 total captures, 1 capture/100 trap nights); for *D. compactus*, 0.99% (28 total captures, 1 capture/100 trap nights). Capture success for the Jim Hogg study site for all heteromyids within all seasons for 2,646 trap nights was 19.16% (507 total captures, 19 captures/100 trap nights); for *C. hispidus*, 8.01% (212 total captures, 8 captures/100 trap nights); for *P. merriami*, 10.20% (270 total captures, 10 captures/100 trap nights); for *D. compactus* 0.94% (25 total captures, 1 capture/100 trap nights).

Additional captures on the Guadalupe County study site included one Hurter's Spadefoot Toad (*Scaphiopus hurterii*) (Curtis et al. 2015) and one Fulvous Harvest Mouse (*Reithrodontomys fulvescens*). On the Jim Hogg study site, the following rodents were captured as a part of the assemblage: four White-footed Deermice (*Peromyscus leucopus*), 14 Northern Grasshopper Mice (*Onychomys leucogaster*), one Hispid Cotton Rat (*Sigmodon hispidus*), one Northern Pygmy Mouse (*Baiomys taylori*), one Southern Plains Woodrat (*Neotoma micropus*). Incidental captures on the Jim Hogg County study site included one Common Spotted Whiptail (*Aspidoscelis gularis*), one Mourning Dove (*Zenaida macroura*), and one Common Ground Dove (*Columbina passerina*).

Landscape Level Analyses

Captures were significantly different per treatment for each species (*C. hispidus*, *P. merriami*, and *D. compactus*) on both study sites (Guadalupe County and Jim Hogg County) (Table 3). For the Guadalupe County study site, the habitats selected by the following species included: *C. hispidus* in Shrub-PaD and *D. compactus* in Grassland-ArD and Shrub-ArD. There were no habitats that were avoided by any species on the Guadalupe County study site. For the Jim Hogg County study site, the habitats selected included: *C. hispidus* in Shrub-Dl, Shrub-Dn, and Grassland-Br; *P. merriami* in Grassland-Br; *D. compactus* in Grassland-Dl and Grassland-Ns. The habitats avoided included: *C. hispidus* in Grassland-Dl; *P. merriami* in Grassland-Dl; *D. compactus* in Shrub-Dl and Grassland-Dn.

Microhabitat Analyses

For the Guadalupe County study site, none of the microhabitat parameters (herbaceous cover of forbs and grasses, bare ground, leaf litter, and densiometer readings representing shrub and canopy cover) were important predictors of capture success for either species (Table 4). For the Jim Hogg County study site, herbaceous cover and bare ground were significant for the capture success of *C. hispidus* with a positive trend observed for herbaceous cover (β = 0.1259, R^2 = 0.1516, P = 0.0276), and a negative trend observed for bare ground (β = -0.2156, R^2 = 0.2477, P = 0.0038). Herbaceous cover and bare ground accounted for approximately 15 and 25% of the variation in the respective models. Herbaceous cover and bare ground were also approaching significance for *P. merriami* and *D. compactus* on the Jim Hogg County study site, with a positive trend observed for herbaceous cover, and a negative trend observed for bare ground. Leaf litter and densiometer readings were not significant for any species on the Jim Hogg County study site. Figures 5-7 display the trendlines and associated R^2 for the microhabitat parameters that are significant or approaching significance for each species associated with the Jim Hogg County study site.

On the Guadalupe County study site, the range of cover for the microhabitat parameters was: herbaceous cover = 5 - 76.5%; bare ground = 17 – 80.5%; leaf litter = 19.5 – 80.5%; and densiometer readings = 0 – 27%. On the Jim Hogg County study site, the range of cover for the microhabitat parameters was: herbaceous cover = 5 - 83%; bare ground = 38 – 97.5%; leaf litter = 2.5 – 42.5%; and densiometer readings = 0 – 7%.

