GENETIC PEDIGREE AND PREY DYNAMICS OF OCELOT AND FINE-SCALE MOVEMENT PATTERNS OF BOBCAT IN SOUTH TEXAS

A Dissertation

by

JENNIFER MARIE KORN

Submitted to the College of Graduate Studies
Texas A&M University-Kingsville
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2013

Major Subject: Wildlife Science

GENETIC PEDIGREE AND PREY DYNAMICS OF OCELOTS AND FINE-SCALE MOVEMENT PATTERNS OF BOBCATS IN SOUTH TEXAS

A Dissertation

by

JENNIFER MARIE KORN

Approved as to style and content by:

Michael E. Tewes

Michael E. Tewes, Ph.D.
(Chairman of Committee)

Randy W. DeYoung, Ph.D.
(Member of Committee)

Jan E. Janečka, Ph.D.
(Member of Committee)

Andrea R. Litt

Andrea R. Litt, Ph.D.
(Member of Committee)

Scott E Henke

Scott E. Henke, Ph.D.
(Head of Department)

LaVonne Fedynich

LaVonne Fedynich, Ed.D.
(Graduate Council Representative)

Mohamed Abdelrahman, Ph.D.
(AVP for Research and Graduate Studies)

December 2013

ABSTRACT

Genetic Pedigree and Prey Dynamics of Ocelot and
Fine-scale Movement Patterns of Bobcat in South Texas
(December 2013)
Jennifer Marie Korn, B.S., UT Arlington; M.S., Texas State University-San Marcos
Chairman of Advisory Committee: Dr. Michael E. Tewes

By the mid-1900s, ocelots (*Leopardus pardalis*) in Texas became isolated as 2 known subpopulations on Yturria Ranch (Yturria) in Willacy County (Willacy), and Laguna Atascosa National Wildlife Refuge (LANWR) in Cameron County (Cameron), Texas. An additional subpopulation has recently been surveyed on East El Sauz Ranch (East), Willacy County. My study consisted of 3 separate components that may be used to determine future conservation strategies for this endangered felid.

First, I assessed genetic diversity, differentiation, dispersal, and the extent of inbreeding. Ocelots on East had the highest diversity, whereas Cameron lost diversity and was most differentiated from Willacy. Differentiation was significant but lower between Yturria and East, and dispersal occurred between sites. No first generation migrants were detected between Willacy and Cameron, but 1 individual captured in Cameron in 2000 had possible immigrant ancestry and a sire from Yturria. All 3 subpopulations contained inbred relationships. Though intermittent dispersal occurred between Yturria and East, there was essentially no dispersal between Willacy and Cameron. Translocation between the subpopulations is a viable conservation strategy.

Second, I measured the response of ocelot prey (i.e., rodents) to drought and rainfall on Yturria and LANWR. Trap success on Yturria indicated that even with long-term, severe drought conditions in the region, local habitat patches maintained stable rodent populations because the site received small periodic rainfall events. Rodent population response was brief on LANWR, which did not receive localized rainfall events. Trap success was higher on sites designated as primary areas for translocated ocelot release, compared to secondary sites. In general, increasing rainfall and lower drought led to increased trap success on LANWR, but without additional rainfall pulses, the response was brief.

Third, I examined fine-scale movement patterns (i.e., tortuosity) of sympatric bobcats (*Lynx rufus*) in fragmented brush strips on King Ranch, Kleberg County, Texas. Male and female bobcats used home ranges at different scales and did not seem to select for brush strips. Male bobcats had larger home ranges and less tortuous movements, whereas female bobcats had smaller home ranges and more tortuous movements.

DEDICATION

This dissertation is dedicated to my family. It has been a long journey from the days when I was a child telling my parents I wanted to "save wild cats." Throughout my years as a graduate student they have been my strongest supporters. Mike and Helen, you taught me how to care about the underdog, even when that meant wild animals that are unable to speak for themselves. I also want to mention my big sister, Michele, for always listening to me, her husband, Nathan, and my nieces Elizabeth and Victoria, and nephew, Max. I'm trying to make a difference in the world so that their generation still has wild cats to appreciate in their natural environment. Additionally, to my big brother, Jason, who once humored me in having a very serious conversation about the physiological possibilities of having a kitty so small you could literally carry it around in your pocket.

Also a very special thanks to my newest friends and family: Abe, Charity, Christopher, and Melanie. You have provided me with unwavering friendship and never once hesitated to include me as one of your family. You have been my rocks in the last year of my dissertation research and writing. Thank you for always having an open ear and open heart.

I love you all and thank you for standing by me throughout all of this.

ACKNOWLEDGMENTS

I would like to thank my committee members Drs. Michael E. Tewes, Randy W. DeYoung, Jan E. Janečka, and Andrea R. Litt for their continued support on this project. This opportunity would not have been possible without Dr. Michael Tewes with whom I had corresponded with many years prior to the beginning of this dissertation. Thank you for providing me with the opportunity to conduct cat research, something that has ultimately been my life goal. Drs. Randy DeYoung and Jan Janečka were instrumental in helping me to understand conservation genetics and the pedigree portion of this dissertation would not have been possible without their patience and assistance. A special thanks to Jan for sharing his previous ocelot genetic data with me for the project. Dr. Andrea Litt has been crucial in understanding population modeling and statistics and I am very grateful for her tutelage.

Ultimately none of this would have been possible without the dedication to ocelot conservation from Mr. Frank Yturria. He has donated large portions of his ranch to be set aside as ocelot habitat in perpetuity. I am extremely grateful for the access to his land to trap and study ocelots, bobcats and rodents throughout the course of this study. He is a pioneer in ranching and habitat management in South Texas and one of the saviors for ocelot conservation.

I want to express a very special thanks to the cat group: Arturo Caso, Lon Grassman, Chad Stasey, Sasha Carvajal-Villarreal, and Joe Holbrook. You provided endless hours of stimulating conversation about cat research and conservation. Joe, thank you for much support as I learned my way in the genetics lab. And I have to call out Arturo for a very heartfelt thank you. My first experience with ocelots in the wild was on a research trip to his family ranch in Mexico more than 10 years ago. This only aided in fanning the flames of my desire to work with wild cats. All these years later Arturo was a patient teacher as he instructed me on wild cat field chemical immobilization techniques of wild cats.

Numerous graduate students have volunteered aiding me in trapping ocelots, bobcats and rodents: Aaron Foley, Joe Holbrook, Chad Stasey, Mark Witecha, Samantha Wisniewski Kahl, Whitney Priesmeyer, Wes Watts, Justin Wied, and others. A warm thanks goes out to all of the graduate students past and present for always making CKWRI, TAMUK and Kingsville feel like family and home. Additionally, the genetic pedigree would not have been entirely possible without the guidance in the lab from Damon Williford, as well as his friendship. Thank you for your patience!

Drs. David G. Hewitt and David Wester provided invaluable assistance and statistical analysis on side projects. I want to sincerely thank the support staff at Caesar Kleberg Wildlife Research Institute, especially Becky Trant, Chris Reopelle and Yolanda Ballard for their friendly smiles and always unlimited assistance with clerical issues. I thank the Institute director, Dr. Fred Bryant, for really trying to put the graduate students first (and killer pool parties).

I want to express thanks to King Ranch, Inc., Marc Bartoskewitz, Oscar Cortez, Matt Schnupp and the leaseholder on my study site at King Ranch for allowing me access to this historic ranch to conduct bobcat movement research. All the entities involved have been extremely helpful and accommodating.

Numerous grants and scholarships made my life as a graduate student possible: Dr. Manuel Pińa and the Hispanic Leaders in Agriculture and Environment at TAMU for my assistantship; Victor Davila and Jim Remelius at Title V/PPOHA for not only a scholarship and travel to national conferences but the grant that made the purchase of GPS collars possible; Gary Waggerman Memorial Scholarship; South Texas Quail Coalition Scholarship; Texas Academy of Science/Texas Organization of Endangered Species Scholarship; Michael and Charles Corbett Scholarship; René Barrientos; Jody Mays, Sonia Najera and the Friends of Laguna Atascosa National Wildlife Refuge for the grants that funded ocelot prey surveys and the ocelot genetic pedigree; and the Houston Safari Club scholarship and small grant.

And ultimately I thank the Lord for providing me with the opportunity to live out my dream of working with wild cats. It is in His name that I try to preserve the wonderful creatures that He created. I hope this is just the beginning of my wild cat research and that I can continue to do it for many years to come.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

POPULATION STATUS OF OCELOT (*LEOPARDUS PARDALIS*) IN TEXAS: STRUCTURE, FAMILY RELATIONSHIPS, AND DISPERSAL

Introduction

Small, isolated populations are particularly vulnerable to the effects of genetic drift and inbreeding (Lacy 1987). Changes in allele frequencies related to drift is negligible in large populations, but in small populations the fixation of deleterious alleles may lead to a decrease in fitness. Inbreeding between related individuals causes an increase in homozygosity and a reduction in genetic variation. The combination of drift and inbreeding can lead to an overall loss of alleles and reduced heterozygosity, and ultimately inbreeding depression (Hedrick & Miller 1992). These effects have been well-documented in populations of wild felids including Florida panther (*Puma concolor coryi*, Roelke *et al.* 1993) and Amur leopard (*Panthera pardus orientalis*, Uphyrkina *et al.* 2002). These felids have undergone drastic reductions in population size due to overhunting or habitat destruction and fragmentation.

The ocelot (*Leopardus pardalis*) is a neotropical felid that ranges from southern Texas to Argentina (Caso 2008). Populations in Texas were designated federally endangered in 1982 (USFWS 1999) after a decline in range and census size as a result of habitat loss and fragmentation. Long-term monitoring of ocelot in Texas has identified three conservation concerns: (1) removal and fragmentation of preferred thornshrub habitat (Tewes & Everett 1986; Jahrsdoerfer & Leslie 1988; Haines *et al.* 2006b), (2) high incidence of road mortality (Haines *et al.* 2005), and (3) loss of genetic diversity over time (Walker 1997; Janečka *et al.* 2011). Landscape alteration of the delta in the Lower Rio Grande Valley (LRGV) for agriculture and

---

Chapter 1 of this dissertation follows the style of the journal of *Molecular Ecology.*

urban development has resulted in almost complete isolation of the remaining ocelots in Texas into two distinct subpopulations. Phylogenetic studies have indicated that any possible historical connectivity with extant populations in Mexico has been discontinued by urbanization and agriculture along the Rio Grande (Janečka *et al.* 2007; Janečka *et al*. 2008).

During the past 30 years, ocelots in Texas have occurred in two known subpopulations on: Yturria Ranch (YTURRIA), Willacy County (WILLACY); and Laguna Atascosa National Wildlife Refuge (LANWR), Cameron County (CAMERON). Molecular studies suggest that these two remnant populations exist in essentially complete isolation and have lost genetic diversity due to decreased gene flow and increased genetic drift and inbreeding (Walker 1997; Janečka *et al*. 2008; Janečka *et al*. 2011). Janečka *et al*. (2008) observed a 23% decrease in expected heterozygosity (H_e) for the CAMERON population between 1986–1989 and 2001–2005. Ocelots sampled in CAMERON and WILLACY during 1991–2005 also had an excess of genetic diversity (H_s), which with the low level of variation, indicated a possible bottleneck (Janečka *et al.* 2008; Janečka *et al.* 2011). These results are consistent with the patterns observed in Amur leopard (Uphrykina *et al*. 2002), Asiatic lion (*Panthera leo persica*, Wildt *et al*. 1987), and Florida panther (Roelke *et al*. 1993), populations which have experienced genetic bottleneck events.

The subpopulation in WILLACY during 1991–1998 retained greater genetic diversity than CAMERON, and was comparable to populations in northern Mexico (Walker 1997; Janečka *et al*. 2011). High densities of ocelots observed from live-trapping, and the greater levels of genetic diversity, suggested that individuals on YTURRIA may be part of a larger, mostly unsampled population in WILLACY, where access to private lands is limited. If YTURRIA is indeed isolated, the status of the WILLACY subpopulation post–2005 may be more severe than previously suspected. Estimates of effective population size (N_e) for WILLACY in 2005 (2.9–3.1) were significantly lower than CAMERON (8.0–13.9, Janečka *et al.* 2008), and both subpopulations were well below 50 individuals, the minimum population size recommended to prevent inbreeding depression (Franklin 1980; Franklin & Frankham 1998). Additionally, genetic diversity in WILLACY decreased from 1996–1998 to 2005. Janečka *et al.* (2008) suggested that the loss of diversity and low N_e for YTURRIA may be indicative of an unstable population or that only a few individuals are monopolizing breeding.

A subpopulation of ocelots previously inaccessible and recently surveyed on the East El Sauz Ranch (EAST) in WILLACY has provided the opportunity to assess genetic diversity, population structure, and its importance to the existing subpopulations (i.e., LAGUNA and YTURRIA). Field observations have indicated movement of ocelots between YTURRIA and EAST which are about 10 km apart. However, LANWR seems completely isolated. A clear depiction of genetic population structure is crucial before making conservation and management decisions (Allendorf & Luikart 2007).

Wild animal populations in need of conservation strategies are typically found to have complex pedigree structures and high levels of inbreeding and relatedness (Oliehoek *et al* 2006). Most wild pedigrees have been for songbirds or large mammals because of their ease in collecting field data that can aid in determining familial relationships in conjunction with genetic data (Pemberton 2008). Extensive demographic information collected from field data was instrumental in creation of the long-term and in-depth pedigree of endangered Florida panther (Johnson *et al*. 2010; Hostetler *et al*. 2013). Pedigrees have also been successfully used on wild carnivore populations of Amur leopard (Uphyrkina *et al*. 2002), bobcat (*Lynx rufus*) in South

Texas (Janečka *et al*. 2006), gray wolf (*Canis lupus*) in Idaho (Stenglein *et al.* 2011), and brown bear (*Ursus arctos*) in Italy (De Barba *et al*. 2010).

My first research objective was to determine extant population structure and genetic differentiation with the addition of the EAST subpopulation. Janečka *et al*. (2011) analyzed ocelots sampled from 1986 to 2005 and determined that CAMERON and WILLACY were two genetically distinct populations ($F_{ST} = 0.16$). The EAST subpopulation is located ~10 km from YTURRIA and ~45 km from LANWR, thus within typical dispersal distance for a medium-sized carnivore. Analysis of population structure will be used to determine if the three subpopulations continue to exist in genetic isolation, or if EAST and YTURRIA occur within one greater WILLACY population.

The second objective was to assess the current levels of genetic diversity and variation (2006–2013) and quantify any further changes since 2005. And the last objective was to evaluate gene flow between the subpopulations and presence of inbreeding measured by creating a partial pedigree and re-assessing the assignment of individuals to the subpopulations with the addition of EAST. Prior to the sampling of ocelots from EAST, Janečka *et al.* (2011) observed no migration between CAMERON and WILLACY, and no mis-assignments of roadkill ocelots collected outside the two subpopulations. Janečka *et al*. (2011) concluded that there was no evidence of dispersal or population connectivity, which was further supported by the high level of differentiation (F_{ST}) and continued loss of genetic diversity. The creation of a partial pedigree using parentage analysis will identify any dispersal between the subpopulations, determine if the loss of diversity is attributable to the monopolization of breeding from few individuals, and identify if and at what level inbreeding has occurred.

The completion of these objectives will allow researchers to provide information on movement between subpopulations, estimate relatedness of individuals, determine population origin of roadkill ocelots, and generate information on temporal changes in genetic variation. The genetic analyses will create the groundwork for long-term monitoring of endangered ocelots in Texas and allow insights into population performance at a fine-scale in the event that translocations are implemented.

Materials and Methods

Study area

The study area consisted of three locations within two counties of the LRGV, Texas, USA. Fig. 1.1). The known ocelot subpopulations in WILLACY occur on two private landholdings: YTURRIA and EAST, and the general area. Ocelots on YTURRIA were sampled from a conservation easement (~2 km^2) located in the San Francisco pasture northeast of Raymondville, Texas, USA. The EAST property is located near Port Mansfield, Texas, USA, and ~10 km from YTURRIA. Ocelot habitat on EAST is separated into two distinct north and south patches and individuals were sampled from both areas.

The known ocelot population in CAMERON occurs on the ~190 km^2 LANWR, northeast of Los Fresnos, Texas, USA, and surrounding areas (Fig. 1.1). Ocelot habitat is scattered across the LRGV, occurring as patches of Tamaulipan thornshrub, a dense low woody stand of honey mesquite (*Prosopis glandulosa*), huisache (*Acacia farnesiana*), and granjeno (*Celtis pallida).* Vegetation on the northern portion of EAST differs slightly with the presence of live oak (*Quercus virginiana*) and a less dense understory.

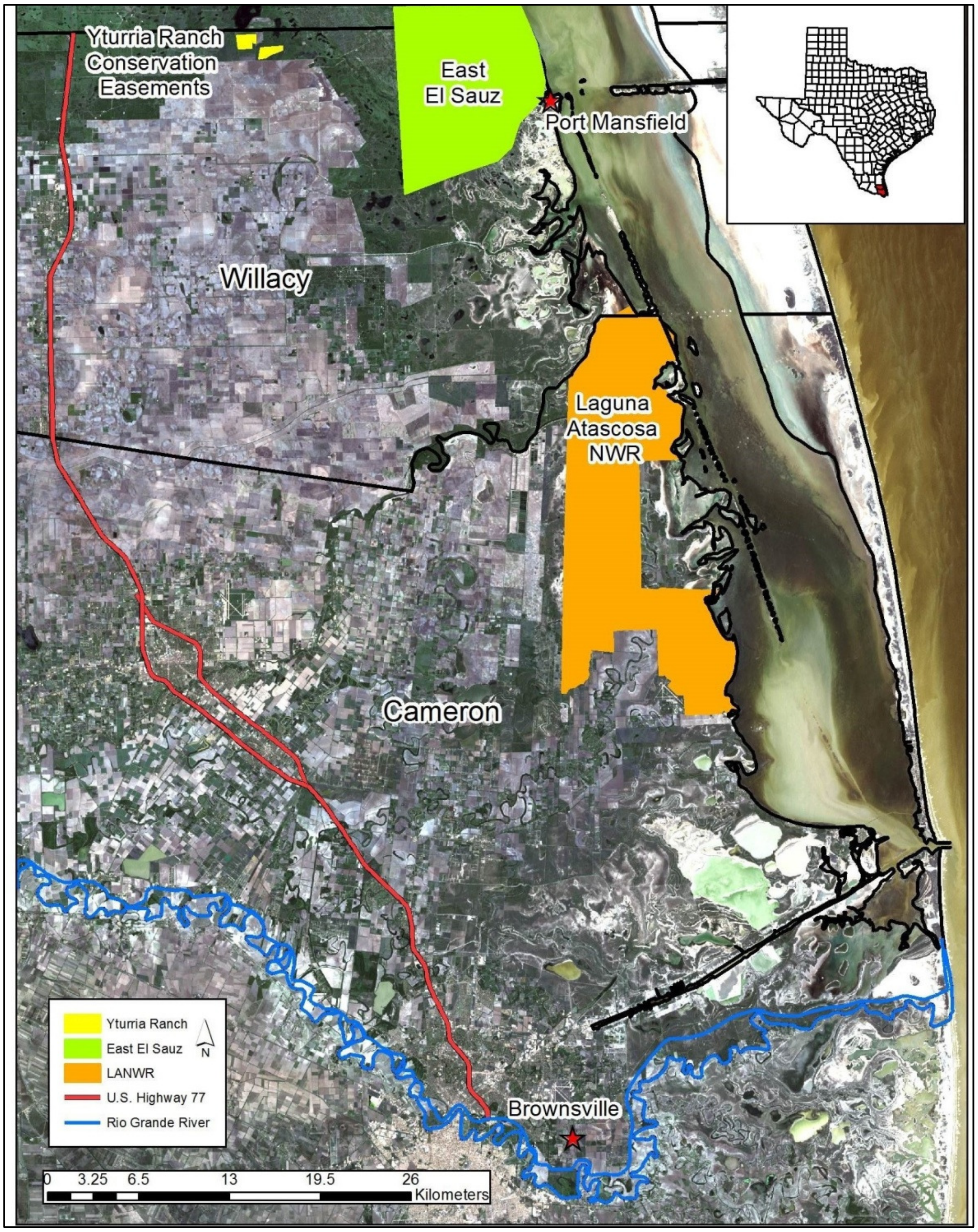

Fig. 1.1 Aerial photo of the Lower Rio Grande Valley (LRGV) in South Texas, indicating the three subpopulations sampled: Laguna Atascosa National Wildlife Refuge (LANWR), Cameron County (CAMERON), and Yturria Ranch (YTURRIA), and East El Sauz Ranch (EAST) in Willacy County (WILLACY).

The entire area is located within the Tamaulipan Biotic Province (Jahrsdoerfer & Leslie 1988) which ranges from southern Texas to northeastern Mexico. The area is characterized by a subtropical, semiarid environment of mild winters and hot summers with mean annual rainfall of 68 cm and mean annual temperatures of 23°C (Norwine & Bingham 1985).

Sample collection, DNA extraction and amplification

Samples were collected during previous radio-telemetry studies dating from 1984 to 2006 (Tewes 1986; Laack 1991; Beltran & Tewes 1995; Horne 1998; Shindle & Tewes 2000; Laack *et al.* 2005; Haines *et al.* 2005; Haines *et al*. 2006a; Haines *et al*. 2006c); samples dating from 2007 to the present were collected as part of current research and monitoring. Live-trapping followed standard capture and sedation protocols (Tewes 1986; Beltran & Tewes 1995; Shindle & Tewes 2000), as well as university Institutional Care and Use Committee protocols (2009-12-17A, 2012-12-20B). Three cc of blood was obtained and stored in Longmire's buffer (Longmire *et al.* 1997); some samples from the 1980s were clotted blood without buffer. Tissue samples were obtained from roadkill individuals.

I extracted DNA from blood and tissue using a commercial kit (Qiagen DNeasy, Valencia, California, USA). Genetic diversity of ocelots in Texas is lower than the closest adjacent populations in Mexico (Janečka *et al.* 2008; Janečka *et al*. 2011), and previous studies were limited by low allelic diversity in microsatellite markers. Thus, I selected the most informative 16 unlinked autosomal microsatellite loci (FCA008, FCA035, FCA045, FCA077, FCA082, FCA090, FCA124, FCA126, FCA133, FCA135, FCA205, FCA208, FCA229, FCA523, FCA1015, FCA1034) based on the number of effective alleles (N) and observed heterozygosity (H_o) in the WILLACY and CAMERON populations (Janečka *et al*. 2011). These were the most variable microsatellites of 41 loci previously screened by Janečka *et al*. (2011) or described by Menotti-Raymond *et al*. (1999) and Menotti-Raymond *et al.* (2003).

I amplified the loci separately using polymerase chain reaction (PCR) in a 10-µl reaction mix containing 5 µl of AmpliTaq Gold® PCR Master Mix (Applied Biosystems, Foster City, California), 0.24 µM of each primer, and 10-50 ng of DNA, adjusted to volume with autoclaved millipore water (dH_2O). Forward primers were labeled with a fluorescent dye on the 5' end (NED, HEX or 6FAM). Samples that amplified poorly were re-amplified, with the addition of 1.0 µl of bovine serum albumin (BSA) to the reaction mix. The PCR conditions started with an initial denaturation at 94°C, followed by 20 cycles each at 94°C for 30s, 62°C for 30s, 61°C for 30 s, 60°C for 30 s, and 72°C for 60 s, then 30 cycles each at 94°C for 30 s, 55°C for 90 s, and 72°C for 60 s, ending with a final extension of 60°C for 10 min, then hold at 4°C.

The PCR products were combined into three multiplex groups, and 1 µl of each mix for each individual was added to a sequencing plate. I created a separate mix of denaturing formamide (10 µl per sample, Hi-Di Formamide, Applied Biosystems) and DNA size standard (0.5 µl per sample, GeneScan ROX 500, Applied Biosystems) and added it to each well. The completed plate was run on an ABI 3130xl DNA Analyzer (Applied Biosystems) to separate the fragments. Each locus was examined in GeneMapper® version 4.0 (Applied Biosystems) to determine allele sizes. Although individuals sampled prior to 2006 were previously analyzed by Walker (1997) and Janečka *et al* (2011), I re-extracted all individuals from their original blood and tissue samples and created new genotypes for all individuals on one analyzer to ensure continuity. Every analysis included a positive and negative control and about 10% of recent samples were re-amplified to calculate a genotyping error rate.

I determined sex of unknown samples and verified sex of all samples that contained labeling errors using a molecular sexing primer designed from the zinc-finger region of the x- and y-chromosomes (Z*fx* and Z*fy*). Reaction mixes and PCR protocols followed Pilgrim *et al.* (2005), which were then run on an ABI 3130 xl DNA Analyzer and sized in GeneMapper®. An ocelot of known sex was included as a positive control on all runs.

Duplicate identification and group organization

Because of the long-term nature of the studies that collected these DNA samples, I checked the data for duplicate individuals using the Identity Analysis function in Program CERVUS 3.0.3 (Field Genetics Ltd., London, England), allowing for fuzzy matching up to two mismatches (Marshall *et al.* 1998). Matches were checked against capture data and other information to determine if the samples were of two individuals. Duplicates were removed from analyses. Genotypes were organized and output files for analyses were created using GenAlex 6.5 (Peakall & Smouse 2012).