Paired Trap Analyses

Capture success did not differ significantly by site (P = 0.7881), but did differ significantly by trap type (P = 0.0005). The fitted predictions for the regression coefficients (β_x), along with the estimated standard error (SE) for each regression coefficient (trap type) are as follows: Sherman trap (β_0 = -4.6111, SE = 0.2595), clean trap (β_1 = -4.0775, SE = 0.5042), Fitch trap (β_2 = -3.6428, SE = 0.4530), long trap = (β_3 = -3.0339, SE = 0.3413), and the specialty bait used within a Sherman trap (β_4 = -5.4027, SE = 0.5011). The predicted probabilities for the capture success of *D. compactus* for each trap type is as follows: Sherman trap = 0.0098, clean trap = 0.0167, Fitch trap = 0.0255, long trap = 0.0459, and the specialty bait used within a Sherman trap = 0.0045. Figure 8 displays the results of the logistic regression (predicted probabilities of capture success), along with the confidence intervals (upper and lower bounds) for each trap type. The long traps had the highest predicted probability of capture success.

Table 3: Results of the chi-square goodness-of-fit tests to determine if captures for each species differed per treatment over all seasons.

Site; Species[1]	χ^2 Test Statistic	df	P-value[2]	Value of Determination[3]	$((O_i-E_i)^2)/E_i$ Values	Obs.[4]	Exp.[5]	Indicates[6]	Treatment
Guadalupe County; *C. hispidus*	11.84	3	0.0080	2.96	6.05	23	13.8	Selection	Shrub-PaD
					2.68	0	2.7	As Expected	Shrub-ArD
					2.57	6	11.4	As Expected	Grassland-PaD
					0.53	1	2.0	As Expected	Grassland-ArD
Guadalupe County; *D. compactus*	8.81	3	0.0319	2.20	0.66	10	12.9	As Expected	Shrub-PaD
					2.48	5	2.5	Selection	Shrub-ArD
					0.66	8	10.7	As Expected	Grassland-PaD
					5.00	5	1.9	Selection	Grassland-ArD
Jim Hogg County; *C. hispidus*	53.56	7	<0.001	6.69	9.47	30	52.2	Avoidance	Grassland-Dl
					1.79	42	51.6	As Expected	Grassland-Ns
					10.37	22	11.2	Selection	Grassland-Br
					0.47	18	21.2	As Expected	Grassland-Dn
					15.74	41	22.3	Selection	Shrub-Dl
					2.66	22	31.1	As Expected	Shrub-Ns
					0.69	14	11.2	As Expected	Shrub-Br
					12.38	23	11.2	Selection	Shrub-Dn

[1] Each study site (Guadalupe County and Jim Hogg County) was analyzed separately.
[2] There is a significant difference between capture success (per species) between treatments for all species on the Guadalupe and Jim Hogg County sites.
[3] The value of determination was calculated by dividing the chi-square test statistic by the number of treatments (assuming all treatments are equal).
[4] The observed value per species per treatment type.
[5] The expected value per species per treatment type.
[6]Indicates selection for or avoidance of the treatment, or a species occurring as expected in this habitat at a rate proportional to its overall availability.

Table 3, Continued.

Site; Species[1]	χ^2 Test Statistic	df	P-value[2]	Value of Determination[3]	$((O_i-E_i)^2)/E_i$ Values	Obs.[4]	Exp.[5]	Indicates[6]	Treatment
Jim Hogg County; *P. merriami*	28.52	7	<0.001	3.56	10.58	40	66.5	Avoidance	Grassland-Dl
					1.61	76	65.7	As Expected	Grassland-Ns
					11.32	27	14.3	Selection	Grassland-Br
					0.91	22	26.9	As Expected	Grassland-Dn
					0.47	32	28.4	As Expected	Shrub-Dl
					0.53	35	39.6	As Expected	Shrub-Ns
					1.56	19	14.3	As Expected	Shrub-Br
					1.56	19	14.3	As Expected	Shrub-Dn
Jim Hogg County; *D. compactus*	14.33	7	0.0456	1.79	2.39	10	6.2	Selection	Grassland-Dl
					3.97	11	6.1	Selection	Grassland-Ns
					2.49	0	2.5	Avoidance	Grassland-Dn
					1.32	0	1.3	As Expected	Grassland-Br
					2.63	0	2.6	Avoidance	Shrub-Dl
					0.12	3	3.7	As Expected	Shrub-Ns
					0.08	1	1.3	As Expected	Shrub-Br
					1.32	0	1.3	As Expected	Shrub-Dn

[1] Each study site (Guadalupe County and Jim Hogg County) was analyzed separately.
[2] There is a significant difference between capture success (per species) between treatments for all species on the Guadalupe and Jim Hogg County sites.
[3] The value of determination was calculated by dividing the chi-square test statistic by the number of treatments (assuming all treatments are equal).
[4] The observed value per species per treatment type.
[5] The expected value per species per treatment type.
[6]Indicates selection for or avoidance of the treatment, or a species occurring as expected in this habitat at a rate proportional to its overall availability.