To assess temporal changes in genetic diversity and variation in relation to previous estimates, I placed ocelots into original groups corresponding to previous studies by Janečka *et al.* (2011). These were individuals live-trapped on LANWR (CAMERON, *n* = 41), YTURRIA and other areas in northern WILLACY (*n* = 28), or near the Port of Brownsville, Texas (*n* = 1). Groups were: CAMERON — 1991–1998 (*n* = 29), and 1999–2005 (*n* = 12); WILLACY — 1991–1998 (*n* = 18), and 2005 (*n* = 10). The selection of microsatellite loci used in analyses differed between the studies, thus, I calculated new estimates of genetic diversity for the previously analyzed samples.

Additional samples collected in live-trapping from 1991 to 2005 not utilized in previous studies (CAMERON, *n* = 13; WILLACY, *n* = 9) were added to the original groups and separate estimates of genetic diversity and variation created for comparison (referred to as adjusted groups). Twelve additional ocelot mortality samples were collected from the following locations in Texas: roadkill — Port Mansfield (*n* = 1), Port Isabel (*n* = 1), Highway 106 in Cameron County (*n* = 1), unknown location (*n* = 3); and other — unknown (*n* = 6).

Current ocelots captured during 2006–2013 (*n* = 31) were placed into groups by location of capture: LANWR (CAMERON, *n* = 15), YTURRIA (*n* = 7), and EAST (*n* = 9). Current ocelots captured on YTURRIA and EAST were also analyzed together as one WILLACY population (*n* = 16).

Genetic diversity

For each sampling group, linkage disequilibrium (LD) was tested between all pairs of loci (*n* = 16) using a likelihood-ratio test in the computer program ARLEQUIN 3.1 (Excoffier *et al* 2005). I performed 16,000 permutations to ensure less than 1% difference between the true value and the null (Guo & Thompson 1992) and set the initial conditions for expectation-maximization (EM) at five. Any departures from Hardy-Weinberg Equilibrium (HWE) were examined at each locus and across all loci in ARLEQUIN using 100,000 Markov chain steps, and 10,000 dememorization steps. The Bonferroni method was used in LD and HWE tests, to correct *P*-values for multiple comparisons (Rice 1989).

Genetic variation was indexed for each group by number of alleles (A), number of effective alleles (A_e), observed heterozygosity (H_o), and expected heterozygosity (H_e) using GenAlEx 6.5. Previous research on ocelots in south Texas found that the CAMERON population has significantly lower H_e, and that WILLACY and CAMERON populations have lost diversity over time (Walker 1997; Janečka 2006; Janečka *et al*. 2008; Janečka *et* al. 2011). Though I used some of the same microsatellite loci used in Janečka *et al*.'s (2011) study, I ultimately chose loci specifically for their highest number of alleles and highest H_e. Because of differences in methods and differences in sample size between the groups, I also estimated allelic richness (A_R) using a rarefaction method in HP-RARE (Kalinowski 2005). To determine if allelic richness differed between the groups within the same time period, or within groups over time, I performed a 1-tailed Wilcoxon Signed Rank Test in Program R 2.15.2 (The R Foundation for Statistical Computing 2012) using the W statistic for small sample size, and set statistical significance as $P \leq 0.05$.

Genetic structure, differentiation, and population structure

Wright's F-statistics (Wright 1951) were used to estimate genetic sub-structure (F_{IS}, inbreeding coefficient) and genetic differentiation (F_{ST}, fixation index) between the subpopulations and over time by analyzing each group separately. A negative F_{IS} value indicates an excess of heterozygotes, and may result from small N_e or genetic drift. When F_{IS} is positive, there is a deficit of heterozygotes, which may indicate inbreeding within a subpopulation or a Wahlund effect (Allendorf & Luikart 2007). Genetic sub-structure (F_{IS}) within each group was calculated for each locus and subpopulation group in Program FSTAT 2.9.3 (Goudet 2002).

Genetic differentiation was evaluated between the subpopulations using pairwise F_{ST}, a measure of the amount of genetic divergence among subpopulations (Allendorf & Luikart 2007) and global F_{ST}. Pairwise comparisons between groups for the two primary sampling sites (CAMERON and WILLACY) were compared within each time period: (1991–1998, 1999–2005, 2006–2013). The current WILLACY group (2006–2013) was also analyzed separately as YTURRIA and EAST with pairwise comparisons between the sites and CAMERON. These were computed in ARLEQUIN over 1,023 permutations and statistical significance determined by comparing observed values to null values. Significance for both tests was evaluated at $P \leq 0.05$.

Previous analyses of population structure found that ocelots consistently grouped with their population of origin, and there was no indication of admixed individuals. To re-evaluate the previous determination of population structure, and examine the extant population structure with the addition of EAST, I employed a Bayesian clustering algorithm in STRUCTURE 2.3.4 (University of Chicago, Chicago, Illinois). All live-captured ocelots sampled between 1991 and 2013 ($n = 122$) were included. This method used a Markov Chain Monte Carlo (MCMC) simulation to determine the optimal number of genetic clusters (K, synonymous with subpopulations) for the data by minimizing HWE and LD (Prichard *et al*. 2000). I used runs with a burn-in of 100,000 repetitions to minimize the effects of the starting configuration, followed by 500,000 MCMC repetitions. I examined $K = 1–5$ genetic clusters, with five independent runs per assumed K, using an admixture model (mixed ancestry) and assuming allele frequencies were correlated. To determine the optimal number of genetic clusters, I averaged the log probability of data [LnP(D)] for each assumed K across the five runs, and computed the standard deviations (*SD*) among runs. Optimal K is indicated at the greatest LnP(D) value, and becomes more variable (increased *SD*) at larger values of K (Pritchard *et al*. 2000).

In practice, the K-values for some data sets may plateau without a clear "best" K value. Evanno *et al*. (2005) have recommended that the rate of change in the likelihood function (ΔK) can be used as an *ad hoc* means of choosing optimal K. I chose the number of genetic clusters where the LnP(D) approached closest to zero or Δ*K* peaked. The model-selected clusters and calculated ancestry proportions (*q*-values) for each individual were then checked against the three known subpopulations. Individuals were classified as resident of a cluster at *q*-values >0.80, and admixed when *q* was 0.25–0.80.

Assignment of unknowns and testing for dispersers

Assignment tests were used to determine origin of ocelots captured outside the three known subpopulations, roadkill individuals and unknown samples (no information on ID, location or date), and to detect for dispersers (i.e., first-generation migrants). I re-assessed the assignment of previously analyzed roadkill ocelots (*n* = 10) with the addition of the EAST subpopulation. These were collected near the following locations in Texas: Port Mansfield (*n* = 5), Lyford (*n* = 1), Sarita (*n* = 2), Highway 186 in WILLACY (*n* = 1), and Rio Hondo (*n* = 1) in CAMERON. One ocelot mortality that occurred in 2010 was collected near Raymondville, Texas.

First, I used a USEPOPINFO model in STRUCTURE to assign individuals of unknown origin (captured outside known sampling sites, roadkill, or unknown) to the three subpopulations (Piry *et al*. 2004). I assumed allele frequencies were correlated, admixture, and set the model to update allele frequencies using only individuals with POPFLAG = 1. I coded known individuals with an integer from one to three for their known origin (LANWR, YTURRIA, and EAST), while unknowns and roadkills were assigned a value of zero. Number of genetic clusters used was based on results of population structure from previous STRUCTURE analyses. The program then used the individuals from known clusters to aid in assignment of unknowns to their optimal cluster or multiple clusters (i.e., the individual may have mixed ancestry).

A separate USEPOPINFO model was used to test for migrants between the subpopulations by testing whether an individual was an immigrant or had recent immigrant ancestry. This procedure works well when the pre-defined populations are very informative (Pritchard *et al*. 2000), as when individuals occur primarily in two to three distinct genetic clusters. I tested values of MIGPRIOR (υ – migration rate) of 0.001–0.10 (Pritchard *et al.* 2000), assumed allele frequencies were correlated and allowed for admixture. In ~30 years of radio-telemetry monitoring of ocelots in South Texas (Tewes 1986; Laack 1991; Beltran & Tewes 1995; Horne 1998; Shindle & Tewes 2000; Laack *et al*. 2005; Haines *et al.* 2005; Haines *et al.* 2006a; Haines *et al*. 2006c), no dispersal has been detected between the sampling sites, thus, υ was expected to be small. Results that differ significantly between different values for υ, indicate that the data may be inadequate for drawing strong conclusions (Pritchard *et al.* 2010). I did not detect substantial differences because of the choice of υ, hence I report results for $\upsilon = 0.05$. Both assignments and tests for dispersers were executed with a burn-in of 100,000, followed by 500,000 MCMC repetitions, and a conservative q-value ≥ 0.90 to indicate assignment.

I also assigned unknown individuals and tested for first-generation migrants using the computer program GeneClass. I selected the modified likelihood ratio analysis (Rannala & Mountain 1997) to assign individuals to reference populations, and used assignment values $\geq 90\%$. To detect for first-generation migrants I used the likelihood computation of Rannala & Mountain (1997), then computed probabilities using a frequency-based algorithm (Paetkau *et al.* 2004) assuming $P \leq 0.05$ over 1,000 Monte Carlo simulations. The proportion of mis-assignments is positively correlated with dispersal (Rannala & Mountain 1997; Paetkau *et al.* 2004), thus, I compared the number of mis-assigned individuals and first-generation migrants between the three subpopulations.

Parentage analysis

I estimated parentage using the likelihood ratio approach in CERVUS (Marshall *et al.* 1998; Kalinowski *et al*. 2007). I assigned parentage using delta values at relaxed (80%) and strict (95%) confidence levels. To assess confidence, I computed delta values with simulations of 10,000 offspring (Jones *et al.* 2010), using allele frequencies from candidate parents (i.e., the group at large without offspring), a 1% genotyping error rate as determined from the data, and proportion of candidate parents sampled (estimated from trapping effort and remote camera survey data). The proportion of candidate parents sampled varied (50–70%) by sampling site. Because of the potential of mating between related individuals in small isolated populations, and the previously demonstrated loss of diversity (Walker 1997; Janečka *et al*. 2008; Janečka *et al*. 2011), I simulated close relatives among candidate parents. I used a maximum likelihood approach in ML-RELATE (Kalinowski *et al*. 2006) to estimate relatedness (r) between pairs of candidates (mothers and fathers separately). I then used the proportion of candidate individuals related at $r \geq 0.25$ as the proportion of relatives among candidate parents. I ran separate simulations for maternity and paternity over 100,000 iterations.

To avoid the inclusion of siblings as candidate parents, offspring were grouped into 5-year groups based on estimated birth years. Simulations, relatedness estimates and parentage was estimated separately for dams and sires by group. When possible, ages were calculated from one of the following ways: individuals caught as kittens, age estimated from live-capture, known deaths from roadkill or other mortalities where ages were estimated from the carcass. When parent-offspring relationships were suspected from demographic or field data (e.g., surveying den sites, remote camera photographs of mother and kitten), they were included as known parents in parentage analyses, then delta values were evaluated to determine if the relationship was correct.

For initial parentage analyses, I placed only known age individuals into 5-year groups for each subpopulation separately. I estimated maternity first, then entered mothers with 95% assignment into the paternity input file as known mothers before estimating paternity. Results were computed for all candidate parents with a positive LOD score and I report results based on confidence of the assignment (80% or 95%). I computed the reproductive input of assigned parents as a proportion of offspring produced from that parent. I ran exploratory analyses for each time period that included both subpopulations, individuals with uncertain ages, and roadkills that were known to be adults. This was used to test for possible parent-offspring assignments between the subpopulations which could indicate gene flow.

Results

Samples, duplicate identification, and group organization

I genotyped 181 individual samples collected from 1986 to 2013. Four individuals sampled in the 1980s failed to amplify or were missing >25% of the genotype, and were not used in further analyses. Removal of duplicates identified in the Identity Analysis resulted in 165 ocelot genotypes (61% male, 36% female, 3% unknown; Supporting Information, Table S1). These 165 individuals were comprised of captures from LANWR and surrounding areas (CAMERON, $n = 85$), captures on YTURRIA and surrounding areas (WILLACY, $n = 58$), roadkill ($n = 16$), and unknown ($n = 6$). Positive and negative PCR controls did not indicate contamination and my genotyping error rate was <1%.

Samples from 1991–2005 were placed into groups by site and time period as previously described. Three samples from the CAMERON 1999-2005 group used in previous studies were previously identified as the incorrect sex. These were corrected and included in the original group. I identified one CAMERON individual as a duplicate with an erroneous ID, so only the original ID and sample was used in the CAMERON 1999-2005 group. Other than these exceptions, individuals included in groups (n = 100) for direct comparison with previous studies were identical.

Adjusted groups that included additional individuals sampled from 1991 to 2005 (n = 22) were analyzed separately for genetic variability and estimates for both were reported. Results for the original and adjusted groups were compared for HWE, LD, F_{ST}, and F_{IS}; I observed no substantial differences, thus results from the adjusted groups were reported. The complete sample of all individuals from 1991 to 2013 (n = 122) was used in analyses of population structure, assignments, and tests for dispersers.

Nine samples that were roadkill with no location information (n = 3), and unknowns with no information other than they were ocelots collected prior to 2005 (n = 6) were only included in assignments tests. Results for samples with missing origin information were less informative and only included in Supporting Information, Table S2. Eighteen individuals were identified by the Identity Analysis to have erroneous IDs and were corrected or removed before further analyses.

Four samples could not be identified with the sexing primers: one roadkill with no origin information, and three unknown tissue samples (Supporting Information, Table S2).

Genetic diversity

One locus (FCA208) departed from HWE in CAMERON 1991-1998, while a different locus (FCA1015) was out of HWE in WILLACY 2006–2013. When that group was examined separately, FCA1015 departed from HWE for the EAST group only. Two pairs of loci

(FCA045-FCA126; FCA126-FCA133) were in LD for CAMERON 2006–2013, one (FCA035-FCA165) in WILLACY 1991–1998, and one (FCA045-FCA165) in YTURRIA 2006–2013.

Higher levels of genetic diversity (H_o and A_R) were observed in ocelots from WILLACY compared to those from CAMERON (Table 1.1). Though micosatellite loci differed between studies, only small differences were detected between groups that were identical to those analyzed by Janečka *et al*. (2011), and adjusted groups with additional ocelots sampled. In general, estimates with additional individuals were higher, but overall conclusions typically did not change. The original group from WILLACY 2005 had the lowest H_e (0.488 ± 0.046) and the lowest A_R (2.8 ± 0.72), similar to estimates from CAMERON (A_R = 2.59–2.9).

Genetic diversity (A_R) decreased from 1991 to 2013 for ocelots in CAMERON, while the subpopulation in WILLACY experienced a sharp decrease in 2005 (Table 1.1). The WILLACY group during 2006–2013 (A_R = 3.34 ± 0.94) appeared to have higher diversity than the previous group in 2005 (A_R = 2.8 ± 0.72). When the 2006–2013 group was examined separately by site, YTURRIA was slightly higher than 2005 (A_R = 2.91 ± 0.80), whereas, EAST was significantly higher (A_R = 3.48 ± 0.98). Consequently, the major contribution of the increased diversity for the 2006–2013 WILLACY group came from the addition of EAST samples.

For the original groups of Janečka *et al*. (2011), genetic diversity was significantly higher in WILLACY 1991–1998 (3.49 ± 0.83, W = -100, P = 0.01, Table 1.2), and 2006–2013 (W = -108, P = 0.002), compared to CAMERON 1991–1998 (2.9 ± 0.65) and 2006–2013 (2.59 ± 0.70). Diversity was not significantly different (W = 22, P = 0.29) between WILLACY 2005 and CAMERON 1999–2005 (2.88 ± 0.79). In the 2006–2013 group, both YTURRIA (W = -59, P = 0.03), and EAST (3.48 ± 0.98, W = -116, P = 0.001) had significantly higher diversity compared to CAMERON.

Table 1.1 Mean estimates (16 loci) of number of alleles (A), number of effective alleles (A_e), allelic richness (A_R)[1], observed (H_o) and expected heterozygosity (H_e), for ocelots sampled from Laguna Atascosa National Wildlife Refuge, Cameron County (CAMERON); and Yturria Ranch (YTURRIA), East El Sauz Ranch (EAST), and surrounding areas in Willacy County (WILLACY) during 1991–2013. Groups 1991 to 2005 correspond to Janečka *et al*. (2011), values in parentheses (when estimates differed) include additional samples within groups (n = 22). Standard errors (SE) and sample sizes (n) indicated.

	n	A	SE	A_e	SE	A_R	SE	H_o	SE	H_e	SE
CAMERON	56 (69)	3.50 (3.63)	0.26	2.56 (2.58)	0.18	2.86 (2.88)	0.65	0.582 (0.587)	0.044 (0.041)	0.579 (0.584)	0.030
1991–1998	29 (35)	3.31 (3.38)	0.22	2.55 (2.58)	0.18	2.90 (2.92)	0.65 (0.63)	0.573 (0.580)	0.046 (0.043)	0.572 (0.581)	0.034 (0.032)
1999–2005	12 (19)	3.38 (3.44)	0.27	2.43 (2.52)	0.19 (0.18)	2.88 (2.89)	0.79 (0.73)	0.583 (0.589)	0.057 (0.048)	0.55 (0.573)	0.035 (0.031)
2006–2013	15	2.81	0.21	2.34	0.17	2.59	0.70	0.597	0.052	0.539	0.035
WILLACY	44 (53)	4.31 (4.44)	0.27	3.03 (3.00)	0.26	3.42 (3.40)	0.81 (0.77)	0.582 (0.598)	0.055 (0.056)	0.628 (0.628)	0.034
1991–1998	18 (25)	4.13 (4.19)	0.29	3.13 (3.09)	0.26 (0.24)	3.49 (3.44)	0.83 (0.81)	0.611 (0.625)	0.051 (0.054)	0.644 (0.639)	0.031 (0.034)
2005	10 (12)	3.19 (3.56)	0.19 (0.18)	2.22 (2.34)	0.21	2.80 (2.98)	0.72 (0.64)	0.575 (0.599)	0.078 (0.075)	0.488 (0.522)	0.046 (0.042)
2006–2013	16	4.00	0.30	2.91	0.26	3.34	0.94	0.555	0.060	0.609	0.038

Table 1.1. (continued)

	n	A	SE	A_e	SE	A_R	SE	H_o	SE	H_e	SE
YTURRIA											
2006–2013	7	3.19	0.25	2.28	0.18	2.91	0.80	0.536	0.067	0.524	0.033
EAST											
2006–2013	9	3.94	0.30	2.98	0.28	3.48	0.98	0.569	0.063	0.648	0.040

[1] Estimates of allelic richness (A^R) were corrected for sample size (smallest $n = 7$) by rarefaction method.
CAMERON - Laguna Atascosa National Wildlife Refuge, Cameron County.
WILLACY - Yturria Ranch and surrounding areas in Willacy County.
YTURRIA - Yturria Ranch, Willacy County.
EAST - East El Sauz Ranch, Willacy County.

Diversity did not significantly decrease within CAMERON, until between 1999–2005 and 2006–2013 (Table 1.2), when diversity was signficantly lower in the latter period ($W = 110$, $P = 0.01$). Diversity significantly declined in WILLACY from 1991–1998 ($W = 110$, $P = 0.002$) to 2005, then was significantly higher during 2006–2013 (i.e., YTURRIA and EAST combined, $W = -98$, $P = 0.01$). Comparing the adjusted groups that included additional samples to original groups, there was not a significant difference between WILLACY 2005 (2.98 ± 0.64) and 2006–2013 ($W = 19$, $P = 0.32$).

The EAST group during 2006–2013 was significantly higher than both CAMERON ($W = -116$, $P = 0.001$) and WILLACY ($W = -104$, $P = 0.002$, Table 1.2). For the entire sample period 1991–2013, WILLACY (3.42 ± 0.81, $W = -108$, $P = 0.003$) retained significantly higher levels of diversity than CAMERON (2.86 ± 0.65).

Genetic structure, differentiation, and population structure

The groups for CAMERON during 1991–1998 and 1999–2005 satisfied HWE ($F_{IS} = 0.02$, $P = 0.69$; $F_{IS} = -0.02$, $P = 0.66$, respectively). The CAMERON 2006–2013 group was negative, though not statistically signficant ($F_{IS} = -0.07$, $P = 0.09$); and WILLACY 2005 was significantly negative ($F_{IS} = -0.13$, $P = 0.02$). Two groups had significantly positive F_{IS} values (WILLACY 1991–1998: $F_{IS} = 0.08$, $P = 0.01$; WILLACY 2006–2013: $F_{IS} = 0.12$, $P = 0.01$), indicating a departure from HWE and a Wahlund effect for the 2006–2013 group. When the WILLACY 2006–2013 group was examined as two separate subpopulations, the YTURRIA group satisfied HWE ($F_{IS} = 0.05$, $P = 0.81$), while EAST did not ($F_{IS} = 0.13$, $P = 0.02$).

Table 1.2 Estimates of allelic richness (A_R) for each group, by locus and overall mean and standard deviation (*SD*). Statistical signficance ($P \leq 0.05$) between comparisons within site and time period, and between sites and time period indicated in superscript; test statistics and *P*-values from Wilcoxon Signed Rank test in R given below. Groups are Laguna Atascosa National Wildlife Refuge, Cameron County (CAMERON); and Yturria Ranch (YTURRIA), East El Sauz Ranch (EAST), and surrounding areas in Willacy County (WILLACY), Texas, for 1991–1998, 1999–2005, and 2006–2013.

	CAMERON (*n* = 56)			WILLACY (*n* = 44)				
Locus	1991–1998^{a} (*n* = 29)	1999–2005^{c} (*n* = 12)	2006–2013^{b,c,f,g} (*n* = 15)	1991–1998^{a,d} (*n* = 18)	2005^{d,e} (*n* = 10)	2006–2013^{b,e} (*n* = 16)	YTURRIA^{f,h} 2006–2013 (*n* = 7)	EAST^{g,h} 2006–2013 (*n* = 9)
FCA008	3.71	3.63	3.86	3.38	3.45	3.53	3.36	3.79
FCA035	3.42	3.09	2.89	3.14	2.95	2.52	2.00	2.82
FCA045	1.98	1.98	1.99	2.97	2.76	2.00	2.00	2.00
FCA077	1.76	1.82	2.00	2.47	2.49	2.31	2.00	2.55
FCA082	2.57	2.83	2.00	3.78	2.98	3.47	2.71	3.63
FCA090	2.69	2.82	2.72	3.71	3.48	4.43	3.43	4.45
FCA124	3.40	3.98	3.61	4.67	4.59	4.85	3.87	4.74
FCA126	3.51	4.19	3.52	4.66	3.44	4.56	4.64	4.70
FCA133	2.54	1.99	2.00	3.19	2.39	2.96	2.93	2.99
FCA165	3.57	3.72	3.28	5.00	2.39	4.54	3.42	5.14
FCA205	2.53	2.42	2.33	3.84	2.26	3.38	2.71	3.73
FCA208	2.91	2.41	2.00	2.95	1.50	2.00	1.93	2.11
FCA229	3.78	3.88	2.92	3.97	2.88	4.11	3.43	4.33
FCA523	2.86	2.93	2.71	2.65	1.96	2.61	2.65	2.55

Table 1.2. (continued)

	CAMERON ($n = 56$)			WILLACY ($n = 44$)				
Locus	1991–1998[a] ($n = 29$)	1999–2005[c] ($n = 12$)	2006–2013[b,c,f,g] ($n = 15$)	1991–1998[a,d] ($n = 18$)	2005[d,e] ($n = 10$)	2006–2013[b,e] ($n = 16$)	YTURRIA[f,h] 2006–2013 ($n = 7$)	EAST[g,h] 2006–2013 ($n = 9$)
FCA1015	1.99	2.00	2.00	2.00	2.91	2.87	2.00	2.93
FCA1034	3.17	2.41	1.63	3.41	2.39	3.26	3.43	3.19
Mean	2.90	2.88	2.59	3.49	2.80	3.34	2.91	3.48
SD	0.65	0.79	0.70	0.83	0.72	0.94	0.80	0.98

[a] 1991–1998: CAMERON—WILLACY, $W = -100$, $P = 0.005$.

[b] 2006–2013: CAMERON—WILLACY, $W = -108$, $P = 0.003$.

[c] CAMERON 1999–2005—2006–2013, $W = 96$, $P = 0.007$.

[d] WILLACY 1991–1998—2005, $W = 110$, $P = 0.002$.

[e] WILLACY 2005—2006–2013, $W = -98$, $P = 0.006$.

[f] 2006–2013: CAMERON—YTURRIA, $W = -59$, $P = 0.03$.

[g] 2006–2013: CAMERON—EAST, $W = -116$, $P = 0.003$.

[h] 2006–2013: YTURRIA—EAST, $W = -104$, $P = 0.002$.

The global F_{ST} (0.12) was signficant ($P = 0.001$), as well as all pairwise comparisons between groups ($P<0.001$). Differentiation almost doubled between CAMERON and WILLACY from 0.15 (1991–1998) to 0.231 (1999–2005). The F_{ST} value for the 2006–2013 group remained high between CAMERON and YTURRIA (0.22), moderate between CAMERON and EAST (0.12), and low between YTURRIA and EAST (0.05). When current YTURRIA and EAST were combined into one WILLACY group (2006–2013), differentiation was moderate with contemporary CAMERON (0.16).

The results for population structure from STRUCTURE indicate some support for multiple scenarios. The mean LnP(D) plateaued at $K = 2$, with only small increases from $K = 3$ to 5 (Fig. 1.2). The plot of the ΔK (Evanno *et al*. 2005) indicated the highest support for $K = 2$ (Fig. 1.2). Evaluation of the ancestry proportions (q-values) for $K = 2$ (Fig. 1.3), showed that most individuals captured in CAMERON (98%) or within WILLACY (95%) assigned to their own genetic clusters ($q \geq 0.80$) which corresponded to the known subpopulations. One individual from CAMERON appeared admixed ($q = 0.60$). Two individuals from WILLACY appeared admixed ($q = 0.48$–0.62).

At $K = 3$ (Fig. 1.3), there was still high assignment of individuals from CAMERON (94%) to one genetic cluster. Three individuals captured in CAMERON assigned just below the threshold ($q = 0.80$–0.87), one appeared admixed between clusters corresponding to CAMERON and WILLACY. There was greater admixture within WILLACY between the two sampling sites of YTURRIA and EAST. In general, the third genetic cluster was comprised of individuals sampled from YTURRIA in 2005 (Fig. 1.3), a similar pattern to that detected by Janečka *et al.* (2011).

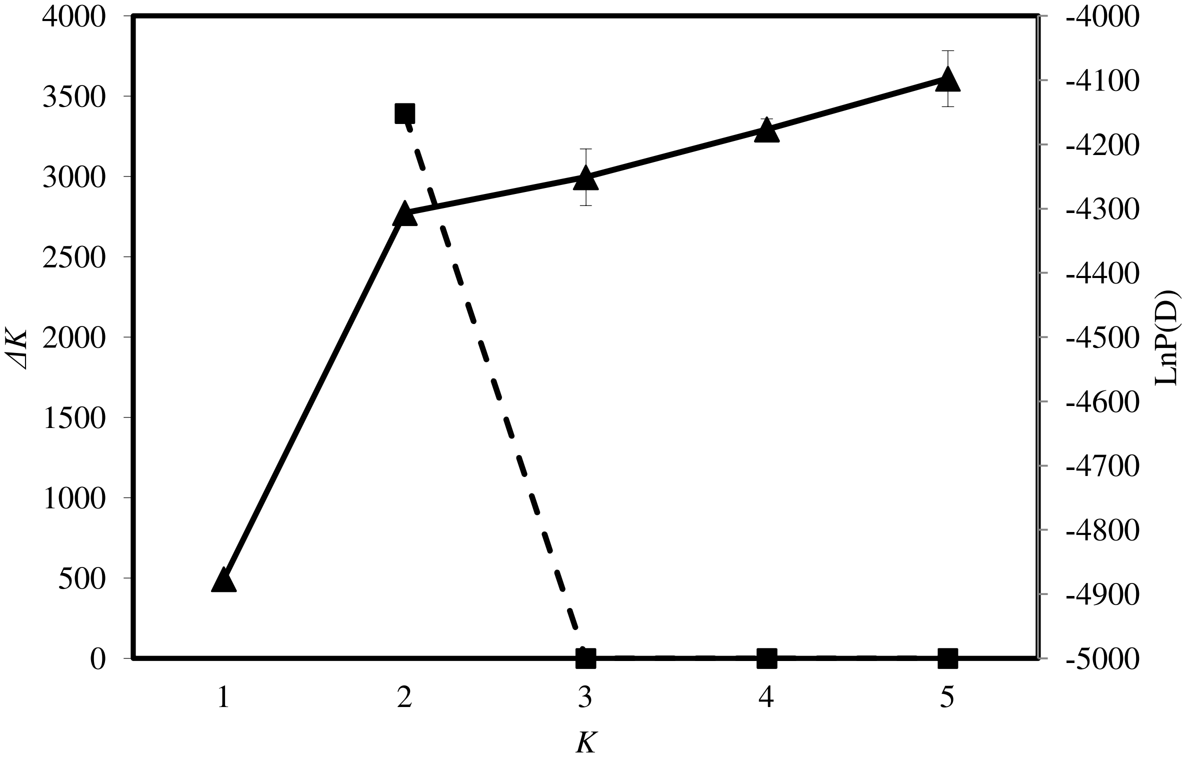

Fig. 1.2 The log probability of the data [LnP(D)] and Δ*K* from STRUCTURE for known ocelots (*n* = 122) sampled from Cameron and Willacy counties, Texas, during 1991–2013. Solid line and secondary vertical axis (right) show the mean LnP(D) for *K* = 1–5 over five independent runs with standard deviation error bars. Dashed line and primary vertical axis (left) indicate estimates of the Δ*K* using the LnP(D) values from STRUCTURE. *K* is the number of genetic clusters.

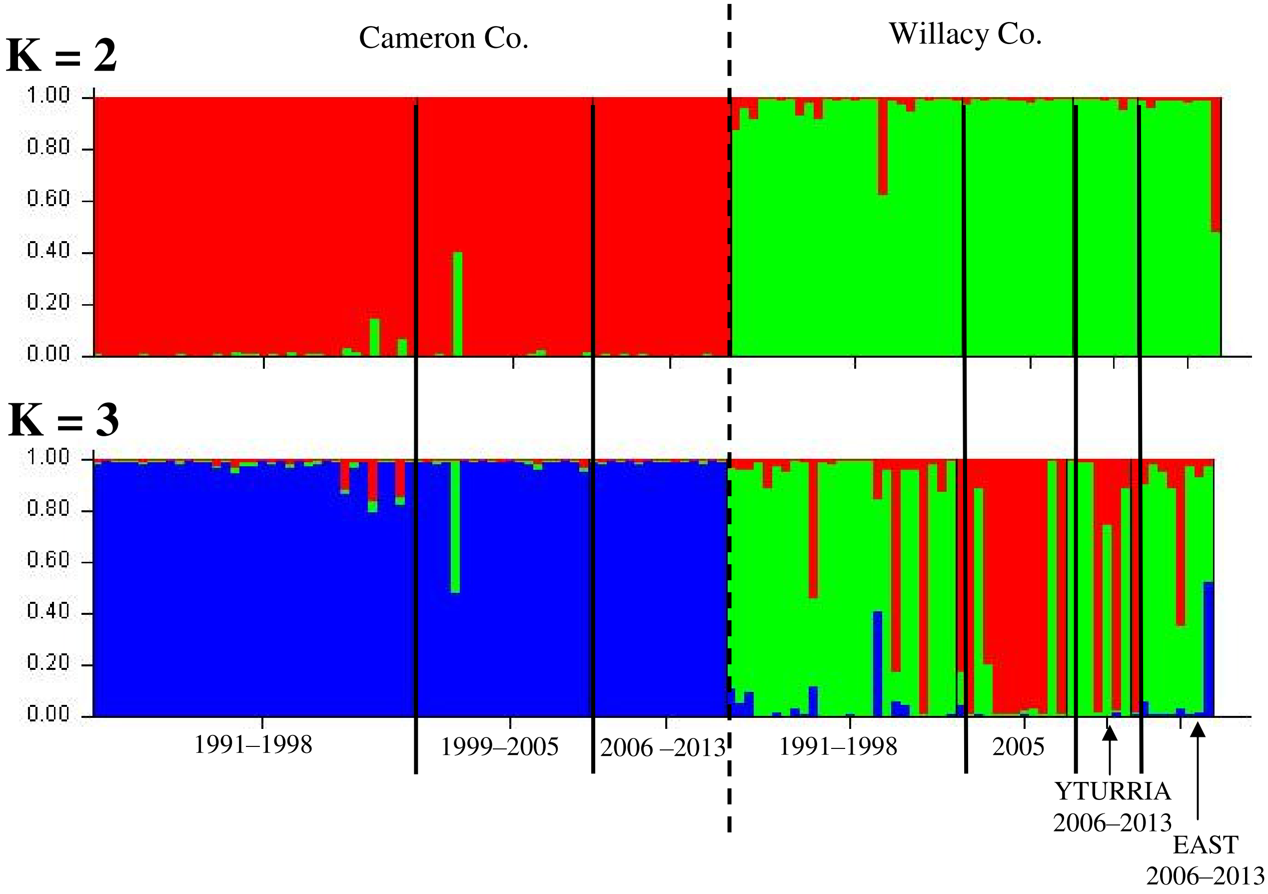

Fig. 1.3 Ancestry proportions (*q*-values) from STRUCTURE for ocelots sampled in Cameron and Willacy (Yturria Ranch [YTURRIA] and East El Sauz Ranch [EAST]) counties, Texas, during 1991–2013 (n = 122). Each column represents *q*-values for one individual for genetic clusters K = 2 (top), K = 3 (middle), and K = 4 (bottom). Sample origin subpopulation and time period designated below.

Because of the higher levels of A_R and H_e in contemporary EAST ocelots, as well as differences in genetic sub-structure (EAST significantly positive, while YTURRIA in equilibrium), I explored population structure within the WILLACY subpopulation. The LnP(D) and ΔK (Fig. 1.4) indicated strong support for $K = 2$, some support for $K = 3$, and greater variability for clusters $K = 4$ or 5. Ancestry proportions for $K = 2$ and 3 (Fig. 1.5) again demonstrated a separate cluster comprised almost completely of individuals captured on YTURRIA in 2005, as well as some individuals captured during 2006–2013. The YTURRIA 2005 group as a separate cluster is further supported by low H_e (0.488–0.522) for individuals from 2005. High levels of admixture between individuals captured on YTURRIA during 1991–1998 and 2006–2013, with those captured on EAST and other surrounding areas during those temporal periods, was supported by field observations (individuals detected residents on a site that was not their capture origin) and the lower levels of genetic differentation ($F_{ST} = 0.05$) between current (2006–2013) YTURRIA and EAST.

Assignment of unknowns and testing for dispersers

After removing 10 samples with missing information (Supporting Information, Table S2), I attempted to assign 14 ocelots from outside the known subpopulations to their most likely origin. The 14 individuals included 10 samples previously analyzed by Janečka *et al.* (2011) consisting of nine roadkill and one captured near the Port of Brownsville. The remaining four samples were of roadkills not included in previous studies ($n = 3$) or that occurred after 2005 ($n = 1$).

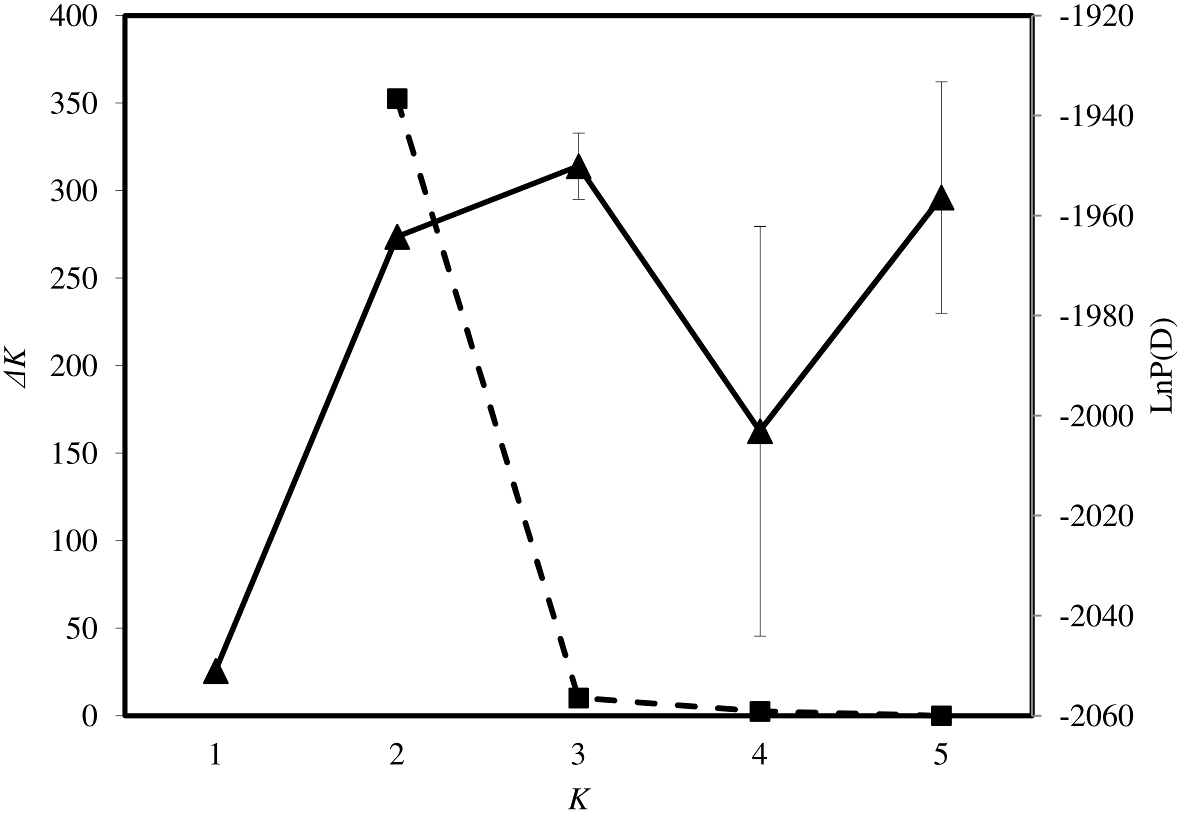

Fig. 1.4 The log probability of the data [LnP(D)] and Δ*K* from STRUCTURE for known ocelots (*n* = 53) sampled from Yturria Ranch, East El Sauz Ranch, and other surrounding areas in Willacy County, Texas, during 1991–2013. Solid line and secondary vertical axis (right) show the mean LnP(D) for *K* = 1–5 over five independent runs with standard deviation error bars. Dashed line and primary vertical axis (left) indicate estimates of the Δ*K* using the LnP(D) values from STRUCTURE. *K* is the number of genetic clusters.

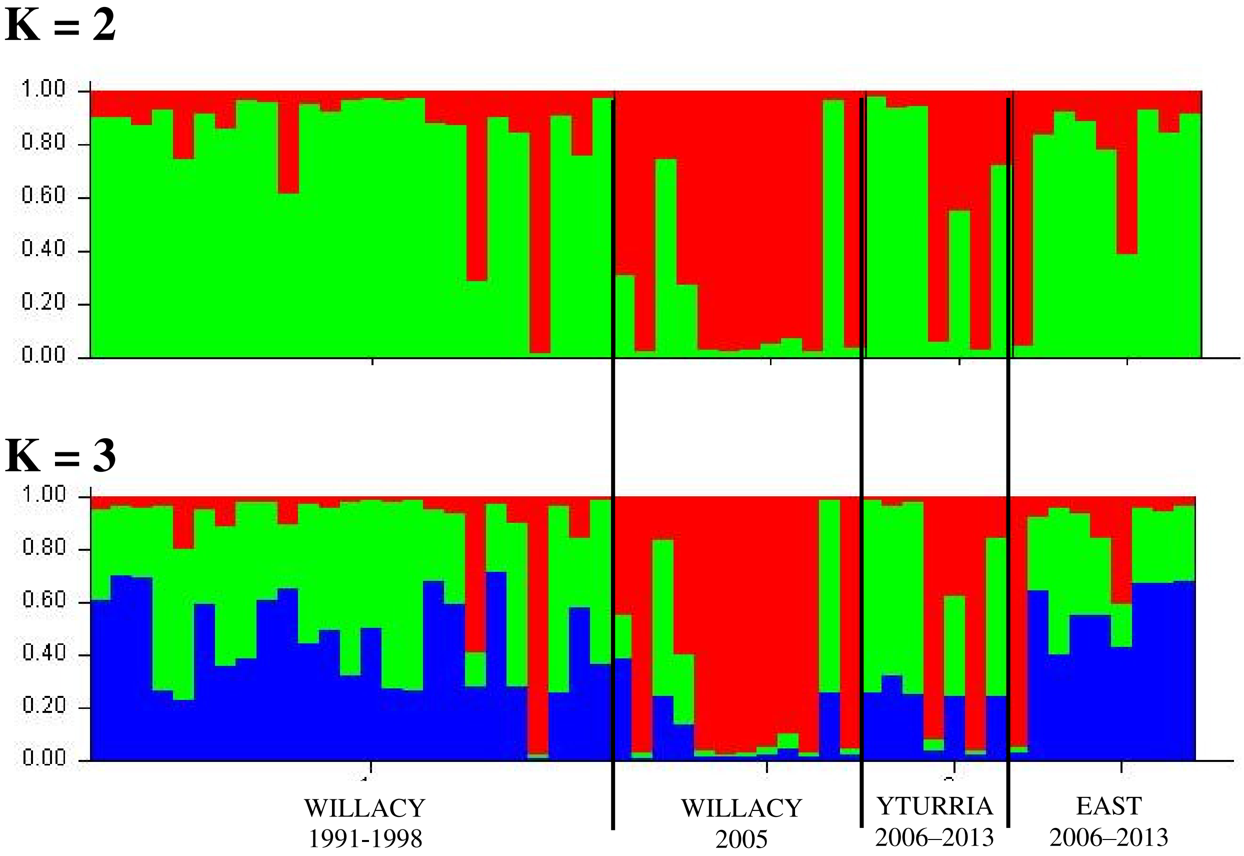

Fig. 1.5 Ancestry proportions (*q*-values) from STRUCTURE for known ocelots (*n* = 53) sampled from Yturria Ranch (YTURRIA) and East El Sauz Ranch (EAST), and other surrounding areas in Willacy County (WILLACY), Texas, during 1991–2013. Each column represents *q*-values for one individual for genetic clusters *K* = 2 (top), and *K* = 3 (bottom). Sample origin subpopulation and time period designated below.

Four individuals were assigned with confidence in STRUCTURE and five in GeneClass (Table 1.3). Four roadkill samples found in Willacy (Sarita, Port Mansfield [*n* = 2] and Lyford) assigned with confidence in STRUCTURE to the EAST subpopulation**.** Four others found near Port Mansfield assigned just below confidence (*q* = 0.70-0.80) to EAST. The GeneClass results for these individuals either assigned to the same location, or appeared admixed between the two WILLACY sites (YTURRIA and EAST).

Four ocelots could not be assigned with confidence with either method. One individual appeared to have admixture between CAMERON and WILLACY according to STRUCTURE, but assigned with confidence to EAST in GeneClass. There were multiple individuals sampled from WILLACY or nearby counties that could not be assigned with confidence to WILLACY or EAST. There were no other mis-assignments between CAMERON and WILLACY.

I did not detect any direct evidence for first-generation migrants between CAMERON and WILLACY using STRUCTURE, though one individual captured on LANWR in CAMERON, may have had partial ancestry from WILLACY. Male ocelot (M238) was captured as a sub-adult (estimated 12-18 mos old) on 12 April 2000. The posterior probability (*P*) indicated that there was a 50% probability for this individual to have a grandparent from YTURRIA, and 30% probability to have a grandparent from EAST. The same individual was identified in GeneClass as either being a first-generation migrant, or having immigrant ancestry from EAST.

Analyses of the two sites (i.e., YTURRIA and EAST) within WILLACY indicated multiple individuals as either migrants or with recent migrant ancestry between the two sites. Program STRUCTURE did not identify any migrant individuals, but GeneClass identified five individuals captured on YTURRIA that were either first-generation migrants, or had immigrant ancestry from EAST or unsampled areas. One individual captured on EAST had a higher

Table 1.3 Genetic assignments from STRUCTURE and GeneClass for 14 unknown origin individuals from Texas radio-collared ($n = 1$) or found as roadkill ($n = 13$) outside of the known ocelot subpopulations during 1988–2010. Reference populations were individuals sampled from Cameron County (Laguna Atascosa National Wildlife Refuge, $n = 69$) and Willacy County (Yturria Ranch, $n = 39$; East El Sauz Ranch, $n = 9$; and surrounding areas, $n = 5$), Texas, during 1991–2013. Assignment values to each subpopulation are estimated ancestry proportions (q-values) from STRUCTURE and likelihood ratio scores from GeneClass (P). Scores $q \geq 0.90$ or $P \geq 90$ indicate substantial support for assignment.

ID	Sex	County	Location	Date	*q* (STRUCTURE)			*P* (GeneClass)		
					Ca	Wi	Ea	Ca	Wi	Ea
Roadkill										
M125	M	Cameron	Port Isabel	10/23/88	0.6	0.1	0.3	99.6	0.1	0.3
M162	M	Willacy	Port Mansfield	11/20/89	0.1	0.3	0.6	0.0	72.1	27.9
M168	M	Willacy	Highway 186	7/11/90	0.1	0.1	0.8	0.0	2.1	97.9
31-AGO-90	M	Kenedy	Sarita	8/31/90	0.4	0.0	0.6	0.0	6.9	93.1
PM1	M	Willacy	Port Mansfield	7/29/91	0.0	0.1	0.9	0.0	36.7	63.3
Port_Man	M	Willacy	Port Mansfield	10/93	0.0	0.2	0.8	0.0	29.7	70.3
PM93	M	Willacy	Port Mansfield	10/93	0.0	0.1	0.9	0.0	49.9	50.1
P-97-14	M	Cameron	Highway 106	4/7/97	0.8	0.1	0.1	100	0.0	0.0
Y962	M	Willacy	Lyford	10/27/97	0.0	0.0	1.0	0.0	86.0	14.1
SARITA	M	Kenedy	Sarita	10/15/97	0.0	0.4	0.5	0.0	85.5	14.6
RK1999	F	Willacy	Highway 186	6/15/99	0.2	0.0	0.7	0.0	0.2	99.8

Table 1.3. (continued)

					q (STRUCTURE)			*P* (GeneClass)		
ID	Sex	County	Location	Date	Ca	Wi	Ea	Ca	Wi	Ea
1/12/04	M	Willacy	Port Mansfield	1/12/04	0.1	0.1	0.9	0.0	80.3	19.7
HWY77RK2010	M	Willacy	Raymondville	12/24/10	0.0	0.8	0.2	0.0	29.7	70.3
Radio-collared										
Port1	M	Cameron	Port of Brownsville	4/27/98	1.0	0.0	0.0	100	0.0	0.0

Ca, Cameron 1991–2013; Wi, Willacy 1991–2005 and Yturria Ranch 2006–2013; Ea, East El Sauz Ranch 2006–2013.

likelihood to be a first-generation migrant or have immigrant ancestry from YTURRIA. There were no individuals captured in WILLACY that appeared to be first-generation migrants or to have any immigrant ancestry from CAMERON.

Parentage analysis

Because field observations (i.e., remote camera surveys and live-trapping) confirm that occasional movement has occurred between the known sites within WILLACY, parentage for the two sites (YTURRIA and EAST) was analyzed together as one WILLACY population. I assessed assignment of maternity or paternity for 140 offspring. Overall, I assigned dams and sires to 52% and 53% of all offspring, respectively. At 95% confidence, I assigned dams to 29% of offspring and sires to 25% (Table 1.4). At 80% confidence, I assigned dams to 24% of offspring and sires to 27%.

For CAMERON, I assigned sires to 58% of offspring and dams to 52% of offspring. At 95% confidence, 28% of offspring were assigned dams, and 25% sires. At 80% confidence, 30% of offspring were assigned dams, and 27% sires. Overall, I assigned a parent pair to 10 LANWR offspring at 95% confidence, and 20 pair at 80% confidence (Table 1.5).

For WILLACY, I assigned sires to 46% of offspring and dams to 53% of offspring (Table 1.4). At 95% confidence, 31% of offspring were assigned dams, and 25% sires. At 80% confidence, 11% of offspring were assigned dams, and 27% sires. Overall, I assigned a parent pair to eight LANWR offspring at 95% confidence, and 13 offspring at 80% confidence (Table 1.5).

Table 1.4 Percentage (%) of parentage assignments at 95% and 80% confidence for 140 possible ocelot offspring (CAMERON, *n* = 81; WILLACY, *n* = 59) from Laguna Atascosa National Wildlife Refuge in Cameron County (CAMERON), and Yturria Ranch, East El Sauz Ranch and surrounding areas in Willacy County (WILLACY), Texas, during 1988–2013.

	80% Sire	80% Dam	95% Sire	95% Dam	Total Sire	Total Dam
CAMERON	27.2	29.6	24.7	28.4	51.9	58.0
WILLACY	27.1	11.1	25.4	30.5	52.5	45.8
TOTAL	27.1	23.6	25	29.3	52.1	52.9

Table 1.5 Parentage assignments for 95 offspring from Laguna Atascosa National Wildlife Refuge, Cameron County (CAMERON, *n* = 59); and Yturria Ranch, East El Sauz Ranch and surrounding areas in Willacy County (WILLACY, *n* = 36), Texas, during 1988–2013. 80% and 95% confidence levels indicated.