Table 4: Summaries of the simple linear regression models used to determine the most important microhabitat predictor of capture success in all seasons for each species.

Site; Species[1]	**Model Coefficients**[2]	**Parameter (Coefficient) Estimates**	**Parameter (Coefficient) Standard Errors**	**t-value**	**P-values**[3]	**R-squared Value**
Guadalupe County; *C. hispidus*	H	0.0075	0.0127	0.59	0.5608	0.0156
	BG	-0.0002	0.0181	-0.01	0.9925	<0.0001
	LL	0.0058	0.0156	0.37	0.7147	0.0062
	densio	-0.0463	0.0371	-1.25	0.2257	0.0660
Guadalupe County; *D. compactus*	H	0.0044	0.0238	0.18	0.8560	0.0015
	BG	0.0162	0.0335	0.48	0.6337	0.0105
	LL	0.0050	0.0291	0.17	0.8658	0.0013
	densio	-0.0434	0.0709	-0.61	0.5467	0.0168
Jim Hogg County; *C. hispidus*	H	0.1259	0.0543	2.32	**0.0276***	0.1516
	BG	-0.2156	0.0686	-3.14	**0.0038***	0.2477
	LL	0.0484	0.1245	0.39	0.7000	0.0050
	densio	-0.2444	0.8035	-0.30	0.7631	0.0031
Jim Hogg County; *P. merriami*	H	0.1182	0.0638	1.85	**0.0736**	0.1028
	BG	-0.1510	0.0861	-1.75	**0.0898**	0.0929
	LL	-0.1402	0.1404	-0.10	0.3259	0.0322
	densio	1.1496	0.8955	1.28	0.2090	0.0521
Jim Hogg County; *D. compactus*	H	0.0166	0.0092	1.79	**0.0830**	0.0968
	BG	-0.0234	0.0123	-1.90	**0.0678**	0.1069
	LL	0.0202	0.0203	0.99	0.3284	0.0319
	densio	-0.0434	0.0709	-0.61	0.5467	0.0168

[1]Each predictor was analyzed separately per species per site
[2]H: herbaceous cover of grasses and forbs; BG: bare ground; LL: leaf litter; densio: densiometer readings
[3]P-values are bold with an asterisk if significant and bold if approaching significance