	80% Confidence		95% Confidence	
ID	Sire	Dam	Sire	Dam
CAMERON (*n* = 59)				
F151	-	-	-	LAC-42
F172	-	-	M132	F88
F176	-	-	M132	F158
F189	-	-	M132	F88
F194	-	-	-	F186
F214	-	-	M170	F194
F223	M132	-	-	F219
F225	-	-	-	F184
F228	-	-	M170	F194
F230	-	-	M170	F228
F235	M299	F230	-	-
F236	M222	F194	-	-
F242	M170	-	-	-
F245	M240	F242	-	-
F247	-	-	-	F225
F249	-	-	M240	F223
F250	-	F184	-	-
F265	-	F167	-	-
F274	M263	F265	-	-
F282	-	F236	-	-

Table 1.5. (continued)

	80% Confidence		95% Confidence	
ID	Sire	Dam	Sire	Dam
CAMERON (continued)				
M100	-	-	LAC-128	-
M132	-	-	-	LAC-68
M170	-	-	-	LAC-68
M174	-	-	M132	-
M175	-	LAC-150	M174	-
M183	-	-	-	F158
M192	-	F184	-	-
M193	-	-	-	F88
M195	M174	F88	-	-
M198	-	-	M191	-
M202	-	-	M183	-
M203	M193	-	-	-
M205	-	-	M203	-
M209	M179	-	-	-
M217	-	-	M132	F184
M218	-	-	M183	-
M224	-	-	-	F167
M226	M174	-	-	F88
M227	M192	F172	-	-
M230	-	F172	M227	-
M237	-	-	M205	F172
M238	Y949[2]	-	-	-
M241	-	-	M239	F219
M243	-	F88	M193	-

Table 1.5. (continued)

	80% Confidence		95% Confidence	
ID	Sire	Dam	Sire	Dam
CAMERON (continued)				
M244	-	F184	-	-
M246	-	F236	-	-
M248	M240	-	-	-
M258	M227	F194	-	-
M259	-	-	-	F235
M263	M227	-	-	-
M266	-	F235	M224	-
M267	-	F235	-	-
M270	M263	F265	-	-
M272	M224	F265	-	-
M273	M227	F265	-	-
M275	M224	F223	-	-
M276	M258	F194	-	-
M279	M258	F247	-	-
M283	-	-	M275	F282
WILLACY (*n* = 36)				
ER1	-	-	RR7	-
ER2	-	-	STC-34	-
F298	-	-	RR4	-
RR7	-	-	-	RR6
Y947	-	YT8	STC-18	-

Table 1.5. (continued)

	80% Confidence		95% Confidence	
ID	Sire	Dam	Sire	Dam
WILLACY (continued)				
Y961/Y11	Y949	-	-	-
Y962	-	-	-	YT8
Y964	Y949	-	-	-
Y973	Y949	-	-	RK1999
Y974	-	-	Y962	Y992
Y975	-	-	Y962	YT8
Y976	-	-	P-95-15	-
Y977	-	Y992	Y947	-
Y992	RR7	-	-	RR6
Y1	Y993-72	-	-	Y971
Y2	Y982	-	-	-
Y3	YT2	-	-	Y947
Y4	Y2	Y992	-	-
Y5	-	Y4	-	-
Y6	Y982	-	-	-
Y7	Y982	Y3	-	-
Y8	Y982	-	-	Y4
Y9	-	-	Y993-72	Y3
Y10	Y982	-	-	Y4
Y12	Y947	RR6	-	-
Y14	Y961	Y3	-	-
Y16	-	Y14	Y12	-
Y17	-	-	Y2	Y1
Y18	-	-	Y2	Y14

Table 1.5. (continued)

	80% Confidence		95% Confidence	
ID	Sire	Dam	Sire	Dam
WILLACY (continued)				
Y21	-	-	Y6	Y1
Y22	Y12[2]	-	Y2[2]	Y16
E-1F	-	-	E-3M	-
E-2M	-	-	-	Y974
E-5F	Y993-72	Y1	-	-
E-7F	1/12/2004	-	-	-
E-10F	-	-	Y7	Y8

[1] M238 captured on Laguna Atascosa National Wildlife Refuge, Cameron County, assigned at 80% confidence a sire, Y949, originally captured on Yturria Ranch, Willacy County.

[2] Y12 assigned as sire at 80% confidence when dam unknown; Y16 assigned as dam at 95% confidence and when analyzed with known sire, Y2 scores zero delta as pair, but 95% confidence as trio.

There was one parent-offspring assignment (80%) between CAMERON and WILLACY (Table 1.5). Within WILLACY, there were eight parent-offspring assignments between individuals captured on YTURRIA and those captured on EAST and other surrounding areas. Three individuals from WILLACY were assigned a parent that was a roadkill (95%, $n = 2$; 80%, $n = 1$) originally found near Port Mansfield. One individual from CAMERON was assigned a sire captured near the Port of Brownsville at 80% confidence.

Most assigned parents produced only 1-2 offspring, but two individuals in CAMERON, female F88 and male M132, produced 17% and 25% of sampled offspring at 95% confidence, respectively. Most candidate parents in WILLACY assigned to fewer than two offspring at 95% confidence, but female Y1 produced 17% of the offspring in that subpopulation.

Both CAMERON and WILLACY contained inbred parent-offspring assignments. The mean and maximum inbreeding coefficient (F) for CAMERON was 0.014 and 0.25, respectively. Six inbred relationships were detected, four between parent-offspring and two between grandparent or great-grandparents (Fig. 1.6).

The mean and maximum F for WILLACY was 0.014 and 0.27, respectively. I detected eight inbred relationships (Fig. 1.7), three between parent-offspring, three between grandparent or great-grandparent, one with half-siblings where one parent was an offspring of an inbred grandparent, and one between parent-offspring where the parent had grandparents which were half-siblings.

Discussion

Ocelots on LANWR in CAMERON have continued to lose genetic diversity over time and become more genetically isolated. There was a 10% decrease in genetic diversity (A_R) in the

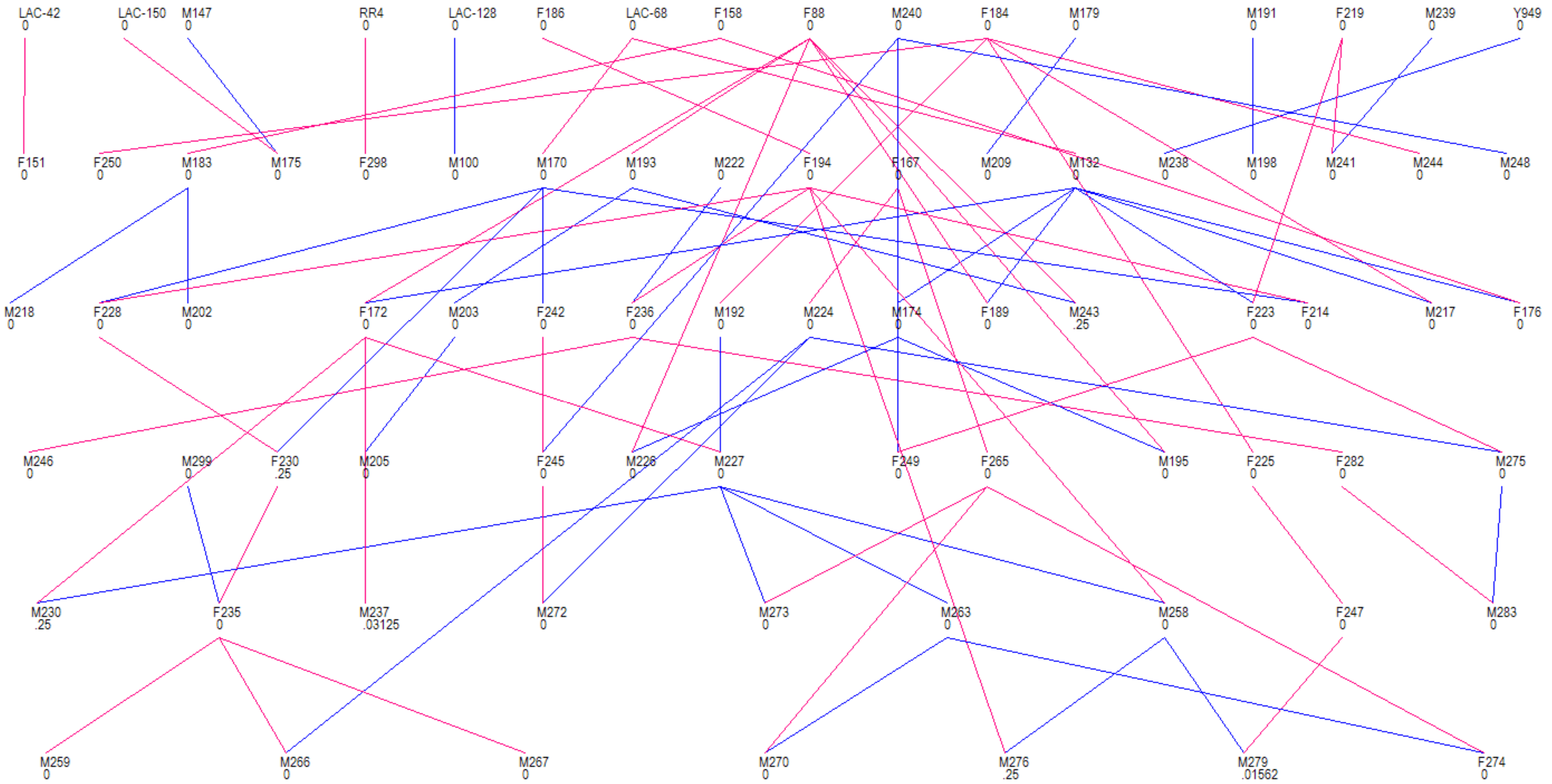

Fig. 1.6 Pedigree chart for 59 individual ocelots sampled from Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, during 1988–2013, assigned at 80% and 95% confidence. Male and female ocelots indicated with blue and pink lines, respectively. Ocelot ID and coefficient of inbreeding coefficient (*F*) in black text.

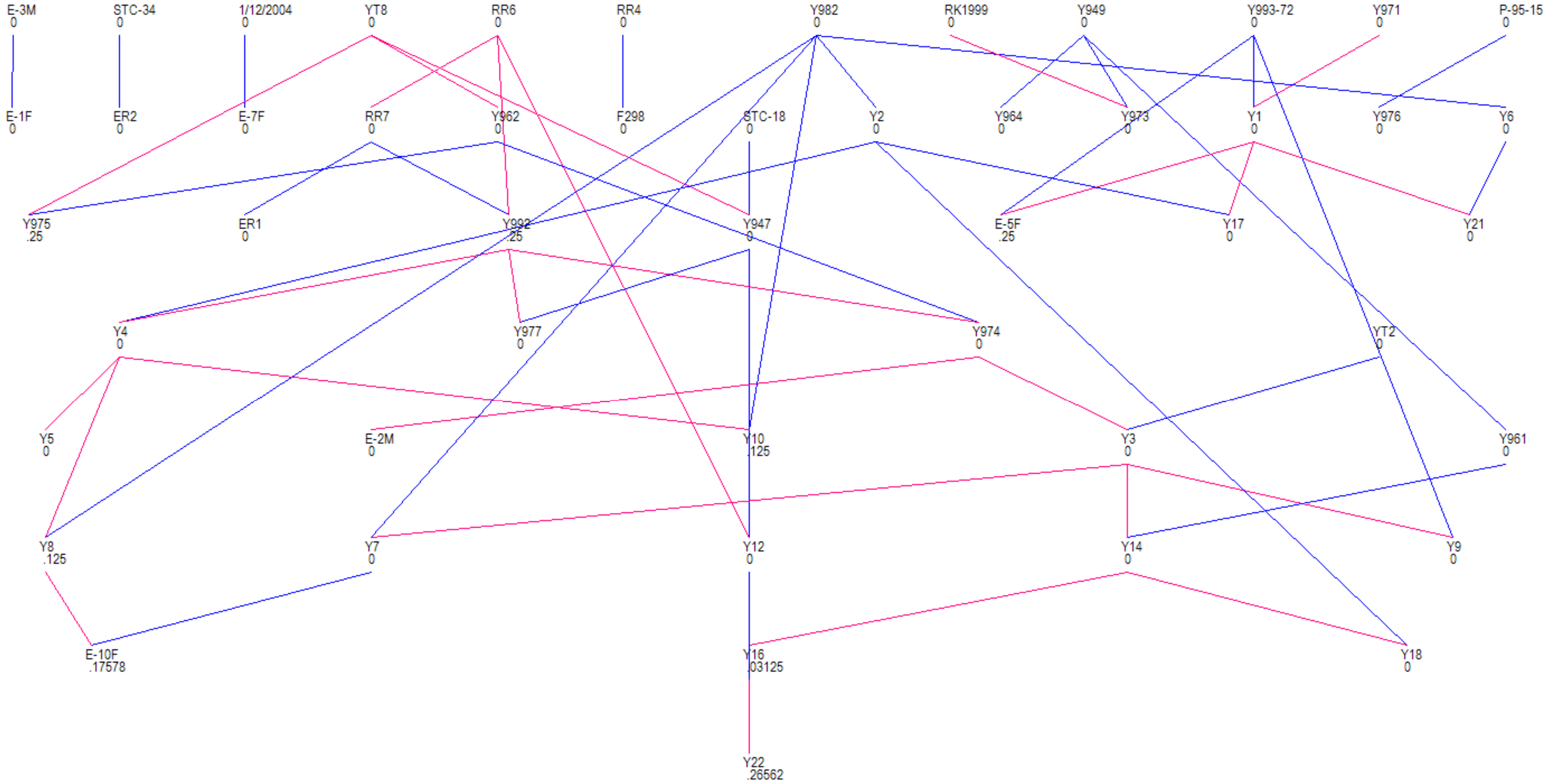

Figure 1.7 Pedigree chart for 36 individual ocelots from Yturria Ranch, East El Sauz Ranch and surrounding areas in Willacy County, Texas, during 1988–2013, assigned at 80% and 95% confidence. Male and female ocelots indicated with blue and pink lines, respectively. Ocelot ID and coefficient of inbreeding coefficient (*F*) in black text.

CAMERON subpopulation from 1999–2005 to 2006–2013. This subpopulation has also remained highly differentiated from ocelots on YTURRIA in WILLACY from 1999–2005 ($F_{ST} = 0.231$) to 2006–2013 ($F_{ST} = 0.222$). These results, in conjunction with a negative F_{IS} in CAMERON during 2006–2013 and previous low estimates of N_e (Janečka *et al.* 2008), all suggest that the population is experiencing severe genetic drift (Allendorf 1986). These factors are consistent with populations that have undergone a bottleneck event, similar to the Amur leopard (Uphyrkina *et al*. 2002), European lynx (Hellborg *et al*. 2002), and Florida panther (Roelke *et al.* 1993; Hedrick 1995).

The WILLACY population historically retained greater diversity than CAMERON, but underwent a major decrease (20%) in genetic diversity (A_R) from 1991–1998 to 2005. The 2005 group had the lowest expected heterozygosity ($H_e = 0.488$), extremely low N_e (Janečka *et al.* 2008), and a significantly negative F_{IS} (-0.126) indicating a possible bottleneck event and genetic drift. The 10 individuals sampled from this period assigned to their own separate genetic cluster, in addition to most of their parents and offspring. The reason for this reduction in population size was unknown, and was postulated to have been a result of thornshrub removal, other habitat management practices, regional drought, reduced rainfall or declining prey populations. At that period the subpopulation was at high risk of extinction without gene flow with ocelots located in CAMERON or other unsampled areas in WILLACY.

Now with the evidence of movement between EAST and YTURRIA, the reduction in heterozygosity and negative F_{IS} for YTURRIA in 2005, could be a result of outbreeding. Of the 10 individuals captured on YTURRIA in 2005, one female ocelot (Y1) assigned at 80% confidence as dam to a current adult female (E-5F) on EAST; and one male ocelot (Y12) was assigned at 95% confidence as offspring to a dam (RR6) captured in the surrounding area. The immigration of 1-2 individuals from EAST or surrounding areas into the YTURRIA subpopulation, when each subpopulation was fixed for different alleles, could have caused the temporary decrease in heterozygosity and the significantly negative F_{IS} value. Additionally, these factors would increase if the genetically divergant immigrants dominated breeding. Of the ocelots sampled in WILLACY during 1983–2013 with sufficient data for parentage analysis, 12 dams were assigned at 95% confidence to 18 individual offspring. Of these 12 dams, seven produced one offspring each, four produced two offspring each, and one (female Y1) produced 3 offspring or 17% of the total offspring. If Y1 was an immigrant to YTURRIA from EAST (which may be indicated by assignment as dam to a female ocelot currently a resident of EAST), and then produced the majority of the offspring over one or many generations it could have caused an excess of heterzygotes and a negative $F_{IS.}$

While WILLACY has historically retained greater diversity, it has not been resistent to inbreeding events. Parentage analyses and construction of a partial pedigree identified six and eight inbred relationships in the CAMERON and WILLACY subpopulations, respectively. Maximum coefficients of inbreeding were similar between the subpopulations (CAMERON, F = 0.25; WILLACY, F = 0.27). Both subpopulations contained mother-son matings (CAMERON = 3, WILLACY = 2), an event usually avoided in carnivores by the dispersal of male offspring from the natal range. Apparently a result of isolation and reduced habitat, biologists on LANWR observed on at least two separate occasions male offspring establishing an adult home range within the boundaries of the mother (J. Mays, pers. comm.). Father-daughter matings are more ecologically probable and CAMERON contained one such relationship, while WILLACY had two. More complex relationships occurred (Oliehoek *et al* 2006) where offspring resulted from an inbred relationship from parents that also were produced from inbred parents and grandparents.

In addition to inbreeding, a concern has been the possibility that only one or two individuals may have monopolized breeding. Female F88 and male M132 in CAMERON, produced 17% and 25% of the offspring assigned in that subpopulation ($n = 59$) at 95% confidence, respectively. Furthermore, one individual in WILLACY produced more than two offspring assigned in that subpopulation at 95% confidence (female Y1 assigned as dam to three individuals).

Overall, ocelots in WILLACY have retained higher levels of genetic diversity than those in CAMERON, but when YTURRIA and EAST were analyzed separately, EAST had significantly greater genetic diversity (A_R) and H_e than both CAMERON and YTURRIA. Though only nine individuals were sampled from EAST during 2006–2013, the subpopulation had 26% and 16% higher A_R than CAMERON and YTURRIA, respectively. Additionally, current ocelots on EAST (2006–2013) had a significantly positive F_{IS}, which could indicate inbreeding or a Wahlund effect. While inbred relationships on EAST were identified in the pedigree, it is also possible there is additional sub-structure if the individuals on EAST are part of larger WILLACY population. Higher levels of diversity and a postive F_{IS} may be an indication that EAST, and to a lesser extent YTURRIA, are actually part of a larger unsampled population of ocelots within WILLACY.

Differentiation between YTURRIA and the recently discovered subpopulation on EAST was low ($F_{ST} = 0.05$), but statistically significant. Bayesian clustering analyses for WILLACY during 1991–2013 revealed the highest support for two genetic clusters, with one cluster consisted of individuals captured on YTURRIA in 2005 and their parents and offspring, and the second cluster consisted of all other individuals captured in WILLACY (YTURRIA, EAST and surrounding areas). Multiple parent-offspring assignments ($n = 8$) between YTURRIA and EAST, and field observations (i.e., remote camera surveys) of individuals ocurring on both sites, indicate there is a moderate level of gene flow between the locations (though typically one direction YTURRIA→EAST) even though they are separated by 10 km of patchy habitat. Two individuals (one male, one female) originally live-trapped and radio-collared on YTURRIA in 2005, were subsequently identified as residents on EAST (2011 to present) where they produced an offspring. Conversely, genetic differentiation was high between CAMERON and EAST ($F_{ST} = 0.16$), confirming the isolation between CAMERON and WILLACY.

In general, ocelots in Texas from 1991 to 2013, occured as three distinct genetic clusters corresponding to individuals sampled from: 1) LANWR in CAMERON during 1991–2013, 2) YTURRIA in WILLACY in 2005 and their offspring, and 3) YTURRIA and surrounding areas in WILLACY during 1991–1998, and YTURRIA and EAST in WILLACY during 2006–2013. At present, ocelots in South Texas exist as two genetically distinct and isolated subpopulations, one of all individuals within CAMERON and one with all individuals in WILLACY (i.e., YTURRIA, EAST, and surrounding areas).

No genetic or spatial evidence has detected gene flow between CAMERON and WILLACY in nearly 30 years of monitoring (Laack 1991; Beltran & Tewes 1995; Horne 1998; Shindle & Tewes 2000; Laack *et al.* 2005; Haines *et al.* 2005; Haines *et al.* 2006a; Haines *et al.* 2006c; Janečka *et al.* 2011). High F_{ST} between the sites, low genetic diversity in CAMERON, significant F_{IS} values, and the lack of assignment of unknown individuals across sampling sites also corroborates that no dispersal has occurred between CAMERON and WILLACY.

However, my analyses identified one individual from CAMERON that may be a recent immigrant or have immigrant ancestry from WILLACY. Genetic cluster analyses assigned a subadult male (M238) captured on LANWR partial origin to the EAST subpopulation (i.e., indicating possible admixture). Additionally, using tests for first-generation migrants, this individual had a higher probability of either being from or having a parent or grandparent from the EAST subpopulation. Finally, in parentage analyses, this individual was assigned at 80% confidence a sire that originated from the YTURRIA subpopulation. This record may be the only recorded gene flow between the two subpopulations in about 30 years of research and monitoring. Unfortunately the continued loss of diversity and high levels of genetic drift and inbreeding indicate that even rare and very low dispersal is not enough to improve genetic diversity of ocelots on LANWR.

Gene flow between populations (e.g., natural migration or artificial translocation of individuals) should alleviate the effects of genetic drift and inbreeding (Ingvarsson 2001). In Texas, ocelots select for dense Tamaulipan thornshrub habitat found in fragmented patches throughout the LRGV (Horne *et al*. 2009). This tendency to be a habitat specialist with increasing agriculture and urbanization in the area has increased the isolation of ocelot subpopulations. These barriers have prevented the subpopulations of ocelots in South Texas from operating as metapopulations and halted or at least drastically reduced any natural gene flow between them. Bayesian clustering and tests for dispersers, and measures of genetic diversity and differentiation provide ample support that the ocelots in WILLACY (YTURRIA and EAST) have no or extremely limited genetic exchange with CAMERON. Additional factors reducing gene flow between the subpopulations include road mortality of dispersers before they can contribute genetically (Haines *et al.* 2005). The individual, M238, was not documented or captured again and did not assign as a parent to other individuals, and may be because this individual did not contribute genetically to the CAMERON population.

The ocelot population in Texas is threatened with extirpation in the near future (Haines *et al*. 2006c) and will likely not persist without genetic restoration and population augmentation by addition of individuals (Hedrick & Kalinowski 2000). Although mitigation of road mortality, creation of corridor habitat between the subpopulations, and restoration of habitat have high priority for ocelot recovery (USFWS 2010), translocation of individuals from outside Texas or between CAMERON and WILLACY is crucial. This artificial gene flow will increase genetic diversity, minimize the effects of genetic drift, and decrease the possibility of inbreeding. Translocation has provided genetic restoration for the critically endangered Florida panther (Pimm *et al.* 2006). In the first seven years after translocation occurred, admixed individuals showed increased survival, population size increased 3-fold, and heterozygosity doubled (Johnson *et al*. 2010). Through parentage assignments I have constructed a partial pedigree for ocelots in Texas than can be used to track the genetic contribution of translocated individuals in additional to continued genetic monitoring.

Ocelots on EAST maintained the highest levels of genetic diversity, and my results indicate they may be part of a larger unsampled population in WILLACY with moderate dispersal with YTURRIA. Although this a positive outlook for ocelots in WILLACY, without gene flow with CAMERON or other populations, the subpopulation on LANWR will continue to decline in genetic diversity, become even more genetically differentiated, and experience increased effects of genetic drift and inbreeding. Currently, there has been no empirical evidence of inbreeding depression, such as the physical and reproductive abnormalities observed in Florida panthers (Roelke *et al.* 1993; Hedrick 1995; Mansfield & Land 2002), though specific montitoring for these factors has not occurred with ocelots. Future research is imperative to monitor the presence of inbreeding depression and any resulting decrease in fitness. Ultimately, with such low levels of diversity, rare to non-existent dispersal, increasing isolation due to loss of habitat and fragmentation, and high road mortality, the ocelot faces extirpation in Texas without immediate conservation management strategies.

References

Allendorf FW (1986) Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology*, **5**, 181–190.

Allendorf FW, Luikart G (2007) *Conservation and the Genetics of Populations*. Blackwell Publishing, Malden, MA.

Beltran, JF, Tewes ME (1995) Immobilization of ocelots and bobcats with ketamine hydrochloride and xylazine hydrochloride. *Journal of Wildlife Diseases*, **31**, 43–48.

Caso A, Lopez-Gonzalez C, Payan E, Eizirik E, de Oliveira T, Leite-Pitman R, Kelly M, Valderrama C (2008) *Leopardus pardalis*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. http://www.iucnredlist.org (accessed on 1 May 2013).

De Barba M, Waits LP, Garton EO, Genovesi P, Randi E, Mustoni A, Groffs C (2010) The power of genetic monitoring for studying demography, ecology and genetics of a reintroduced brown bear populations. *Molecular Ecology*, **19**, 3938–3951.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology*, **14**, 2611–2620.

Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online,* **1**, 47–50.

Franklin IR (1980) Evolutionary changes in small populations. In: *Conservation biology: An evolutionary-ecological perspective*. (eds Soule ME, Wilcox BA), pp. 135–150. Sinauer Associates, Sunderland.

Franklin IR & Frankham R (1998) How large must populations be to retain evolutionary potential? *Animal Conservation*, **1**, 69–71.

Goudet J (2002) FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3.2). Available from http://www2.unil.ch/popgen/softwares/fstat.htm.

Guo S, Thompson E (1992) Performing the exact test of Hardy-Weinburg proportion for multiple alleles. *Biometrics*, **48**, 361–372.

Haines AM, Tewes ME, Laack LL (2005) Survival and cause-specific mortality of ocelots in southern Texas. *Journal of Wildlife Management*, **69**, 255–263.

Haines AM, Grassman LI, Tewes ME, Janečka JE (2006a) The first ocelot (*Leopardus pardalis*) monitored via GPS telemetry. *European Journal of Wildlife Research*, **52**, 216–218.

Haines AM, Janečka JE, Tewes ME, Grassman LI, Morton P (2006b) The importance of private lands for ocelot *Leopardus pardalis* conservation in the United States. *Oryx*, **40**, 90–94.

Haines AM, Tewes ME, Laack LL, Horne JS, Young JH (2006c) A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States. *Biological Conservation*, **132**, 424–436.

Hedrick PW (1995) Gene flow and genetic restoration: The Florida panther as a case study. *Conservation Biology*, **9**, 9969–1007.

Hedrick PW, Miller PS (1992) Conservation genetics: technique and principles. *Ecological Applications*, **2**, 30–46.

Hedrick PW, Kalinowski ST (2000) Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics* **31**, 139–162.

Hellborg L, Walker CW, Rueness EK, Stacy JE, Kojola I, Valdmann H, Vila C, Zimmermann B, Jakobsen KS, Ellegren H. (2002) Differentiation and levels of genetic variation in northern European lynx (*Lynx lynx*) populations revealed by microsatellites and mitochondrial DNA analysis. *Conservation Genetics,* **3**, 97–111.

Horne JS (1998) *Habitat Partitioning of Sympatric Ocelot and Bobcat in Southern Texas*. MS Thesis, Texas A&M University-Kingsville, Texas.

Horne JS, Haines AM, Tewes ME, Laack LL (2009) Habitat partitioning by sympatric ocelots and bobcats: implications for recovery of ocelots in southern Texas. *Southwestern Naturalist* **54**, 119–126.

Hostetler JA, Onorato DP, Jansen D, Oli MK (2013) A cat's tale: the impact of genetic restoration on Florida panther population dynamics and persistence. *Journal of Animal Ecology,* **82**, 608–620.

Ingvarsson PK (2001) Restoration of genetic variation lost–the genetic rescue hypothesis. *Trends in Ecology & Evolution*, **16**, 62–63.

Jahrsdoerfer SE, Leslie Jr. DM (1988) Tamaulipan brushland of the Lower Rio Grande Valley of south Texas: description, human impacts, and management options. US Fish and Wildlife Service, *Biological Report*, **88**, 1–63.

Janečka JE (2006) *Conservation genetics and ecology of the ocelot with recovery implications in Texas*. PhD Dissertation, Texas A&M University-Kingsville and Texas A&M University, Texas.

Janečka JE, Blankenship TL, Hirth DH, Tewes ME, CW Kilpatrick, Grassman, Jr. LI (2006) Kinship and social structure of bobcats (*Lynx rufus*) inferred from microsatellite and radio-telemetry data. *Journal of Zoology (London)*, **269**, 494–501.

Janečka JE, Walker CW, Tewes ME, Caso A, Laack LL, Honeycutt RL (2007) Phylogenetic relationships of ocelot (*Leopardus pardalis albescens*) populations from the Tamaulipan Biotic Province and implications for recovery. *Southwestern Naturalist,* **52**, 89–96.

Janečka JE, Tewes ME, Laack LL, Grassman LI, Haines AM, Honeycutt RL (2008) Small effective population sizes in two remnant ocelot populations (*Leopardus pardalis albescens*) in the United States. *Conservation Genetics*, **9**, 869–878.

Janečka JE, Tewes ME, Laack LL, Caso A, Grassman Jr. LI, Haines AM, Shindle DB, Davis BW, Murphy WJ, Honeycutt RL (2011) Reduced genetic diversity and isolation of remnant ocelot populations occupying a severely fragmented landscape in southern Texas. *Animal Conservation,* **14**, 608–619.

Johnson WE, Onorato DP, Roelke ME, Land ED, Cunningham M, Belden RC, McBride R, Jansen D, Lotz M, Shindle D, Hoawrd J, Wildt DE, Penfold LM, Hostetler JA, Oli MK, O'Brien SJ (2010) Genetic restoration of the Florida panther. *Science*, **329**, 1641–1645.

Jones AG, Small CM, Paczolt KA, Ratterman NL (2010) A practical guide to methods of parentage analysis. *Molecular Ecology*, **10**, 6–30.

Kalinowski ST (2005) HP-RARE 1.0: a computer program for performing rarefaction on measures of allelic richness. *Molecular Ecology Notes*, **5**, 187–189.

Kalinowski ST, Wagner AP, Taper ML (2006) ML-Relate: a computer program for maximum likelihood estimations of relatedness and relationship. *Molecular Ecology Notes*, **6**, 576–579.

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, **16**, 1099–1106.

Laack LL (1991) *Ecology of the Ocelot (Felis pardalis) in South Texas*. MS Thesis, Texas A&I University, Kingsville, Texas.

Laack LL, Tewes ME, Haines AH, Rappole J (2005) Reproductive life history of ocelots *Leopardus pardalis* in southern Texas. *Acta Theriologica,* **50**, 505–514.

Lacy RC (1987) Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology*, **1,** 143–158.

Longmire JL, Maltbie M, Baker RJ (1997) Use of "lysis buffer" in isolation and its implications for museum collections. *Occasional Papers, The Museum of Texas Tech University* **163**, 1–3.

Mansfield KG, Land ED (2002) Cryptorchidism in Florida panthers: prevalence, features, and influence of genetic restoration. *Journal of Wildlife Diseases,* **38**, 693–698.

Marshall TC, Slate J, Kruuk LEB, Pemberton JM (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology,* **7**, 639–655.

Menotti-Raymond MA, David VA, Lyons LA, et al. (1999) A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). *Genomics*, **57,** 9–23.

Menotti-Raymond MA, David VA, Chen ZQ, et al. (2003) Second generation integrated genetic linkage/radiation hybrid maps of the domestic cat (*Felis catus*). *Journal of Heredity*, **94**, 95–106.

Norwine J, Bingham R (1985) Frequency and severity of drought in south Texas. In: *Livestock and Wildlife Management During Drought* (editor Brown R), pp.1–19. Caesar Kleberg Wildlife Research Institute Press, Kingsville, Texas.

Oliehoek PA, Windig JJ, van Arendonk JAM, Bijma P (2006) Estimating relatedness between individuals in general populations with a focus on their use in conservation programs. *Genetics*, **173**, 483–496.

Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate using assignment methods: a simulation-based exploration of accuracy and power. *Molecular Ecology* **13**, 55–65.

Peakall R, Smouse PE (2012) GenAlEx 6.5: Genetic Analysis in Excel. Population Genetic Software for Teaching and Research - An Update. *Bioinformatics,* **28**, 2537–2539.

Pemberton JM (2008) Wild pedigrees: the way forward. *Proceedings of the Royal Society B*, **275**, 613–621.

Pilgrim KL, McKelvey KS, Riddle AE, MK Schwartz (2005) Felid sex identification based on noninvasive genetic samples. *Molecular Ecology Notes,* **5**, 60–61.

Pimm, SL, Dollar L, Bass Jr. OL (2006) The genetic rescue of the Florida panther. *Animal Conservation*, **9**, 115–122.

Piry S, Alapetite A, Cornuet J-M, Paetkua D, Baudouin L, Estoup A (2004) GeneClass2: A software for genetic assignment and first-generation migrant detection. *Journal of Heredity,* **95**, 536–539.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics,* **155**, 945–959.

Pritchard JK, Wen X, Falush D (2010) Documentation for structure software: version 2.3. University of Chicago, Chicago, Illinois, 1–36.

Rannala R, Mountain JL (1997) Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences of the USA*, **94**, 9197–9201.

Rice WR (1989) Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Roelke ME, Martenson JS, O'Brien SJ (1993) The consequences of demographic reduction and genetic depletion in the endangered Florida panther. *Current Biology,* **3**, 340–350.

Shindle DB, Tewes ME (2000) Immobilization of wild Ocelots with tiletamine and zolazepam in southern Texas. *Journal of Wildlife Diseases,* **36**, 546–550.

Stenglein JL, Waits LP, Ausband DE, Zager P, Mack CM (2011) Estimating gray wolf pack size and family relationships using noninvasive genetic sampling at rendezvous sites. *Journal of Mammalogy*, **92**, 784–795.

Tewes ME (1986) Ecological and behavioral correlates of ocelot spatial patterns. PhD Dissertation, University of Idaho, Moscow, Idaho.

Tewes ME, Everett DD (1986) Status and distribution of the endangered ocelot and jaguarundi in Texas. In: *Cats of the world: biology, conservation, and management*. (eds Miller SD, Everett DD), pp. 147–158. National Wildlife Federation, Washington.

Uphyrkina O, Miquelle D, Quigley H, Driscoll C, O'Brien SJ (2002) Conservation genetics of the Far Eastern leopard (*Panthera pardus orientalis*). *Journal of Heredity,* **93**, 303–311.

USFWS (1999) *Endagered and Threatended Wildlife and Plants*. US Fish and Wildlife Service, Washington, DC.

USFWS (2010) Draft ocelot (*Leopardus pardalis*) recovery plan, first revision. US Fish and Wildlife Service, Southwest Region, Albuquerque, New Mexico.

Walker CW (1997) *Patterns of Genetic Variation in Ocelot (Leopardus pardalis) Populations for South Texas and Northern Mexico*. PhD Dissertation, Texas A&M University-Kingsville and Texas A&M University, College Station, Texas.

Wildt DE, Bush M, Goodrowe LK, Packer C, Pusey AE, Brown JLL, Joslin P, O'Brien SL (1987) Reproductive and genetic consequences of founding isolated lion populations. *Nature,* **329**, 328–331.

Wright S (1951) The genetical structure of populations. Annals of Eugenics, **15**, 323–354.

Supporting Information

Table S1. Complete list of ocelots used in analyses (*n* = 165), sampled in Texas during 1984-2013 with ocelot ID, sex, sample type (capture, roadkill, or unknown [UNK]), date collected and location collected (LANWR, YTURRIA, EAST, or if surrounding areas indicated by county only [WILLACY or CAMERON]). Roadkill and unknown samples listed separately.

ID	Sex	Sample type	Date collected	Location collected
CAMERON (*n* = 85)				
LAC-100	M	Capture	2/21/1989	LANWR
LAC-128	M	UNK	4/14/1989	LANWR
LAC-150	F	UNK	8/4/1989	LANWR
LAC-42	F	Capture	1/30/1989	LANWR
LAC-50	F	Capture	6/18/1986	LANWR
LAC-68	F	Capture	UNK	LANWR
LAC-71	F	Capture	11/22/1987	LANWR
F88	F	UNK	12/8/1994	LANWR
F115	F	Capture	10/18/1989	LANWR
F151	F	Capture	3/1/1990	LANWR
F158	F	Capture	11/9/1989	LANWR
F167	F	Capture	2/18/1994	LANWR
F172	F	Capture	4/20/1996	LANWR
F176	F	Capture	4/16/1992	LANWR
F182	F	Capture	4/19/1992	LANWR
F184	F	Capture	UNK	LANWR
F186	F	Capture	5/11/1993	LANWR
F189	F	Capture	2/19/1994	LANWR
F194	F	Capture	11/7/1995	LANWR
F197	F	Capture	3/13/1996	LANWR
F201	F	Capture	UNK	LANWR
F214	F	Capture	12/15/1996	LANWR

Table S1. (continued)

ID	Sex	Sample type	Date collected	Location collected
CAMERON (continued)				
F219	F	Capture	5/7/1997	LANWR
F223	F	UNK	3/27/1999	LANWR
F225	F	Capture	2/13/01	LANWR
F228	F	Capture	11/22/98	LANWR
F230	F	Capture	UNK	LANWR
F235	F	Capture	12/19/2002	LANWR
F236	F	Capture	4/6/2000	LANWR
F242	F	Capture	11/27/2001	LANWR
F245	F	Capture	12/11/2003	LANWR
F247	F	Capture	1/10/2004	LANWR
F249	F	Capture	2005	LANWR
F250	F	Capture	2/18/2005	LANWR
F265	F	Capture	2/19/2008	LANWR
F271	F	Roadkill	10/18/2009	LANWR
F274	F	Capture	12/4/2010	LANWR
F282	F	Capture	3/13/2013	LANWR
M100	M	Capture	3/28/1990	LANWR
M132	M	Capture	3/18/1995	LANWR
M147	M	Capture	7/10/1989	LANWR
M165	M	Roadkill	1/8/1992	LANWR
M170	M	Capture	11/24/1992	LANWR
M174	M	Capture	1/13/1992	LANWR
M175	M	Capture	4/30/1991	LANWR
M179	M	Capture	11/22/1992	LANWR
M183	M	Capture	1/25/1994	LANWR
M191	M	Capture	2/23/1995	LANWR
M192	M	Capture	UNK	LANWR
M193	M	Capture	UNK	LANWR
M195	M	Capture	UNK	LANWR
M198	M	Capture	3/14/1996	LANWR

Table S1. (continued)

ID	Sex	Sample type	Date collected	Location collected
CAMERON (continued)				
M202	M	Capture	UNK	LANWR
M203	M	UNK	UNK	LANWR
M205	M	Capture	1/22/1999	LANWR
M209	M	Capture	5/28/1996	LANWR
M217	M	Capture	4/23/1997	LANWR
M218	M	Capture	5/11/1997	LANWR
M222	M	Capture	12/7/1997	LANWR
M226	M	Capture	5/6/1998	LANWR
M230	M	UNK	12/3/2000	LANWR
M224	M	Capture	4/23/2002	LANWR
M227	M	Capture	5/9/1998	LANWR
M237	M	Capture	2/10/2001	LANWR
M238	M	UNK	12/3/2000	LANWR
M239	M	Capture	5/2/2001	LANWR
M240	M	Capture	UNK	LANWR
M241	M	Capture	4/28/2001	LANWR
M243	M	Capture	1/29/2003	LANWR
M244	M	Capture	1/11/2004	LANWR
M246	M	Capture	1/10/2004	LANWR
M248	M	Capture	UNK	LANWR
M258	M	Capture	10/28/2007	LANWR
M259	M	Capture	3/19/2007	LANWR
M263	M	Capture	2/1/2008	LANWR
M266	M	Capture	10/1/2008	LANWR
M267	M	Capture	11/17/2008	LANWR
M270	M	Capture	4/12/2009	LANWR
M272	M	Capture	1/20/2010	LANWR
M273	M	Mortality	11/16/2010	LANWR
M275	M	Capture	1/31/2011	LANWR
M276	M	Capture	2/23/2011	LANWR

Table S1. (continued)

ID	Sex	Sample type	Date collected	Location collected
CAMERON (continued)				
M279	M	Capture	3/9/2012	LANWR
M283	M	Capture	3/28/2013	LANWR
Port1	M	Capture	4/27/1998	Port of Brownsville
WILLACY (n = 58)				
STC-18	M	Capture	8/23/1984	YTURRIA
STC-32	M	Capture	9/29/1985	YTURRIA
STC-33	M	Capture	9/29/1985	WILLACY
STC-34	M	Capture	9/29/1985	WILLACY
ER1	M	Capture	5/17/1991	EAST
ER2	F	Mortality	5/20/1991	EAST
F298	F	Capture	2/4/1998	YTURRIA
M297	M	Capture	1/31/1998	YTURRIA
RR4	M	Capture	10/26/1991	WILLACY
RR6	F	Capture	6/27/1991	WILLACY
RR7	M	Capture	6/28/1991	WILLACY
Y946	M	Capture	2/18/1994	YTURRIA
Y947	M	Capture	1/28/1994	YTURRIA
Y949	M	Capture	1/5/1994	YTURRIA
Y961	M	Capture	1/27/1997	YTURRIA
Y964	M	Capture	5/1/1996	YTURRIA
Y971	F	Capture	UNK	YTURRIA
Y972	M	Capture	1/25/1997	YTURRIA
Y973	M	Capture	1/26/1997	YTURRIA
Y974	F	Capture	1/26/1997	YTURRIA
Y975	M	Capture	1/26/1997	YTURRIA
Y976	F	Capture	5/7/1997	YTURRIA
Y977	F	Capture	5/7/1997	YTURRIA
Y981	M	Capture	1/28/1998	YTURRIA

Table S1. (continued)

ID	Sex	Sample type	Date collected	Location collected
WILLACY (continued)				
Y982	M	Capture	1/29/1998	YTURRIA
Y983	M	Capture	1/31/1998	YTURRIA
Y984	F	Capture	2/4/98	YTURRIA
Y992	F	Capture	3/21/1999	YTURRIA
Y993	F	Capture	3/24/1999	YTURRIA
Y993-72	M	Capture	UNK	YTURRIA
YT2	M	Capture	4/19/1991	YTURRIA
YT8	F	Capture	5/13/1991	YTURRIA
Y1	F	Capture	3/6/2006	YTURRIA
Y2	M	Capture	3/23/2011	YTURRIA
Y3	F	Capture	2/7/2005	YTURRIA
Y4	F	Capture	2/8/2005	YTURRIA
Y5	M	Capture	2/9/2004	YTURRIA
Y6	M	Capture	3/4/2006	YTURRIA
Y7	M	Capture	2/10/2005	YTURRIA
Y8	F	Capture	2/10/2005	YTURRIA
Y9	F	Capture	2/10/2005	YTURRIA
Y10	M	Capture	3/2/2005	YTURRIA
Y12	M	Capture	3/6/2007	YTURRIA
Y14	F	Capture	2/22/2010	YTURRIA
Y16	F	Capture	4/24/2012	YTURRIA
Y17	M	Capture	4/11/2012	YTURRIA
Y18	M	Capture	3/8/2012	YTURRIA
Y21	F	Capture	3/8/2012	YTURRIA
Y22	F	Capture	4/24/2012	YTURRIA
E-1F	F	Capture	3/10/2012	EAST
E-2M	M	Capture	3/13/2011	EAST
E-3M	M	Capture	3/15/2011	EAST
E-4M	M	Capture	3/18/2012	EAST
E-5F	F	Capture	4/3/2011	EAST

Table S1. (continued)

ID	Sex	Sample type	Date collected	Location collected
WILLACY (continued)				
E-6M	M	Capture	4/3/2011	EAST
E-7F	F	Capture	3/18/2012	EAST
E-8M	M	Capture	2/20/2013	EAST
E-10F	F	Capture	4/25/2013	EAST
ROADKILL (*n* = 16)				
M125	M	Roadkill	10/23/1988	Port Isabel
M162	M	Roadkill	11/20/1989	Port Mansfield
M168	M	Roadkill	7/11/1990	Port Mansfield
31-AGO-1990	M	Roadkill	8/31/1990	Sarita
PM1	M	Roadkill	7/29/91	Port Mansfield
Port_Man	M	Roadkill	October 1993	Port Mansfield
PM93	M	Roadkill	October 1993	Port Mansfield
P-95-15	M	Roadkill	5/9/95	UNK
P-95-150	UNK	Roadkill	5/8/95	UNK
P-97-13	F	Roadkill	4/4/96	UNK
P-97-14	M	Roadkill	4/7/97	Near LANWR
SARITA	M	Roadkill	10/15/97	Sarita
Y962	M	Roadkill	10/27/97	Lyford
RK1999	F	Roadkill	6/17/99	Port Mansfield
1/12/2004	M	Roadkill	1/12/04	Port Mansfield
HWY77RK20101224	M	Roadkill	12/24/10	Raymondville
UNKNOWN (*n* = 6)				
11218-001	UNK	UNK	UNK	UNK
16665-001	M	UNK	UNK	UNK
18151-001	UNK	UNK	UNK	UNK
18156-001	UNK	UNK	UNK	UNK
NO_ID2	M	UNK	UNK	UNK

Table S2. Genetic assignments from STRUCTURE and GeneClass for nine individuals with unknown origin collected in Texas as roadkill with no other information ($n = 3$) or collected in Texas but with no information on collection type, location, or date ($n = 6$) during 1983–2013. Reference populations were individuals sampled from Cameron County (Laguna Atascosa National Wildlife Refuge, $n = 69$) Willacy County (Yturria Ranch, $n = 39$; East El Sauz Ranch, $n = 9$; and surrounding areas, $n = 5$), Texas, during 1991–2013. Assignment values to each subpopulation are estimated ancestry proportions (*q*-values) from STRUCTURE and likelihood ratio scores from GeneClass (*P*). Scores $q \geq 0.90$ or $P \geq 90$ indicate substantial support for assignment. When sex or date unknown, indicated with 'UNK'.

			q (STRUCTURE)			*P* (GeneClass)		
ID	Sex	Date	Ca	Wi	Ea	Ca	Wi	Ea
Roadkill								
P-95-15	M	5/9/95	0.01	0.02	0.97	0.0	99.9	0.1
P-95-150	UNK	5/8/95	0.76	0.05	0.20	100.0	0.0	0.0
P-97-13	F	4/4/96	0.53	0.05	0.43	0.5	56.8	42.7
Unknown								
11218-001	UNK	UNK	0.56	0.42	0.02	67.2	32.5	0.3
16665-001	M	UNK	0.98	0.01	0.01	100.0	0.0	0.0
18151-001	UNK	UNK	0.65	0.30	0.05	99.1	0.0	0.9
18156-001	UNK	UNK	0.87	0.01	0.12	100.0	0.0	0.0
NO_ID2	M	UNK	0.02	0.03	0.96	0.0	16.0	84.0

CHAPTER II

COMPARATIVE RESPONSES OF OCELOT (*LEOPARDUS PARDALIS*) PREY TO DROUGHT IN SOUTH TEXAS

Long-term studies have shown that populations of small mammals (e.g., rodents) may be highly affected by precipitation patterns (Madsen and Shine 1999; Ernest et al. 2000; Brown and Ernest 2002; Morrison et al. 2002; Bradley et al. 2006). The Tamaulipan Biotic Province of South Texas is characterized by irregular rainfall patterns and periodic drought (Jahrsdoerfer and Leslie 1988) with below-average precipitation, and plant and animal communities of the region are highly adapted to this erratic, semiarid ecosystem. Periods of severe drought can cause a decline in rodent populations as food and cover are reduced, leading to a decrease in survival (Singleton et al. 2010). When resources are limited, reproduction may cease or decline dramatically as embryos are absorbed, and litter size is reduced (Bradley et al. 2006).

Conversely, rainfall events can trigger a response from primary producers and consumers such as plants and rodents, which then result in a period of high abundance (Schwinning and Sala 2004; Tewes and Hornocker 2008). Herbaceous vegetation in arid and semiarid regions respond to these episodic pulses by growing and producing seeds rapidly (Holmgren et al. 2006). These complex dynamics have been studied extensively in deserts (Whitford 1976; Brown 1989; Brown and Zeng 1989; Brown and Heske 1990; Predavac 1994) and tropical ecosystems (Sheppe 1972; Cheeseman and Delaney 1979; Lima et al. 1999; Jaksic and Lima 2003), but less so in semiarid, subtropical regions such as South Texas (Windberg 1998; Bradley et al. 2006).

Communities of small mammals of this region serve as prey for many common carnivores (e.g., coyote [*Canis latrans*], bobcat [*Lynx rufus*]), and endangered ocelot

---

Chapter 2 of this dissertation follows the style of the *Journal of Mammalogy*.

(*Leopardus pardalis*). The ocelot is a medium-sized neotropical felid that ranges from South Texas to Argentina. Federally endangered within their range in Texas, about 50–100 individuals persist in South Texas (M. Tewes, pers. comm.). Long-term research has focused on ecological responses of ocelots to issues such as prey decline and drought (USFWS 2010). Rodents and lagomorphs are the main prey item of ocelots, with the most energetically profitable species being the hispid cotton rat (*Sigmodon hispidus*, hereinafter referred to as cotton rat; Tewes and Hornocker 2008), Southern Plains woodrat (*Neotoma micropus*, hereinafter referred to as woodrat), and eastern cottontail (*Sylvilagus floridanus*).

Optimal foraging theory predicts that ocelots will choose prey with the maximum energetic input (digestible energy content of prey) that requires the least energetic output by the ocelot (Tewes and Hornocker 2008). In general, this means that ocelots choose the largest prey that can be captured with the least effort (Tewes and Hornocker 2008). Cotton rats are about 60–150 g in body mass and can be extremely abundant in Texas. Cottontails and woodrats have greater body mass, but may not be as readily encountered as a result of low trapping rates, and therefore less likely to be surveyed for prey availability studies.

Ocelots also will consume herpetofauna and birds, but in lower quantities, particularly when primary prey are abundant (Emmons 1987). When abundance of primary prey species decrease, such as during drought, bobcat diets shift to less profitable prey (Blankenship 2000). Blankenship (2000) recorded a prey shift in bobcats during a decline in primary prey: >90% of scats indicated presence of birds, typically an infrequent prey item (Tewes et al. 2002; Tewes and Hornocker 2008). A comparison of bobcat stomachs between wet and dry years showed that during wet periods, the two species of cotton rat and cottontail comprised most (96%) of the bobcat diet exclusively. During dry periods, bobcats consumed 21 different species of prey, with the majority still being cotton rats and cottontails (Beasom and Moore 1977). .

I conducted mark-recapture surveys on 2 sites where ocelots occurred to assess fluctuations in rodent abundance and population demographics in response to drought and rainfall,. The first objective was to examine timing and magnitude of fluctuations of rodent populations with varying precipitation. Bradley et al. (2006) suggested that rodent populations may not be greatly affected by drought conditions if a minimum threshold level of rainfall occurs, or if drought is of short duration. Granivorous species (i.e., heteromyids) may be less affected by drought and low rainfall because seed crops persist longer than herbaceous vegetation (Whitford 1976). Windberg (1998) observed a greater proportion of the granivorous heteromyid (kangaroo rat [*Dipodomys* spp.]) in years with decreased precipitation. Conversely, populations of the herbivorous cotton rat are strongly correlated with fluctuations in precipitation (Strecker 1929; Odum 1955; Windberg 1998). Periods of low rainfall reduce forage quantity and quality, and populations typically respond with a rapid decline ("crash") in abundance (Bradley et al. 2006). Precipitation may then occur as a pulse (isolated rainfall event) or longer duration wet period, which are then rapidly followed with an irruption ("boom") in population size (Windberg 1998; Morrison et al. 2002; Bradley et al. 2006). Deer mice (*Peromyscus* spp.) are omnivorous and habitat generalists, and may have little direct relationship with rainfall. Thus, changes in abundance may not be detectable until a longer duration of extreme conditions has occurred.