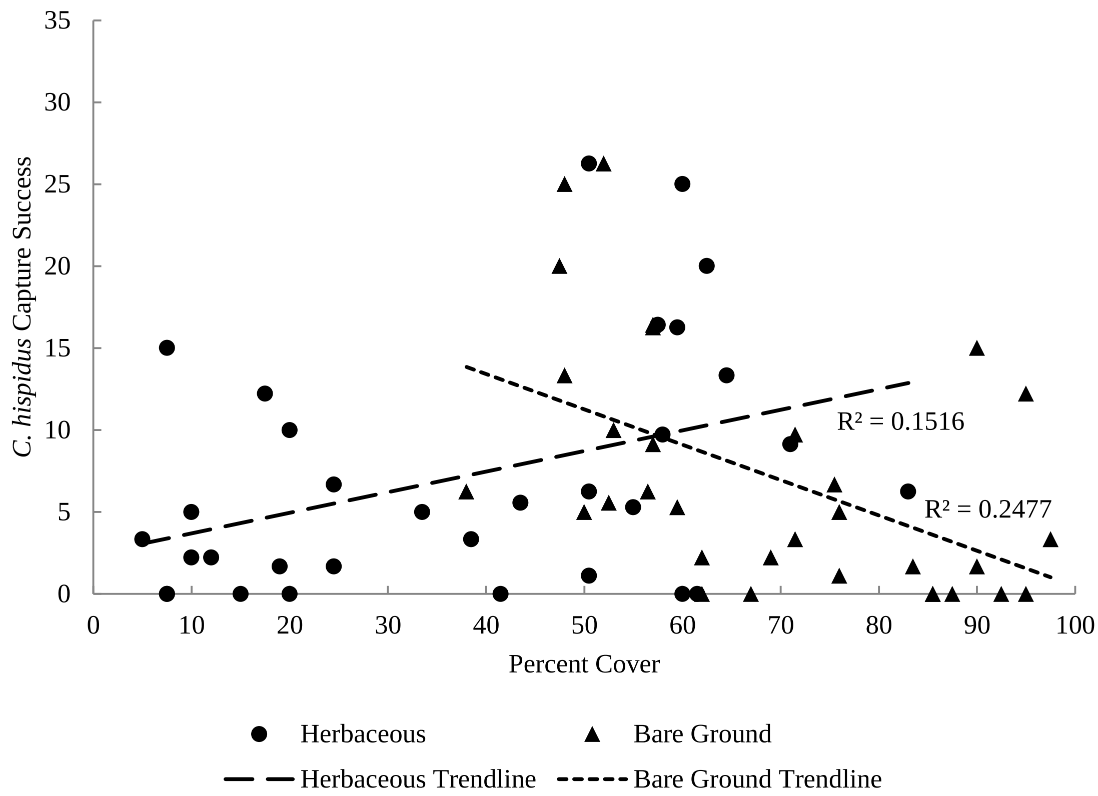

Figure 5. Percent cover of the significant parameters for capture success of *Chaetodipus hispidus*. As herbaceous cover increases and bare ground decreases, capture success of *C. hispidus* increases.