The second objective was to estimate how population demographics (age, sex, and reproductive condition) of three targeted species (cotton rat, Mexican spiny pocket mouse [*Liomys irroratus*, hereinafter referred to as Mexican spiny], and deer mouse) were affected by season, drought, and rainfall. Peak reproduction periods for cotton rats in southern latitudes occur in spring and fall (Cameron and Spencer 1981), with breeding year-round possible when resources are abundant (e.g., high rainfall periods). Therefore, spring and fall seasons should correspond to higher captures of adults and reproductively-active individuals, whereas summer and winter should have an influx of juveniles dispersing into the population. Drought conditions may alter these assumptions, resulting in reduced breeding or no breeding in spring–summer, and result in a higher proportion of adult captures. In contrast, high rainfall may lead to the capture of reproductively-active adults and juveniles throughout the year. Reproductive activity for Mexican spiny pocket mouse peaks from August to November (Dowler and Genoways 1978), thus adults and reproductively-active individuals should be captured in greater proportion in summer–fall, and juveniles in winter. Deer mouse reproduction in northern regions is highly seasonal, whereas deer mice in southern regions are reproductively active throughout the year regardless of small changes in resource conditions (Lackey et al. 1985). Thus, increases in captures of juveniles may occur in any season after breeding has been successful, and may not be affected by minimal changes in rainfall and drought conditions.

MATERIALS AND METHODS

Study area.—The study area consisted of 2 sites located in Willacy and Cameron counties in the Lower Rio Grande Valley (LRGV) of southern Texas. The study site in Willacy County consisted of a ~2 km^2 federal conservation easement on private lands within the Yturria Ranch, Raymondville, Texas (Fig. 2.1). The other study site in Cameron County included the ~190 km^2 Laguna Atascosa National Wildlife Refuge (LANWR), 23 km northeast of Los Fresnos, Texas (Fig. 2.1). Ocelot habitat is greatly reduced and scattered across the LRGV, occurring primarily as patches of Tamaulipan thornshrub. Habitat consists of low, dense stands of honey mesquite (*Prosopis glandulosa*), various *Acacia* spp. and *Mimosa* spp., granjeno

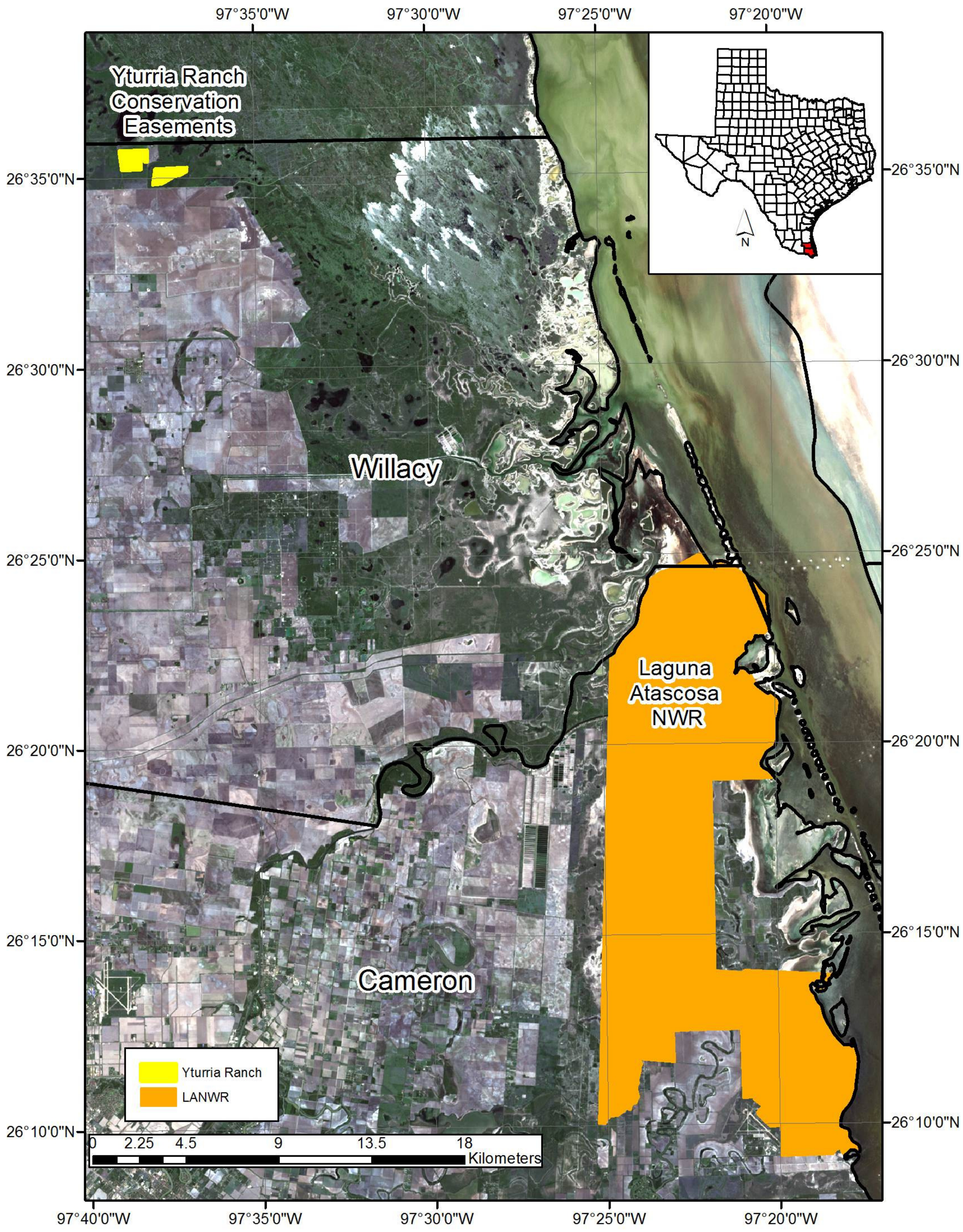

Figure 2.1.—Aerial photograph of the Lower Rio Grande Valley in South Texas where rodent trapping surveys occurred from 2009–2013 on Yturria Ranch (yellow), Willacy County and Laguna Atascosa National Wildlife Refuge (orange), Cameron County.

(*Celtis pallida*), other shrub and succulent species, and intermittent grasses (Jahrsdoerfer and Leslie 1988; Shindle and Tewes 1998). The entire area is located within the Tamaulipan Biotic Province which ranges from southern Texas to northeast Mexico. The area is characterized by a semiarid, subtropical environment of mild winters and hot summers with mean annual rainfall of 68 cm and mean annual temperatures of 23°C (Norwine and Bingham 1985). Precipitation in the LRGV is irregular, alternating between periods of higher than average rainfall and periods of drought.

Small mammal trapping.—On Yturria Ranch, 4 transects of 50 Sherman traps each (*n* = 200) were placed about 2 m apart on fencelines adjacent to or on trails within the conservation easements (i.e., ocelot habitat) from October 2008 to October 2009. Transect locations followed those from previous surveys on the site from July 2006 to August 2008. Trapping from October 2008 to November 2009 occurred on the original 4 transects of 50 traps each (*n* = 200) delineated in previous surveys (Fig. 2.2). Because of low capture rates, a fifth transect and additional traps were added in January 2010; thus 5 transects of 60 traps (*n* = 300) were surveyed through March 2013. Beginning January 2009, rodents were marked individually and demographic data were collected. Sessions from July 2006 to October 2008 and the session from July 2009 did not use individual marking, therefore trap success estimates are based on total captures that combine initial captures and recaptures of rodents. These sessions were removed from analyses of relative abundance as they may overestimate the number of individuals present. Survey sessions from January 2009 to March 2013 were included in demographic analyses. All trapping was conducted seasonally (e.g., 4 times a year in winter, spring, summer, and fall).

Rodent surveys on LANWR consisted of 7 transects (Fig. 2.3) partitioned between 2 types of possible ocelot translocation release sites (primary–first choice for release of

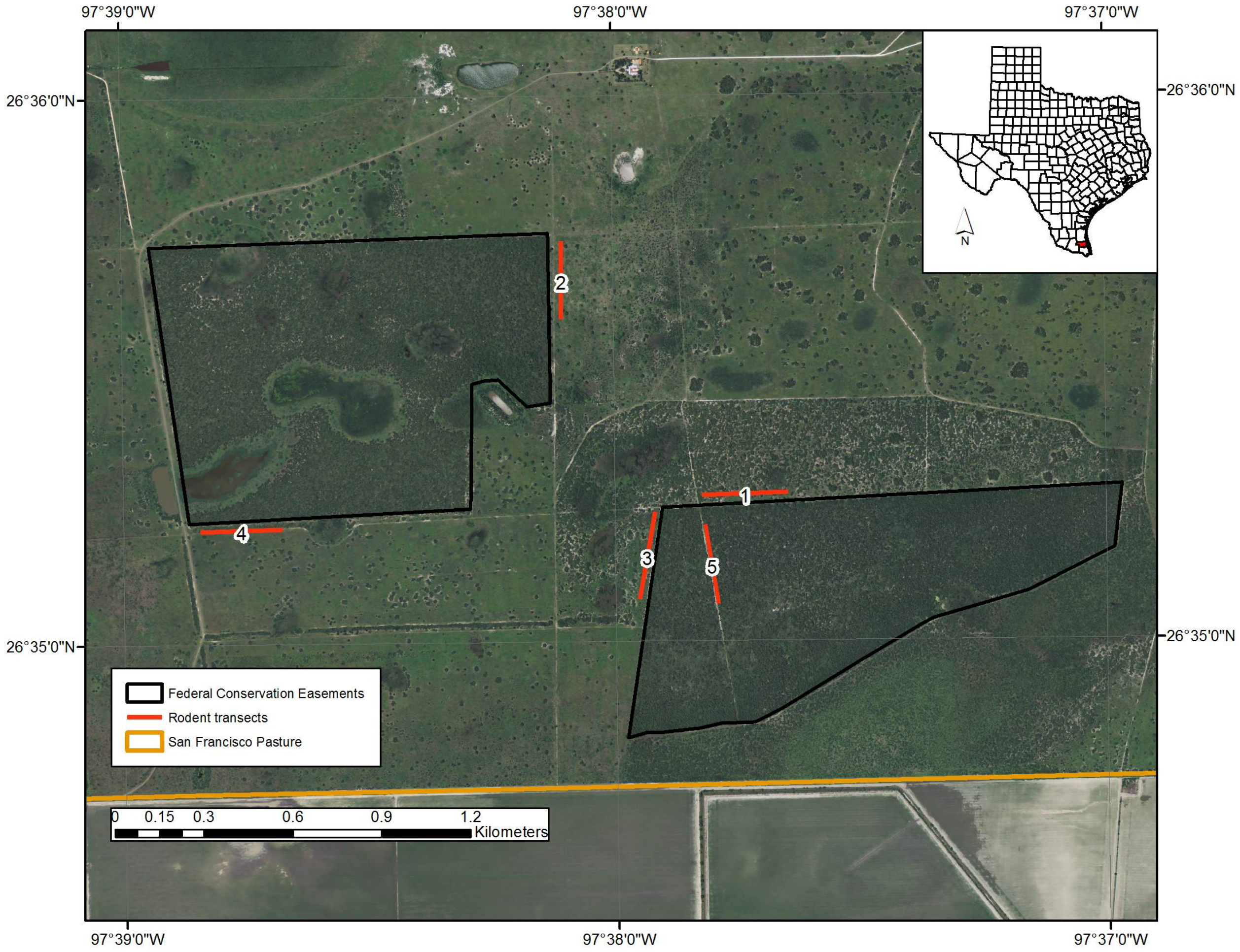

Figure 2.2.—Aerial photograph of rodent transects located on Yturria Ranch, Willacy County, Texas. Count surveys occurred on transects 1–4 (red) from July 2006 to October 2008 and July 2009. Mark-recapture surveys occurred on transects 1–4 (red) from January 2009 to March 2013; and on transect 5 from January 2010 to March 2013.

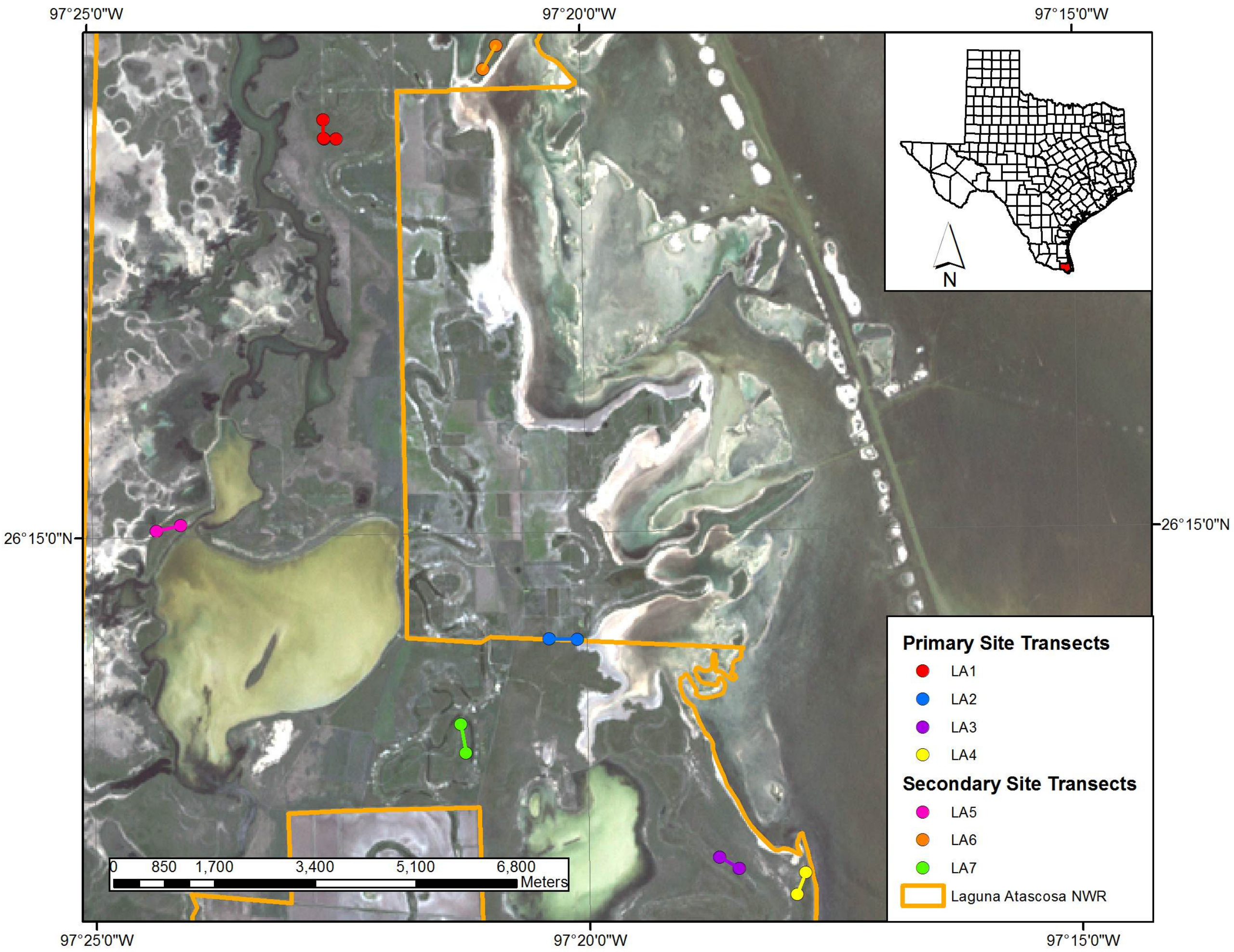

Figure 2.3.—Aerial photograph of rodent transects located on Laguna Atascosa National Wildlife Refuge (NWR), Cameron County, Texas. Mark-recapture surveys occurred seasonally from June 2010 to May 2012. LA1, LA5, and LA6 were not sampled during fall 2011.

translocated ocelots; secondary–second choice for release of ocelots). Primary release sites (n = 4; LA1, LA2, LA3, LA4) were sampled each calendar season. Secondary release sites (n = 3; LA5, LA6, LA7) were surveyed once during fall and once during spring. All surveys occurred from June 2010 to May 2012. Three transects (LA1, LA5, and LA6) could not be sampled during fall 2011 because of restricted access due to hunting in the area. Fifty Sherman traps were set on each transect located along roads and fencelines adjacent to or within ocelot habitat (primary: n = 200 traps; secondary: n = 150 traps). All survey sessions used mark-recapture methods and were included in all analyses.

Traps were baited with a seed mixture and checked the following day at sunrise over 4 consecutive trap nights at Yturria Ranch and LANWR. Polyester batting was added to the traps to reduce hypothermic mortality when temperatures were below 10°C. I identified the species of captured rodents and collected data on sex, age (i.e., adult or juvenile based on size and body mass), and reproductive condition. Non-reproductive rodents were designated non-parous, whereas active males had abdominal or descended testes, and active females were parous, pregnant, or lactating. Because of few individuals within each category, individuals were grouped as non-parous or parous for each sex for statistical analyses.

During mark-recapture surveys, each rodent was marked with a unique double-mark consisting of a numbered metal ear tag (Monel tag #1005-1, National Band and Tag Co., Newport, KY) and permanent marker coloring the underbelly. Species with small ears or body size (e.g., northern pygmy mouse [*Baiomys taylori*], fulvous harvest mouse [*Reithrodontomys fulvescens*, hereinafter referred to as harvest mouse], hispid pocket mouse [*Chaetodipus hispidus*, hereinafter referred to as pocket mouse], Merriam's silky pocket mouse [*Perognathus merriami*], and Mexican ground squirrel [*Spermophilus mexicanus*]) were not given ear tags, but marked with two unique colors for individual identification. Incidental captures of juvenile cottontails were given color marks only.

Individuals were immediately released near the point of capture. All capture and handling techniques followed American Society of Mammalogists Guidelines (Sikes et al. 2011) and were approved by Texas A&M University-Kingsville Institutional Care and Use Committee (2009-12-17A, 2010-06-21A, and 2012-12-20C).

Statistical analyses.—Relative abundance of rodents was estimated using trap success. Number of trap nights and number of transects varied over time and between sites, thus the total number of unique individuals captured for analysis could have biased surveys later in the study after transects and traps were added. Consequently, trap success was defined as the number of unique individuals captured per 100 trap nights, expressed as a percentage, which reduced bias between different sample sizes. I measured relative abundance using overall trap success (community-level) by season and year, as well as for individual species (population-level). I determined if rainfall differed between drought periods, years, and seasons using a 1-way analysis of variance (ANOVA).

I assessed the response of rodents to changes in drought and rainfall using separate linear regressions to test whether trap success (response variable) varied by rainfall (explanatory variable) or drought (explanatory variable). Rainfall was defined as total precipitation (mm) accumulated in the previous three months prior to the survey session. This lag time accounted for the time vegetation responds to rainfall, and rodents to increase reproduction (Bradley et al. 2006). Precipitation data for Yturria Ranch came from a monitored rain gauge located on a nearby ranch (~5 km from transects), and data for LANWR came from an onsite Remote Automated Weather Station (~1–10 km from transects). The Palmer Modified Drought Index

(PMDI) was used to indicate drought, and is a meteorological scale modified from the Palmer Drought Severity Index that is produced by the National Climatic Data Center. The PMDI is a continuous measure, has a more normal distribution, and is used in areas with frequent transition periods (Heddinghaus and Sobol 1991). Monthly indices are created for regional divisions within states by weighting moisture supply (precipitation and loss of soil moisture) and demand (evapotranspiration, recharge of soil moisture, and runoff), with temperature (in the calculation of evapotranspiration). Values typically range between -5 and 5, but can occur up to ±7 in some cases. Any positive value is considered "not in drought", whereas values below zero indicate drought conditions. Though precipitation is one component used to calculate PMDI, localized rainfall events are necessarily reflected in regional PMDI (Schwinning and Sala 2004) . Therefore, I assessed response of rodents to rainfall and PMDI separately.

Simple linear regression analyses were conducted at the community-level for both study sites using cumulative trap success of all species. Individual target species and those with sufficient sample size were used at the population-level.

I used an ANOVA to examine differences in trap success by season and year on Yturria Ranch. A pooled t-test was used to determine if trap success differed between the translocation sites (primary or secondary) on LANWR. I used an ANOVA to test whether trap success varied by season or year, and a pooled t-test for drought (Y/N), and drought during the previous 3 months (Y/N) on study sites Yturria Ranch and LANWR separately.

A Tukey-Kramer Honestly Significant Difference (T-K HSD) test was used to identify the significantly different group. Simple linear regressions, ANOVA, and pooled t-tests were performed in program JMP 10.0.2 (SAS Institute, Inc., Cary, North Carolina). Estimates were reported with 95% confidence intervals (*CI*) and statistical significance reported at $P \leq 0.05$.

For demographic analyses at both sampling sites, I used multiple logistic regression to predict whether males, adults, or reproductively active individuals could be predicted by 4 covariates. The response variable were each individual unique capture. The covariates of interest were season (categorical), rainfall (continuous), PMDI (continuous), and whether drought was present during the 3 months prior to the trap session (continuous), and the interactions between these variables. I coded 3-month previous drought (Y = 1, N = 0) based on PMDI data. Drought conditions occur on a gradient from extreme drought at the lowest negative values to extreme wet at the highest positive values. Therefore, any value below zero indicated that the environment was stressed because of drought. All values below zero were coded as 1 for analyses. Year was not chosen as a covariate because the drought covariates accounted for this effect.

Models were chosen from the full set of candidate models (*n* = 15, Table 2.1) based on Akaike's Information Criterion corrected for small sample size ($\mathrm{AIC_C}$) and $\Delta\mathrm{AIC_C} = 2$. I present model-averaged coefficients and their unconditional standard errors (*SE*, Burnham and Anderson 2002). Overall probability ($\hat{P}$) of capturing males, adults, and reproductively active individuals was calculated (Eq. 2.1), as well as for each survey session. I also calculated the overall odds ratio (Eq. 2.2) and for each survey session. The $\mathrm{AIC_C}$ model selection and model averaging was performed in R 2.13.0 (R Foundation for Statistical Computing, Vienna, Austria) and statistical significance was considered at $P \leq 0.05$.

Equation 2.1.

$$\hat{P} = \frac{1}{1 + e^{-1\,(\hat{\beta}_0\,\mathrm{X} + \hat{\beta}_{Rain}\mathrm{X} + \hat{\beta}_{PMDI}\mathrm{X} + \hat{\beta}_{PMDI3}\mathrm{X} + \hat{\beta}_{Spring}\mathrm{X} + \hat{\beta}_{Summer}\mathrm{X} + \hat{\beta}_{Winter}\mathrm{X})}}$$

Equation 2.2.

$$\text{Odds ratio} = \frac{\hat{P}success}{(1 - \hat{P}success)}$$

Table 2.1.—Full set of candidate models (*n* = 15) used in multiple logistic regression analyses to determine if rodent demographics (sex, age, and reproductive condition) could be predicted by total precipitation recorded in the 3 months prior to the survey (Rain), drought (Palmer Modified Drought Index [PMDI]), drought in previous 3 months (PMDI3), and season (Season) on Yturria Ranch, Willacy County; and Laguna Atascosa National Wildlife Refuge, Cameron County, Texas. Species modeled for both study sites were: hispid cotton rat (*Sigmodon hispidus*), Mexican spiny pocket mouse (*Liomys irroratus*), and deer mouse (*Peromyscus* spp.).

#	Model
1	Rain
2	PMDI
3	PMDI3
4	Season
5	Rain + PMDI
6	Rain + PMDI3
7	Rain + Season
8	Rain + PMDI + PMDI3
9	Rain + PMDI + Season
10	Rain + PMDI3 + Season
11	PMDI + PMDI3
12	PMDI + Season
13	PMDI3 + Season
14	PMDI + PMDI3 + Season
15	Rain + PMDI + PMDI3 + Season

RESULTS

Yturria Ranch.—For the entire study period (2008–2013), I captured 1,513 individuals from 11 species over 16,113 trap nights (Table 2.2). The 11 species captured consisted of 6 cricetids (cotton rat, woodrat, deer mouse, harvest mouse, northern pygmy mouse and northern grasshopper mouse [*Onychomys leucogaster*]), 3 heteromyids (Mexican spiny, pocket mouse, and Merriam's silky pocket mouse), 1 sciurid (Mexican ground squirrel), and 1 lagomorph (eastern cottontail). Incidental captures were primarily birds (e.g., olive sparrow [*Arremonops rufivirgatus*]), and snakes, lizards, and 1 desert shrew (*Notiosorex crawfordi*). Surveys from October 2008 and July 2009 did not use unique marking techniques, so data were examined for overestimation because of counting unmarked individuals multiple times. Examination of the data from these sessions led to the exclusion of October 2008 and the inclusion of July 2009 for analyses with mark-recapture surveys.

Simple linear regression analyses were applied at the community-level using cumulative trap success for all species. Regression analyses were applied at the population-level on Yturria Ranch for 5 species that were either targeted (i.e., cotton rat, Mexican spiny, and deer mouse) or had adequate sample sizes for analysis (i.e., pocket mouse, harvest mouse). Six species did not have enough captures consistently across seasons and years to be included in the analyses (i.e., woodrat, northern pygmy mouse, Merriam's silky pocket mouse, northern grasshopper mouse, Mexican ground squirrel, and eastern cottontail).

Increasing PMDI values (i.e., decreasing drought severity) were positively correlated with increasing rainfall (t_{13} = 3.29, P = 0.006, R^2 = 0.46). For every 1 mm increase in rainfall, there was a 0.01 unit increase in PMDI (CI = 0.005–0.02, Fig. 2.4). Rainfall differed significantly between years ($F_{3,11}$ = 7.05, P = 0.007), and T-K HSD indicated 2010 had significantly higher rainfall than 2009, 2011, or 2012. Additionally, rainfall was significantly

Table 2.2.—Trap success (number of unique individuals/100 trap nights), for each species ($n = 11$) captured on Yturria Ranch, Willacy County, Texas, by year (2009–2013) and season (winter, spring, summer, and fall). Species are *Baiomys taylori* (BATA), *Chaetodipus hispidus* (CHHI), *Liomys irroratus* (LIIR), *Neotoma micropus* (NEMI), *Onychomys leucogaster* (ONLE), *Perognathus merriami* (PEME), *Peromyscus* spp. (PESP), *Reithrodontomys fulvescens* (REFU), *Sigmodon hispidus* (SIHI), *Spilosoma mexicanus* (SPME), and *Sylvilagus floridanus* (SYFL). Rainfall (RAINFALL, mm) corresponds to total precipitation recorded in the 3 months prior to the survey and regional Palmer Modified Drought (PMDI) to the month of the survey.

	BATA	CHHI	LIIR	NEMI	ONLE	PEME	PESP	REFU	SIHI	SPME	SYFL	TOTAL	RAINFALL (mm)	PMDI
2009														
Winter	0	0	1.64	0	0.20	0	7.36	2.45	9.82	0	0	23.72	22.86	1.8
Spring	0.70	0.42	0.42	0	0	0.56	0.98	0	3.37	0	0	6.46	10.16	-2.13
Summer	1.02	0.13	0.38	0	0	0.25	1.27	0.13	1.40	0	0	4.6	43.18	-3.15
Fall	0	0.78	1.82	0	0	0.13	1.30	0.13	0.52	0.26	0	4.94	74.93	-2.46
2010														
Winter	0.09	0	0.18	0	0	0	1.27	0.09	0	0	0	1.63	241.3	0.74
Spring	0	0.75	1.17	0.33	0	0.08	0.83	0	0.17	0	0	3.34	241.3	3.14
Summer	0	1.53	2.29	0.17	0	0.08	0.25	0	5.27	0	0	9.6	482.6	4.27
Fall	0.26	1.05	2.64	0.35	0	0	2.81	0.97	11.42	0	0	19.51	367.03	1.38
2011														
Winter	1.19	0.09	1.45	0	0	0	4.18	2.47	7.34	0	0	16.72	66.04	-0.88
Spring	1.17	0.45	0.90	0	0	0	1.35	0.63	7.99	0.09	0	12.57	0	-3.74

Table 2.2. (continued)

	BATA	CHHI	LIIR	NEMI	ONLE	PEME	PESP.	REFU	SIHI	SPME	SYFL	TOTAL	RAINFALL (mm)	PMDI
2011 (cont.)														
Summer	1.9	0.26	0.85	0.43	0	0	0.60	0	7.08	0.09	0.09	11.26	207.01	-2.04
Fall	3.33	0.83	3.92	0.24	0.36	0	6.90	0.36	11.89	0.12	0	27.94	85.09	-4.25
2012														
Spring	0.09	0.52	1.13	0.17	0	0	2.53	0	0	0.17	0.09	4.71	123.83	-2.02
Summer	0.26	0.35	0.86	0.17	0	0	1.30	0	0	0.43	0.08	3.45	111.76	-3.21
Fall	0.18	1.45	1.36	0.09	0.18	0	2.27	0	0	0.09	0	5.64	100.33	-4.21
2013														
Winter	0.09	0.58	0.19	0	0.48	0.19	2.70	0	0	0.19	0	4.34	25.4	-4.61

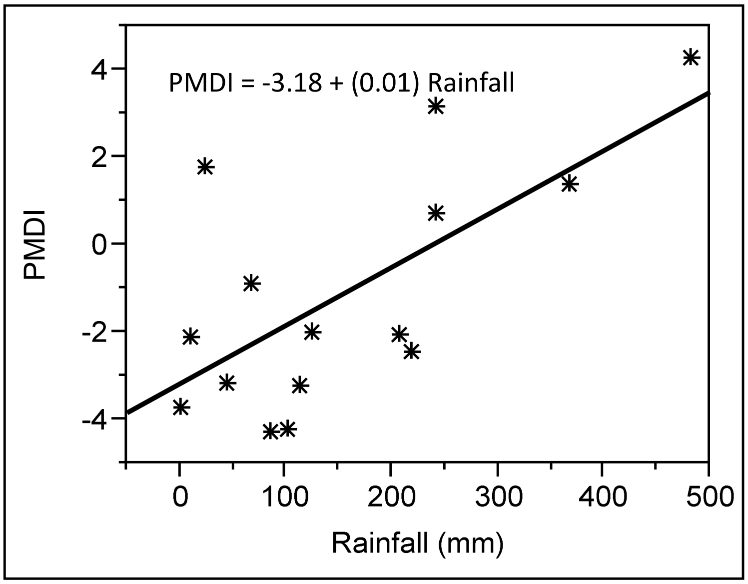

Figure 2.4.—Positive linear correlation between Palmer Modified Drought Index (PMDI) and rainfall (mm) on Yturria Ranch, Willacy County, Texas, from January 2009 to March 2013. For every 1 mm increase in rainfall, there was a 0.01 (*CI* = 0.005–0.02) increase in PMDI.

higher when "not in drought" (t_{13} = -2.82, P = 0.01). Rainfall did not differ significantly by season ($F_{3,11}$ = 0.63, P = 0.61) or by season when the wet year (i.e., 2010) was excluded ($F_{3,7}$ = 1.29, P = 0.35). Drought (as defined by PMDI) was significantly different between years ($F_{3,11}$ = 8.18, P = 0.004); T-K HSD revealed that 2010 was "not in drought," whereas the other 3 survey years were of similar drought severity. During "not in drought" periods, rainfall did not differ significantly by season ($F_{3,6}$ = 0.90, P = 0.50), but rainfall was generally higher in summer and fall.

Trap success was not correlated with rainfall (t_{13} = -0.45, P = 0.66), PMDI (t_{13} = 0.10, P = 0.92), or drought (t_{13} = - 0.38, P = 0.71). Trap success also did not differ significantly if drought occurred in the 3 months prior to the survey (t_{13} = -1.46, P = 0.17), but tended to increase when drought did not occur prior to surveys. Trap success was not significantly different between years ($F_{3,11}$ = 1.74, P = 0.22), although total trap success for 2011 was 68.5% compared to 39.7%, 34.1%, and 13.8% for 2009, 2010, and 2012, respectively. Trap success was not significantly different between seasons ($F_{3,12}$ = 0.83, P = 0.5), but I observed the highest success during the fall sessions.

Rainfall and trap success data from Yturria Ranch showed that dry periods did not necessarily correspond to the most severe PMDI values. Therefore, I explored analyses of wet and dry periods separately. Wet periods were those with significant rainfall events during drought periods (PMDI<0). Trap success was positively correlated with increasing PMDI in dry periods (t_4 = 3.42, P = 0.03, R^2 = 0.75). Trap success increased by 2.9% (CI = 0.54–5.25, Fig. 2.5A) for every 1 unit increase in PMDI. There was no correlation between trap success and rainfall during dry periods (t_4 = 0.24, P = 0.82). In wet periods, there was no relationship

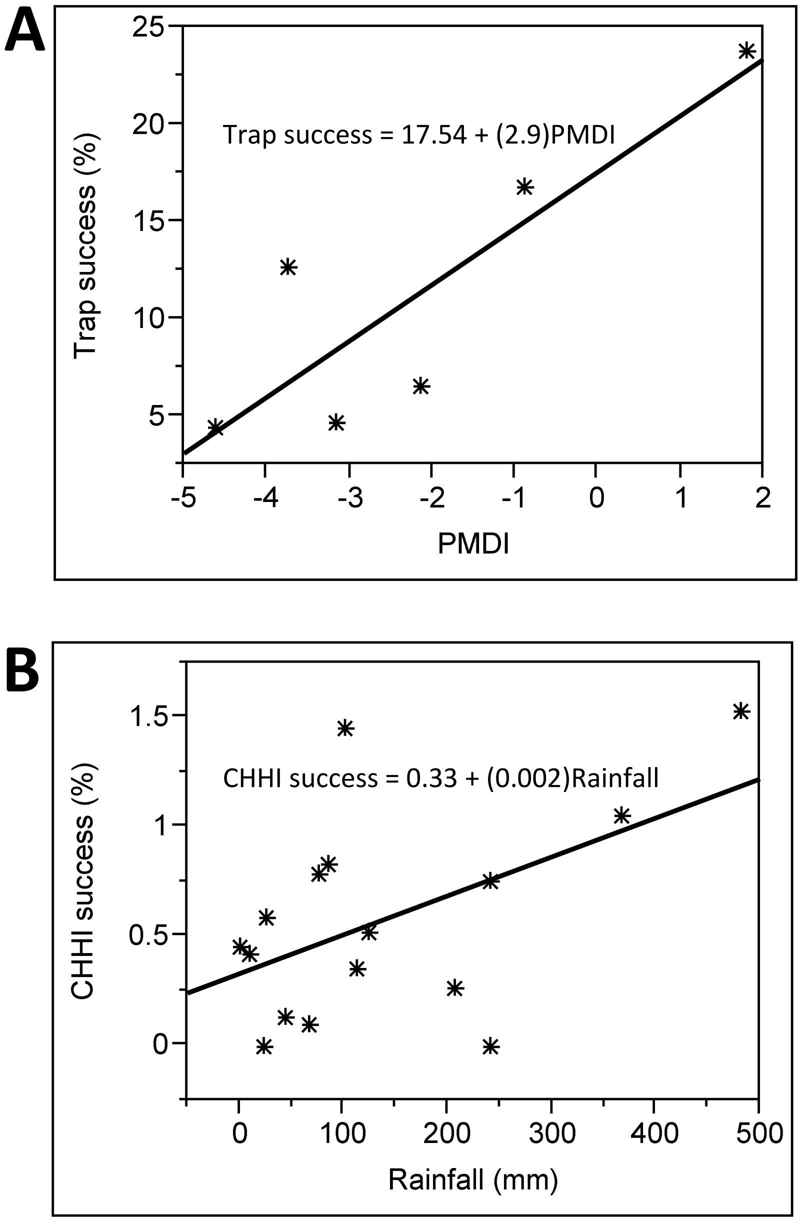

Figure 2.5.—(A) Positive linear correlation between dry periods and drought (Palmer Modified Drought Index [PMDI]) on Yturria Ranch, Willacy County, Texas, from January 2009 to March 2013. For every 1 unit increase in PMDI, there was a 2.9 % (*CI* = 0.5–5.25) increase in trap success. (B) Positive linear correlation between trap success of hispid pocket mouse (CHHI) and rainfall (mm) on Yturria Ranch. For every 1 mm increase in rainfall, there was a 0.002% (*CI* = 9.61e-5–0.003) increase in CHHI trap success.

between trap success and PMDI (t_8 = -0.48, P = 0.64) or between trap success and rainfall (t_8 = 0.08, P = 0.94).

Trap success was significantly different among individual species ($F_{4,70}$ = 6.52, P <0.001). The T-K HSD test indicated that trap success of cotton rat was higher than harvest mouse, pocket mouse, and Mexican spiny, but not deer mouse. Trap success was positively correlated with increasing rainfall for pocket mouse (t_{13} = 2.26, P = 0.04, R^2 = 0.28). For every 1 mm increase in rainfall, there was a 0.002% increase in trap success (CI = 9.61e-5–0.003, Fig. 2.5B). There was no correlation between trap success and rainfall for Mexican spiny (t_{13} = 1.03, P = 0.32) or cotton rat (t_{13} = 0.20, P = 0.85). A slightly negative, but not significant, correlation was indicated between trap success and rainfall for deer mouse (t_{13} = -1.31, P = 0.21) and harvest mouse (t_{13} = -0.92, P = 0.34). Highest trap success for harvest mouse for the study occurred during winter 2009 (2.45%) and winter 2011 (2.47%). After removal of the 2 outliers, there was no relationship between this species and rainfall (t_{11} = 0.34, P = 0.74).

Drought (defined by PMDI < 0) was not a significant factor for trap success for any species: pocket mouse (t_{13} = 0.50, P = 0.62), Mexican spiny (t_{13} = 0.32, P = 0.76), deer mouse (t_{13} = 0.27, P = 0.79), harvest mouse (t_{13} = 0.81, P = 0.81), or cotton rat (t_{13} = 0.34, P = 0.74). The occurrence of drought in the 3 months prior to the trapping session did not significantly affect trap success for pocket mouse (t_{13} = -0.60, P = 0.56), Mexican spiny (t_{13} = -1.25, P = 0.23), deer mouse (t_{13} = -0.92, P = 0.37), or cotton rat (t_{13} = -1.51, P = 0.15). Trap success was significantly higher for harvest mouse when drought did not occur in the previous 3 months.

Trap success was not significantly different between years for pocket mouse ($F_{3,11}$ = 1.03, P = 0.42), but success in 2010 and 2012 was about 2 times higher than in 2009 and 2011. It also was not significantly different for Mexican spiny ($F_{3,11}$ = 0.42, P = 0.74), deer mouse

($F_{3,11} = 0.55$, $P = 0.66$), or harvest mouse ($F_{3,11} = 0.70$, $P = 0.57$). Trap success was different, though not significantly between years for cotton rat ($F_{3,11} = 3.06$, $P = 0.07$). Trap success peaked during fall 2011 (11.9%), even though the region was in severe drought (-4.25). After this population high, no cotton rats were captured on surveys from winter 2012 through winter 2013.

Trap success varied significantly between seasons for pocket mouse ($F_{3,12} = 3.24$, $P = 0.06$), Mexican spiny ($F_{3,11} = 2.92$, $P = 0.08$), and harvest mouse ($F_{3,11} = 4.39$, $P = 0.03$), but not for deer mouse ($F_{3,11} = 2.54$, $P = 0.11$), or cotton rat ($F_{3,11} = 0.40$, $P = 0.76$). The T-K HSD analysis revealed that for pocket mouse, trap success was highest in fall, lowest during winter, and moderate for spring and summer. Though not significant, T-K HSD indicated that Mexican spiny trap success was about 2 times greater during fall as compared to summer and winter, and lowest during spring by about 3-fold. Trap success for harvest mouse was significantly higher during winter than any other season.

Wet or dry periods did not significantly affect trap success for Mexican spiny ($t_{13} = 1.27$, $P = 0.23$), deer mouse ($t_{13} = -1.85$, $P = 0.41$), or cotton rat ($t_{13} = -0.95$, $P = 0.36$). Trap success was significantly higher during wet periods for pocket mouse ($t_{13} = 2.28$, $P = 0.04$), and significantly higher during dry periods for harvest mouse ($t_{13} = -2.45$, $P = 0.03$).

Trap success on Yturria Ranch was not significantly correlated with year, season, or drought, but it typically peaked in fall of each year. The highest trap success occurred in fall 2011 (27.9%) during regional drought, but followed significant rainfall events. A hurricane and tropical storm produced large quantities of precipitation on the site in June and September 2010, respectively (Fig. 2.6).

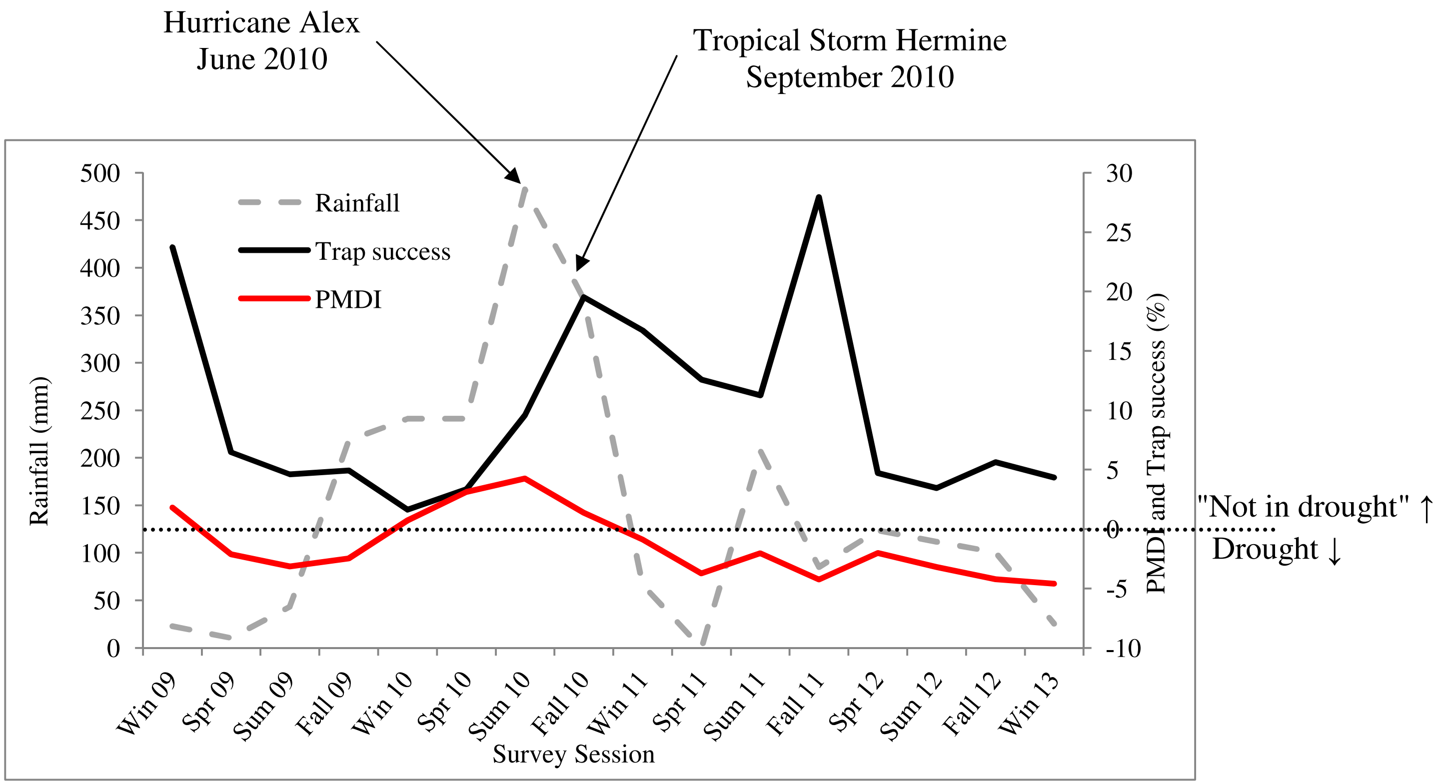

Figure 2.6.—Patterns of rodent trap success (%) on Yturria Ranch, Willacy County, Texas, from January 2009 to March 2013 (solid black line; right vertical axis). Rainfall (mm) was greatest in 2010 and included precipitation from Hurricane Alex (June) and Tropical Storm Hermine (September), and had multiple localized pulse events in 2011 (grey dashed line; left vertical axis). Drought (Palmer Modified Drought Index [PMDI]) conditions occurred at any value below 0 (below black dotted line), and "not in drought" above 0 (red line; right vertical axis). Extreme drought and extreme wet conditions occurred ~ -4.0, and ~4.0, respectively.

The top competing models in multiple logistic regression analyses for cotton rat, pocket mouse, and deer mouse included all covariates, except for male pocket mouse, and adult deer mouse, which did not include season (Appendix I). No cotton rats were captured from spring 2012 to winter 2013. Probability of catching a male cotton rat from winter 2009 to fall 2011 ranged from 12% (winter 2010) to 55% (spring 2011). Probability of catching an adult cotton rat was relatively constant with the lowest in spring 2010 (52%), but was typically 80–100% throughout the year. Probability of catching a reproductively active cotton rat was usually low in winter (2009 = 8%, 2011 = 7%), and highest in spring (37–63%). The highest capture probability was winter 2010 (91%) after the beginning of a high rainfall period that occurred through 2010 (Table 2.3).

Probability of capturing a male Mexican spiny was lowest in summer 2010 (10%) and highest in winter 2013 (68%). For adults, probability of success ranged from 5% (summer 2009) to 100% (fall 2010, winter 2011, winter 2013). Probability for reproductively active Mexican spiny was lowest in the winter season (18–27%) and highest in spring (77–87%), even during drought or low rainfall conditions (Table 2.3).

Probability of capturing a male deer mouse was consistent in spring, summer, and fall (57–67%), and lowest in winter after wet periods (39%). Probability of capture success for adults was >98% throughout the study, but was 47% in winter 2009. Highest probability of capturing a reproductively active deer mouse was in summer (79–98%), and lowest in winter (2009 = 10%, 2011 = 5%, 2013 = 7%), except winter 2010 when it reached 50% after high rainfall occurred (Table 2.3).

Probability of capturing a male Mexican spiny or adult deer mouse was not dependent on season, but all models for all species included rainfall, PMDI, and occurrence of drought in the

Table 2.3.—Probability ($\hat{P}$) and odds ratio (OR) of capturing a male, adult, or reproductively active (Repro) hispid cotton rat, hispid pocket mouse, and deer mouse by season (winter, spring, summer, and fall), and year (2009–2013) on Yturria Ranch, Willacy County, Texas. Rainfall (mm) is total precipitation recorded in the 3 months prior to the survey and regional Palmer Modified Drought Index (PMDI) to the month of the survey. Total estimates across the entire time period for each species are given below.

			Hispid cotton rat						Mexican spiny pocket mouse					
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
2009														
Winter	22.86	1.8	0.36	0.56	0.71	2.49	0.08	0.08	0.29	0.42	0.86	5.95	0.21	0.27
Spring	10.16	-2.13	0.46	0.85	0.93	13.73	0.47	0.89	0.55	1.22	0.50	1.02	0.86	6.40
Summer	43.18	-3.15	0.42	0.72	0.78	3.63	0.16	0.19	0.63	1.69	0.05	0.05	0.68	2.15
Fall	74.93	-2.46	0.37	0.58	0.88	7.61	0.18	0.22	0.59	1.44	0.16	0.19	0.34	0.51
2010														
Winter	241.3	0.74	0.12	0.14	1.00	847.32	0.91	10.27	0.40	0.66	0.98	45.26	0.21	0.26
Spring	241.3	3.14	0.55	1.20	0.52	1.09	0.63	1.74	0.18	0.22	0.94	15.03	0.77	3.30
Summer	482.6	4.27	0.39	0.63	0.55	1.23	0.83	4.90	0.10	0.11	0.81	4.24	0.48	0.91
Fall	367.03	1.38	0.40	0.66	0.67	2.02	0.38	0.62	0.17	0.21	1.00	287.36	0.22	0.28
2011														
Winter	66.04	-0.88	0.31	0.45	0.92	11.05	0.07	0.07	0.35	0.54	1.00	4241.90	0.18	0.22
Spring	0.0	-3.74	0.45	0.82	0.96	22.68	0.37	0.58	0.67	2.00	0.95	18.45	0.87	6.93
Summer	207.01	-2.04	0.32	0.48	0.93	14.16	0.56	1.28	0.51	1.02	0.38	0.62	0.65	1.89
Fall	85.09	-4.25	0.34	0.53	0.94	16.79	0.15	0.17	0.64	1.78	0.90	9.08	0.36	0.56

Table 2.3. (continued)

			Hispid cotton rat						Mexican spiny pocket mouse					
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
2012														
Spring	123.83	-2.02	0.0	0.0	0.0	0.0	0.0	0.0	0.55	1.22	0.96	22.29	0.86	6.05
Summer	111.76	-3.21	0.0	0.0	0.0	0.0	0.0	0.0	0.59	1.47	0.28	0.40	0.68	2.09
Fall	100.33	-4.21	0.0	0.0	0.0	0.0	0.0	0.0	0.63	1.71	0.93	13.06	0.36	0.55
2013														
Winter	25.4	-4.61	0.0	0.0	0.0	0.0	0.0	0.0	0.68	2.12	1.00	3446.10	0.27	0.37

			Deer mouse					
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
2009								
Winter	22.86	1.8	0.41	0.70	0.47	0.90	0.10	0.11
Spring	10.16	-2.13	0.62	1.62	0.94	17.12	0.63	1.72
Summer	43.18	-3.15	0.58	1.37	0.98	43.66	0.79	3.71
Fall	74.93	-2.46	0.62	1.64	0.97	29.92	0.48	0.94
2010								
Winter	241.3	0.74	0.53	1.13	0.85	5.68	0.50	0.98
Spring	241.3	3.14	0.57	1.35	0.91	10.49	0.82	4.51
Summer	482.6	4.27	0.60	1.49	0.93	13.81	0.98	44.51
Fall	367.03	1.38	0.63	1.67	0.99	72.96	0.67	2.04

Table 2.3. (continued)

Season	Rainfall (mm)	Deer mouse PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
2011								
Winter	66.04	-0.88	0.39	0.65	0.99	99.25	0.05	0.06
Spring	0.0	-3.74	0.64	1.74	0.98	55.92	0.50	1.01
Summer	207.01	-2.04	0.64	1.75	0.98	40.48	0.91	10.27
Fall	85.09	-4.25	0.65	1.86	0.99	123.41	0.36	0.57
2012								
Spring	123.83	-2.02	0.67	2.00	0.96	26.92	0.74	2.85
Summer	111.76	-3.21	0.61	1.56	0.98	63.18	0.83	4.84
Fall	100.33	-4.21	0.66	1.91	0.99	128.62	0.38	0.61
2013								
Winter	25.4	-4.61	0.51	1.02	0.99	122.62	0.07	0.08

TOTALS BY SPECIES

Hispid cotton rat						Mexican spiny pocket mouse						Deer mouse					
$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
0.27	0.37	0.99	120.32	0.90	8.68	0.52	1.07	0.21	0.26	0.93	13.87	0.40	0.68	0.60	1.50	0.83	4.74

previous 3 months before surveys. The greatest probability of capturing a juvenile cotton rat was highest in spring 2010, which was then followed by increasing probability of adults and high trap success in fall 2010; the result of an influx of new individuals after breeding. This period also corresponded with the highest rainfall and PMDI values of the study period (Fig. 2.7)

The relationship was less clear for Mexican spiny, and seemed to fluctuate in a relatively predictable pattern regardless of minor pulses in rainfall or drought. This pattern changed slightly during the wet period of 2010 when there was a prolonged period of high adult presence. The greatest probability of capturing a female (summer 2010) was immediately following a peak in reproductive activity (spring 2010), which seemed correlated with abundant precipitation (Fig. 2.8).