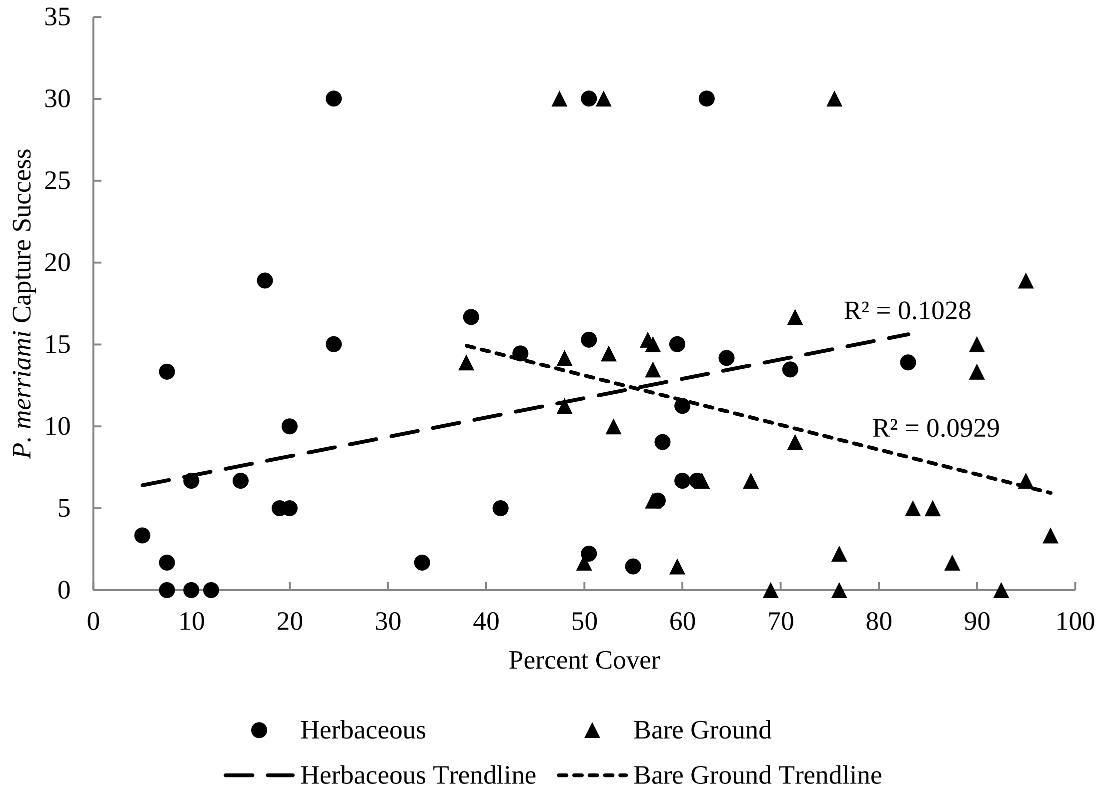

Figure 6. Percent cover of the parameters approaching significance for the capture success of *Perognathus merriami*. As herbaceous cover increases and bare ground decreases, capture success of *P. merriami* increases.

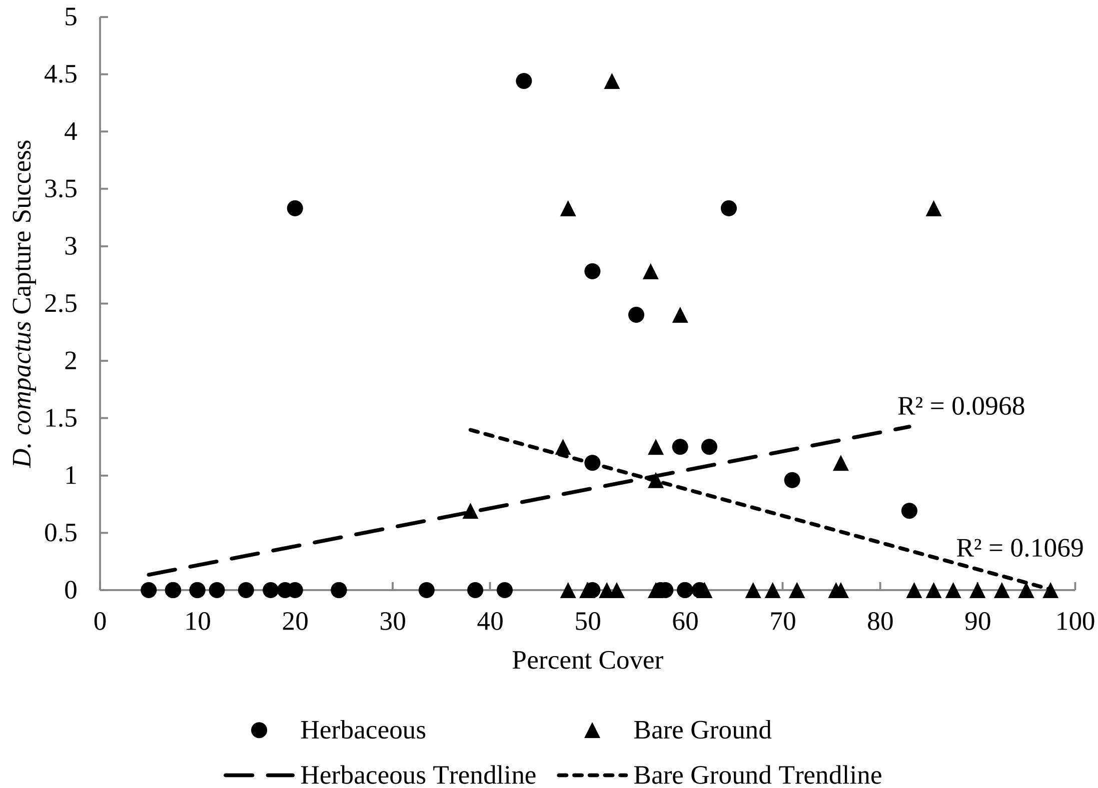

Figure 7. Percent cover of the parameters approaching significance for the capture success of *Dipodomys compactus*. As herbaceous cover increases and bare ground decreases, capture success of *D. compactus* increases. Note that capture success is at a reduced scale, as compared to the previous two figures.

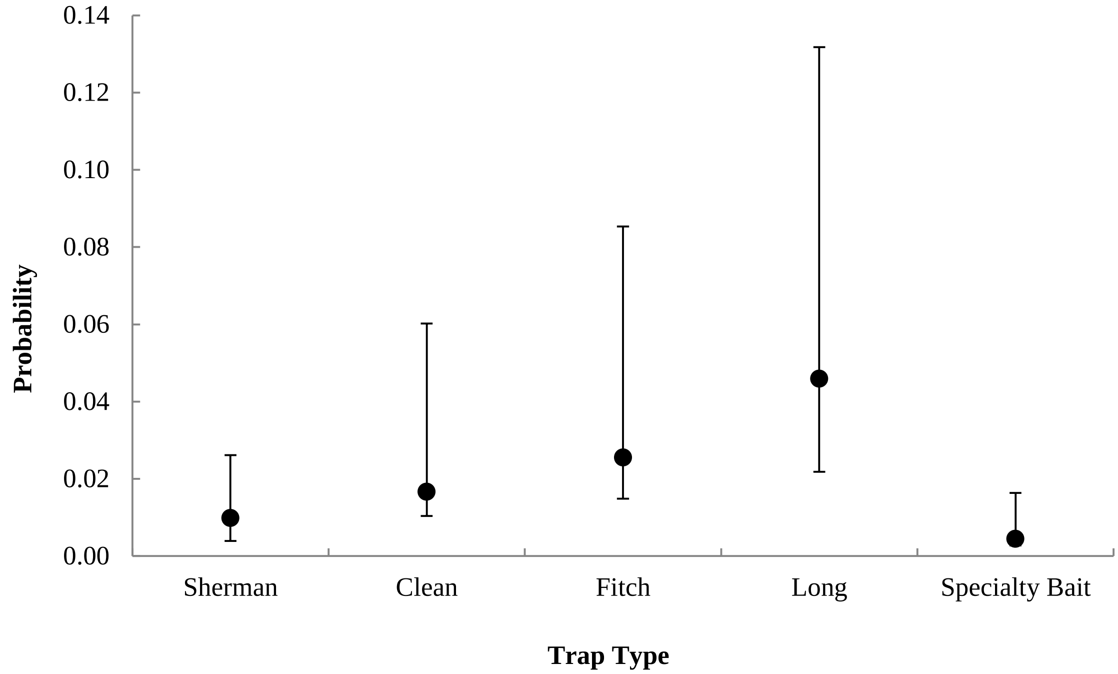

Figure 8. Logistic regression analysis displaying the predicted probabilities of capture success of *Dipodomys compactus* (represented by dots) for each trap type (Sherman trap = 0.0098, clean trap = 0.0167, Fitch trap = 0.0255, long trap = 0.0459, and the specialty bait used within a Sherman trap = 0.0045). Vertical bars represent the confidence intervals (upper and lower bounds) for each trap type.

V. DISCUSSION

Landscape Level Analyses

In this study I sought to determine the extent that heteromyid species were utilizing different habitat types. For the Guadalupe County study site, *C. hispidus* selected for the Shrub-PaD land cover class and soil type combination (Patilo soils within shrub only), whereas *D. compactus* selected for both Grassland-ArD and Shrub-ArD land cover class and soil type combinations (all Arenosa soil types on the study site). Both species were captured in the Grassland-PaD land cover class and soil type combination at the expected frequencies, suggesting that these two species (*C. hispidus* and *D. compactus*) occurred together in this habitat at a rate proportional to its overall availability.

For the Jim Hogg County study site, *C. hispidus* selected for both the Shrub-Dl and Shrub-Dn land cover class and soil type combinations (two of the four shrub habitat types) along with the Grassland-Br land cover class and soil type combination. Similarly, *P. merriami* selected for Grassland-Br land cover class and soil type combination. Alternatively, *D. compactus* selected for both Grassland-Dl and Grassland-Ns land cover class and soil type combinations (two of the four grassland habitats). Both *C. hipsidus* and *P. merriami* avoided the Grassland-Dl land cover class and soil type combination, in contrast to *D. compactus*, which selected for that land cover class and soil type combination. Furthermore, *C. hispidus* selected for the Shrub-Dl land cover class and soil type combination that *D. compactus* avoided. These patterns may reflect the different microhabitat preferences of these taxa. The land cover class and soil type combinations in which all three heteromyids neither selected for nor avoided included the Shrub-Ns and Shrub-Br, suggesting all three species occurred together in this habitat at a rate proportional to its overall availability.

If a heteromyid occurred at the expected frequency, or greater than the expected frequency within a habitat in which a second heteromyid occurred at the expected frequency, or greater than the expected frequency, then that suggests coexistence. Heteromyids may coexist within these productive habitats due to ample structure on a microhabitat scale (i.e. microhabitat segregation), or due to differences in their microhabitat use (Brown and Harney 1993). If one land cover class and soil type combination was selected for by one species, and avoided by another species, then this suggests potential habitat partitioning by heteromyids. In this case, habitat structure on a microhabitat scale may not be conducive for the coexistence of more than one heteromyid.

Microhabitat Analyses

Microhabitats are the precise places in which animals occur, and microhabitat data are important to collect to predict occurrence (Inger and Wilson 1996). Both herbaceous cover and bare ground were important predictors of occurrence for *C. hispidus* only on the Jim Hogg County study site. For all seasons combined, as both herbaceous cover increased and bare ground decreased, capture success for *C. hispidus* increased. Microhabitat parameters were not important predictors of occurrence for *P. merriami* or *D. compactus*. However, values were approaching significance for *P. merriami* and *D. compactus* for herbaceous cover and bare ground. A weak relationship exists in the sense that as both herbaceous cover increased and bare ground decreased, the capture success for both *P. merriami* and *D. compactus* increased. These findings support previous research that quadrupedal heteromyids are largely associated with dense vegetation (Rosenzweig and Winakur 1969, Rosenzweig 1973, Lemen and Rosenzweig 1978). Further, these results are similar to Oakley's (2012), in which *D. compactus* burrows were present in areas with high forb cover. However, Oakley (2012) also found that *D. compactus* burrows were present in areas with a high percentage of bare ground in contrast to the results presented here. Likewise, the results of this study appear to contradict previous research that bipedal heteromyids are largely associated with open habitat and sparse vegetation (Rosenzweig and Winakur 1969, Rosenzweig 1973, Lemen and Rosenzweig 1978). However, it is important to note that in areas with *D. compactus* captures, herbaceous cover ranged from 20-83%, with an average of 56% cover and bare ground ranged from 38-85.8%, with an average of 57.8% cover, which is congruent with the general statement of open habitat with sparse vegetation. The occurrence of *D. compactus* may require an equal amount of coverage of both herbaceous cover and bare ground. Density of herbaceous vegetation (stems/m^2) may be a better indicator than percent cover to determine occurrence. Densiometer readings were taken at approximately one meter heights, and therefore may not have captured the shrub cover component on a microhabitat scale in which it relates to heteromyid use.

Microhabitat parameters were not important predictors of occurrence on the Guadalupe County study site, perhaps because in areas suitable for heteromyids, the landscape is managed for cattle and hunting and therefore homogenized. The Jim Hogg County study site is more natural, and therefore, offers more heterogeneity for heteromyid species, as compared to the Guadalupe County study site. A heterogenous landscape provides more options for the segregation of coexisting species within different microhabitats (Brown and Harney 1993). However, our scale of measure for microhabitat parameters may not have captured the reason for significance or non-significance because all traps were set in suitable habitats. If all sampled habitats are suitable for heteromyids, then they may effectively be occurring together within these suitable habitats at a broad spatial scale, regardless of possible differences at the microhabitat level.

Paired Trap Analyses

The predicted probability of success of capture of *D. compactus* by trap type was highest with the long traps (0.0459, Fig.8). These results suggest that the long traps with regular oats and mixed bird seed will have a higher probability of capture success for *D. compactus*. However, capture success with the long traps was close to the upper limit documented for *D. compactus* in other studies that used (standard) Sherman traps (Baumgardner and Schmidly 1985, Rissel 2011, Phillips 2012). The extra-large (7.62x9.525x30.48 cm) folding H. B. Sherman kangaroo rat trap, constructed "especially for capturing the kangaroo rat" has similar size dimensions to the long trap utilized in the study (extra-large [10.16x11.43x38.1 cm] folding H. B. Sherman trap). It is usually more convenient to carry and set smaller traps because they weigh less and take up less space during transport. However, if *Dipodomys* are targeted, setting fewer large-sized traps is a more efficient strategy than setting more smaller-sized traps to increase capture success of this "trap-shy" (xenophobic) species. The lowest probability of capture success of *D. compactus* was evident with the specialty bait (oats, peanut butter, and vanilla extract mixture), perhaps because it would not be advantageous to kangaroo rats to cache seeds or other food items that have a high oil composition. Kangaroo rats maintain their seed caches (larderhoards) to reach an intermediate level of moldiness for the production of beneficial byproducts (Reichman et al. 1986, Reichman and Price 1993). Sterile seeds are moved to high humidity locations, and seeds that have molded to preferred levels are moved to low humidity locations (Reichman and Price 1993). In addition, external cheek pouches may have been favored by natural selection over internal pouches to conserve body water (Brylski 1993), and kangaroo rats may prefer to collect dry seeds in their external fur-lined cheek pouches versus oily seeds.

Capture Success

Capture success for *C. hispidus* was lower on the Guadalupe County study site (1.07%) than the Jim Hogg County study site (8.01%). Although capture success for *P. merriami* (10.2%) was higher than that of *C. hipsidus* on the Jim Hogg County study site, this value is not higher than what is reported in the literature for *P. merriami* congeners (Reichman and Van De Graaff 1973, Rosenzweig 1973). Anecdotally, intraspecific pairs of *P. merriami* were captured in a single Sherman trap eight times over the course of the winter and spring trapping events in Jim Hogg County. For six of the pairs, social traveling may explain the capture of these individuals (Taulman et al. 1994), as they did not appear injured and the pairs dispersed together upon release. For two of the pairs, intraspecific competition may have been the reason for capture, as one individual from the pair was alive and one individual was dead.

Trapping success for *D. compactus* (0.99% in Guadalupe County and 0.94% in Jim Hogg County) was similar to previous trapping efforts in Guadalupe County (2%, Phillips 2012) and in Jim Hogg County (<5%, Baumgardner and Schmidly 1985). Trapping success in Jim Hogg County was lower than in Guadalupe County because *D. compactus* was not captured in traps during the winter trapping event, even though at every trapping location, bait was taken at the trap entrance. Because kangaroo rat activity was observed (i.e., tracks, tail drags, fresh excavations at burrow entrances) in the absence of a capture, I placed cameras at several burrow locations across the site on the last trap night in the winter to try to document kangaroo rat behavior. Photos and videos documented kangaroo rats actively taking bait at the trap entrance, climbing on top of traps, sand bathing, defending territory, and clearing burrow entrances. It is uncertain why D. *compactus* were active around the traps but reluctant to enter during the winter season. Activity was documented at dusk (approximately 1830 hours) until high humidity caused the camera lens to fog over at approximately 0230 hours. Other heteromyids (i.e., *C. hispidus* and *P. merriami*) were not observed on cameras during this time, but were captured in traps. Therefore, these species must have been captured after 0230 hours. Future studies related to temporal partitioning could be conducted to determine the extent to which coexisting heteromyids utilize a shared resource.

Conclusions

This study provides ecological data as a contribution to the literature for heteromyids on the Central and South Texas mainland. On the landscape scale, heteromyids occurred as expected within the majority of suitable land cover and soil types. However, some habitat partitioning may exist in land cover and soil types in which it was determined that one species avoided the habitat type and another species selected for the habitat type. Herbaceous cover and bare ground also appear to be important predictors of occurrence for heteromyids on the microhabitat scale. The positive trend for herbaceous cover and the negative trend for bare ground appears to support previous research that quadrupedal heteromyids are associated with areas of dense cover. The weak trends for *D. compactus* appear to contradict previous research that bipedal heteromyids are associated with sparse cover and open areas; however, most *D. compactus* captures occurred in areas with an approximate even mix of herbaceous cover and bare ground. Future studies should consider using extra-large sized traps baited with oats and mixed bird seed in order to increase capture success of the trap-shy *D. compactus* within suitable habitats.

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