The greatest probability of capturing a juvenile deer mouse was in winter 2009 ($\hat{P}$ = 53%), but all other surveys were comprised primarily of adults ($\hat{P} \approx$ 100%). Reproductively-active individuals had the highest probability of being trapped in summer of each year, with distinct declines in winter 2009, 2011, and 2013 (Fig. 2.9).

LANWR.—From 2010–2012, I captured 1,001 individuals from 10 species over 8,166 trap nights on primary and secondary sites (Table 2.4). Small mammal captures consisted of the same species found on Yturria Ranch, except that no hispid pocket mouse were detected on LANWR surveys. Incidental captures were less frequent and consisted of primarily birds and snakes.

At the population-level on LANWR, 3 species were assessed (e.g., cotton rat, Mexican spiny, and deer mouse), and 7 species lacked adequate captures for analyses (e.g., woodrat, harvest mouse, northern pygmy mouse, Merriam's silky pocket mouse, northern grasshopper mouse, Mexican ground squirrel, and eastern cottontail).

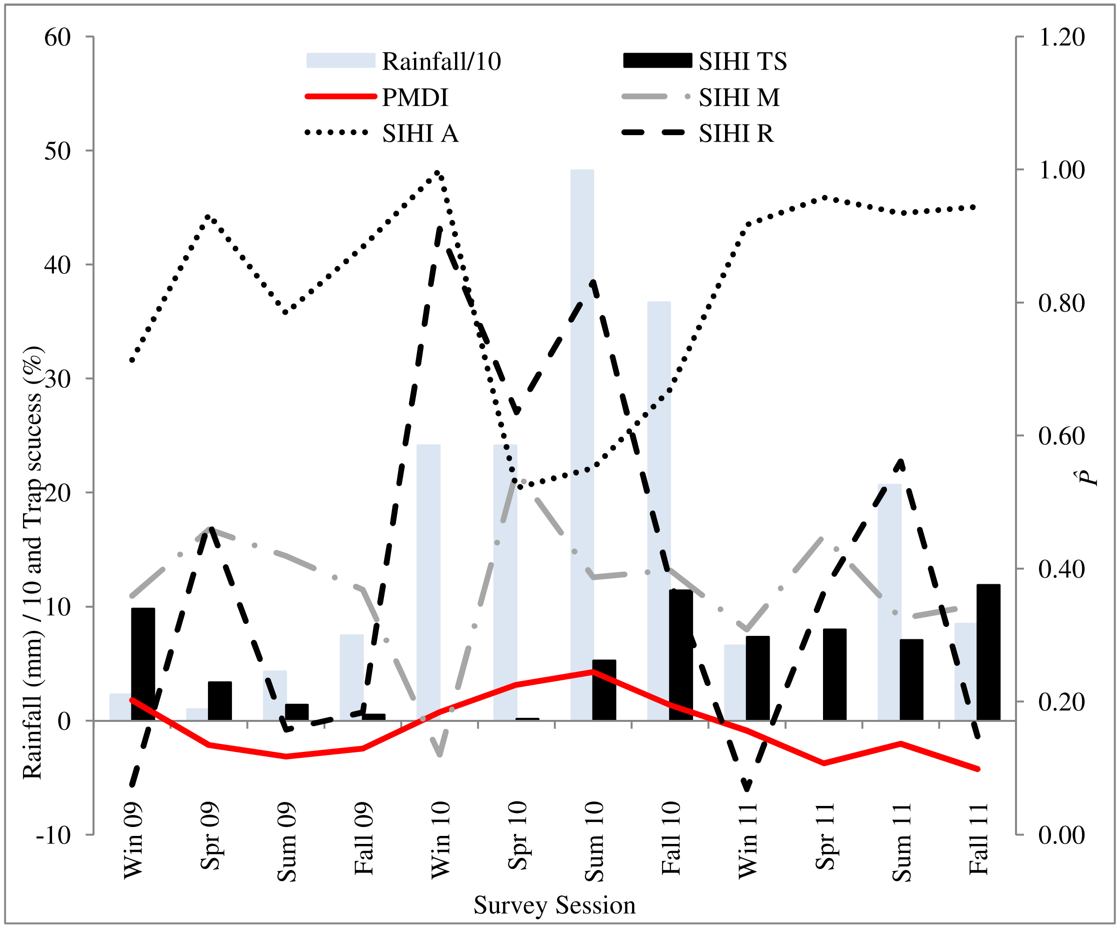

Figure 2.7.—Probability ($\hat{P}$) of capturing (dashed lines; right vertical axis) a male (M), adult (A), or reproductively active (R) hispid cotton rat (SIHI) on Yturria Ranch, Willacy County, Texas, by survey session from January 2009 to November 2011. Trap success (TS; %), rainfall (mm) as 1/10 of total precipitation recorded in 3 months prior to survey, and Palmer Modified Drought Index (PMDI; red line) are projected on the left vertical axis.

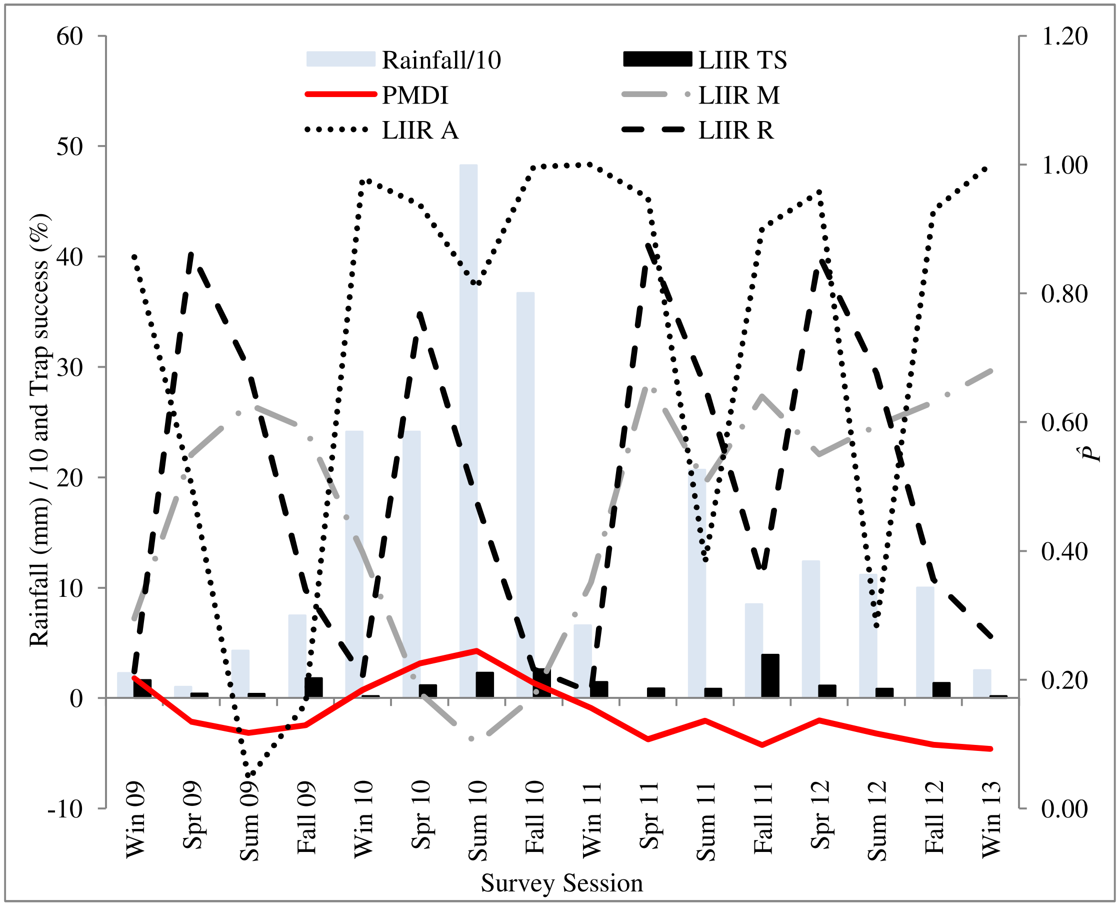

Figure 2.8.—Probability ($\hat{P}$) of capturing (dashed lines; right vertical axis) a male (M), adult (A), or reproductively active (R) Mexican spiny pocket mouse (LIIR) on Yturria Ranch, Willacy County, Texas, by survey session from January 2009 to March 2013. Trap success (TS; %), rainfall (mm) as 1/10 of total precipitation recorded in 3 months prior to survey, and Palmer Modified Drought Index (PMDI; red line) are projected on the left vertical axis.

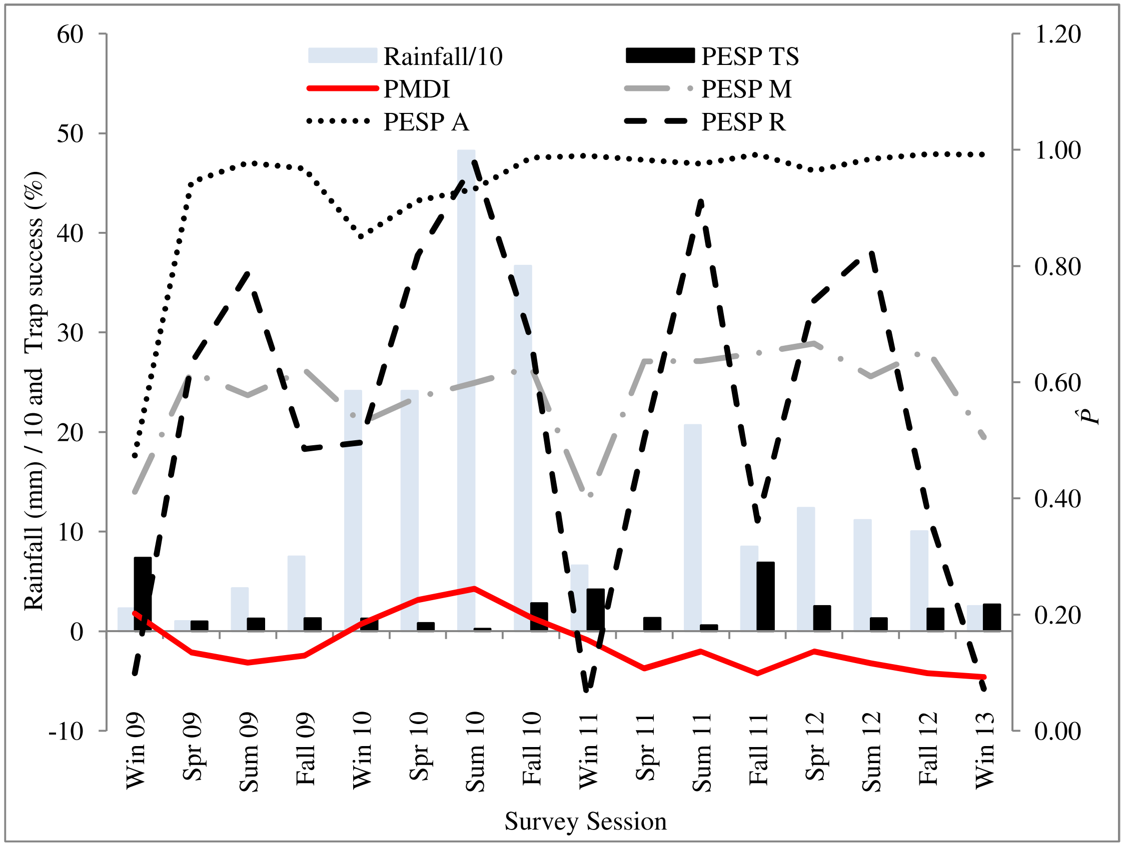

Figure 2.9.—Probability ($\hat{P}$) of capturing (dashed lines; right vertical axis) a male (M), adult (A), or reproductively active (R) deer mouse (PESP) on Yturria Ranch, Willacy County, Texas, by survey session from January 2009 to March 2013. Trap success (TS; %), rainfall (mm) as 1/10 of total precipitation recorded in 3 months prior to survey, and Palmer Modified Drought Index (PMDI; red line) are projected on the left vertical axis.

Table 2.4.—Trap success (number of unique captures/100 trap nights), for each individual species ($n = 10$) captured on Laguna Atascosa National Wildlife Refuge by site (primary and secondary), year (2010–2012) and season (winter, spring, summer, and fall). Species are *Baiomys taylori* (BATA), *Liomys irroratus* (LIIR), *Neotoma micropus* (NEMI), *Onychomys leucogaster* (ONLE), *Perognathus merriami* (PEME), *Peromyscus* spp. (PESP), *Reithrodontomys fulvescens* (REFU), *Sigmodon hispidus* (SIHI), *Spilosoma mexicanus* (SPME), and *Sylvilagus floridanus* (SYFL). Rainfall (RAINFALL, mm) corresponds to total precipitation recorded in the 3 months prior to the survey and Palmer Modified Drought Index (PMDI) to the month of the survey.

	BATA	LIIR	NEMI	ONLE	PEME	PESP	REFU	SIHI	SPME	SYFL	TOTAL	RAINFALL (mm)	PMDI
PRIMARY													
2010													
Summer	0.13	1.30	0.26	0.00	0.13	1.95	0.13	14.97	0.00	0.00	18.88	295.95	3.37
Fall	0.00	1.44	0.65	0.00	0.00	3.92	0.13	13.99	0.00	0.00	20.13	325.35	1.38
2011													
Winter	0.14	3.30	0.14	0.00	0.00	9.49	0.96	7.43	0.00	0.00	21.46	38.10	0.07
Spring	0.00	2.37	0.15	0.00	0.00	3.11	0.44	4.14	0.15	0.15	10.50	14.48	-2.93
Summer	0.00	1.42	0.28	0.43	0.00	1.42	0.28	6.10	0.43	0.00	10.35	102.87	-3.27
Fall	0.00	2.72	0.57	0.00	0.00	4.58	0.00	2.01	0.00	0.00	9.89	61.97	-4.25
2012													
Winter	0.00	1.68	0.00	0.26	0.39	4.38	0.26	2.06	0.00	0.00	9.02	169.44	-1.98
Spring	0.13	1.73	0.40	0.00	0.13	2.12	0.40	3.98	0.00	0.00	8.90	141.48	-2.45

Table 2.4. (continued)

	BATA	LIIR	NEMI	ONLE	PEME	PESP	REFU	SIHI	SPME	SYFL	TOTAL	RAINFALL (mm)	PMDI
SECONDARY													
2010													
Fall	0.00	0.71	0.00	0.18	0.00	4.45	0.53	8.36	0.00	0.00	14.23	325.35	1.38
2011													
Spring	0.00	2.37	0.14	0.00	0.00	3.11	0.44	4.14	0.15	0.15	10.50	14.48	-2.93
Fall	0.00	1.01	0.00	0.00	0.00	2.70	0.00	0.34	0.00	0.00	4.05	61.97	-4.25
2012													
Spring	0.00	0.72	0.72	0.00	0.36	0.72	0.00	0.18	0.00	0.00	1.97	157.25	-2.45

Trap success differed significantly between translocation site types ($t_{10} = 2.33$, $P = 0.04$), and T-K HSD indicated trap success was higher on primary sites. The sites were analyzed separately, with results from primary sites reported first. On primary sites, PMDI was positively correlated with increasing rainfall ($t_6 = 2.73$, $P = 0.03$, $R^2 = 0.55$). For every 1 mm increase in rainfall, there was a 0.02 ($CI = 0.001–0.03$, Fig. 2.10A) unit increase in PMDI. Rainfall differed significantly between years ($F_{2,5} = 43.21$, $P = 0.001$), and T-K HSD revealed that the 3 study years differed significantly from each other (2010>2012>2011). Rainfall was not significantly different between drought and "not in drought" ($t_6 = -1.6$, $P = 0.16$), though it was typically 2 times higher when "not in drought". Rainfall did not differ significantly between seasons ($F_{3,4} = 0.44$, $P = 0.74$). Drought was significantly different between years ($F_{2,5} = 7.08$, $P = 0.04$) and T-K HSD indicated that 2010 was significantly "not in drought", whereas 2011 and 2012 were of similar drought severity. There were not adequate survey sessions during "not in drought" periods to statistically examine whether rainfall differed between drought periods.

Trap success on primary sites was positively correlated with increasing rainfall, though not significant ($t_6 = 1.16$, $P = 0.29$, $R_2 = 0.18$). Removal of an outlier sample from winter 2011 resulted in a significant, though small, correlation between trap success and increasing rainfall ($t_5 = 3.56$, $P = 0.02$, $R^2 = 0.72$). For every 1 mm increase in rainfall, there was a 0.04% ($CI = 0.01–0.06$, Fig. 2.10B) increase in trap success. Though winter 2011 was preceded by 38.1 mm of rainfall, it had the highest trap success following extremely high rainfall in 2010 (summer = 295 mm, fall = 325 mm).

Trap success was positively correlated ($t_6 = 3.75$, $P = 0.01$, $R^2 = 0.70$) with decreasing drought severity (i.e., increasing PMDI). For every 1 unit increase in PMDI, there was 1.75% ($CI = 0.61–2.89$, Fig. 2.11) increase in trap success. Trap success was not significantly different

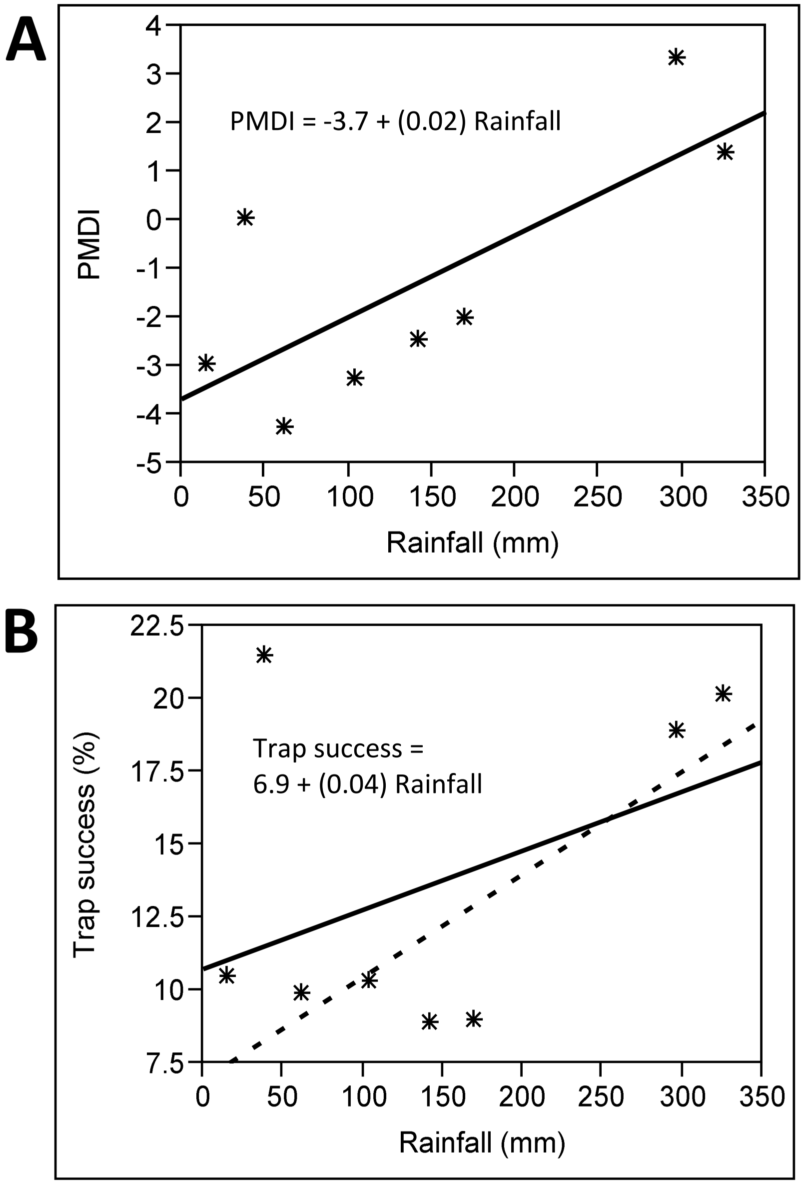

Figure 2.10.—(A) Positive linear correlation ($t_6 = 2.73$, $P = 0.03$, $R^2 = 0.55$) between drought (Palmer Modified Drought Index [PMDI]) and rainfall (mm) on Laguna Atascosa National Wildlife Refuge from June 2010 to May 2012. For every 1 mm increase in rainfall, there was a 0.02 unit (*CI* = 0.002–0.03) increase in PMDI. (B) Positive linear correlation between trap success (%) and rainfall (mm). Non-significant relationship (solid line), and significant ($t_5 = 3.56$, $P = 0.02$, $R^2 = 0.72$, dashed line) after removal of outlier from winter 2011. For every 1 mm increase in rainfall, there was a 0.04% (*CI* = 0.01–0.06) increase in trap success.

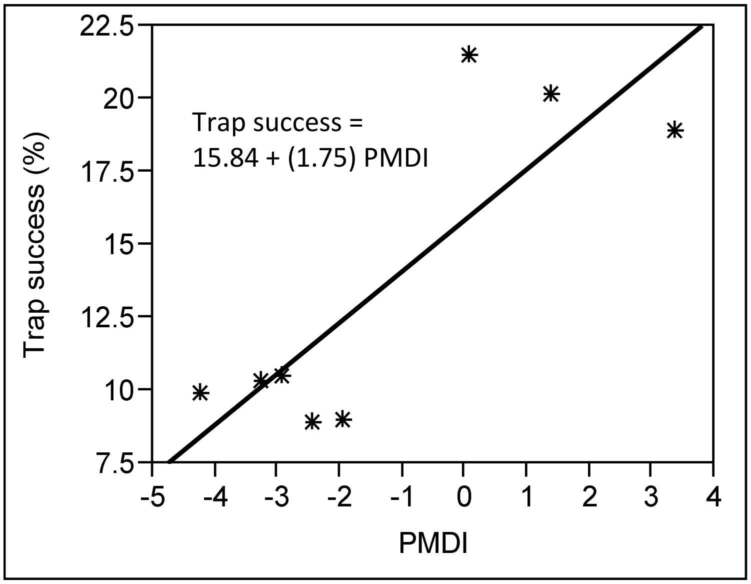

Figure 2.11.—Positive linear correlation ($t_6 = 3.75$, $P = 0.10$, $R^2 = 0.70$) between trap success (%) and increasing Palmer Modified Drought Index (PMDI) on primary sites at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, from June 2010 to May 2012. For every 1 unit increase in PMDI, there was a 1.75% (CI = 0.61–2.89) increase in trap success.

between years ($F_{2,5}$ = 3.0, P = 0.14), but I observed highest success in 2010, which then declined through 2012. Trap success did not differ significantly between seasons ($F_{3,4}$ = 0.33, P = 0.80). Caution should be applied with using estimates between years and seasons with low samples. Additional surveys may be needed to measure the effect of these variables on trap success. Trap success on primary sites was significantly higher when "not in drought" (t_6 = -14.88, P<0.0001), and when drought was not present 3 months prior to the survey (t_6 = -14.88, P<0.0001). Trap success was about 2 times higher when "not in drought".

There were only 4 survey sessions on secondary sites, thus I could not examine relationships between trap success and year, season, or drought. There was no significant relationship between trap success and rainfall (t_2 = 2.4, P = 0.14) or PMDI (t_2 = 2.76, P = 0.11). Trap success on secondary sites was highest in fall 2010 (14.2%) following 325 mm of rainfall. Severe drought and low rainfall in 2011 resulted in the lowest trap success in spring 2012 (1.9%).

Total trap success was lower overall on secondary sites compared to primary sites and was not correlated with rainfall or drought (Fig. 2.12A,B), though sample size was small with 4 surveys. Additional trapping sessions on secondary sites are needed to clarify these patterns.

Trap success differed significantly on primary sites between the 3 species ($F_{2,21}$ = 4.37, P = 0.03). The T-K HSD test revealed that trap success of cotton rat was significantly higher than Mexican spiny, but deer mouse was not different from Mexican spiny. Trap success for Mexican spiny differed between the sites (t_{10} = -3.14, P = 0.01). There was a significant negative linear relationship on primary sites between Mexican spiny trap success and rainfall (t_6 = -2.76, P = 0.03, R^2 = 0.56). For every 1 mm increase in rainfall, there was a 0.005% (CI = -0.009– -0.001, Fig. 2.13A) decrease in trap success. There was no significant relationship

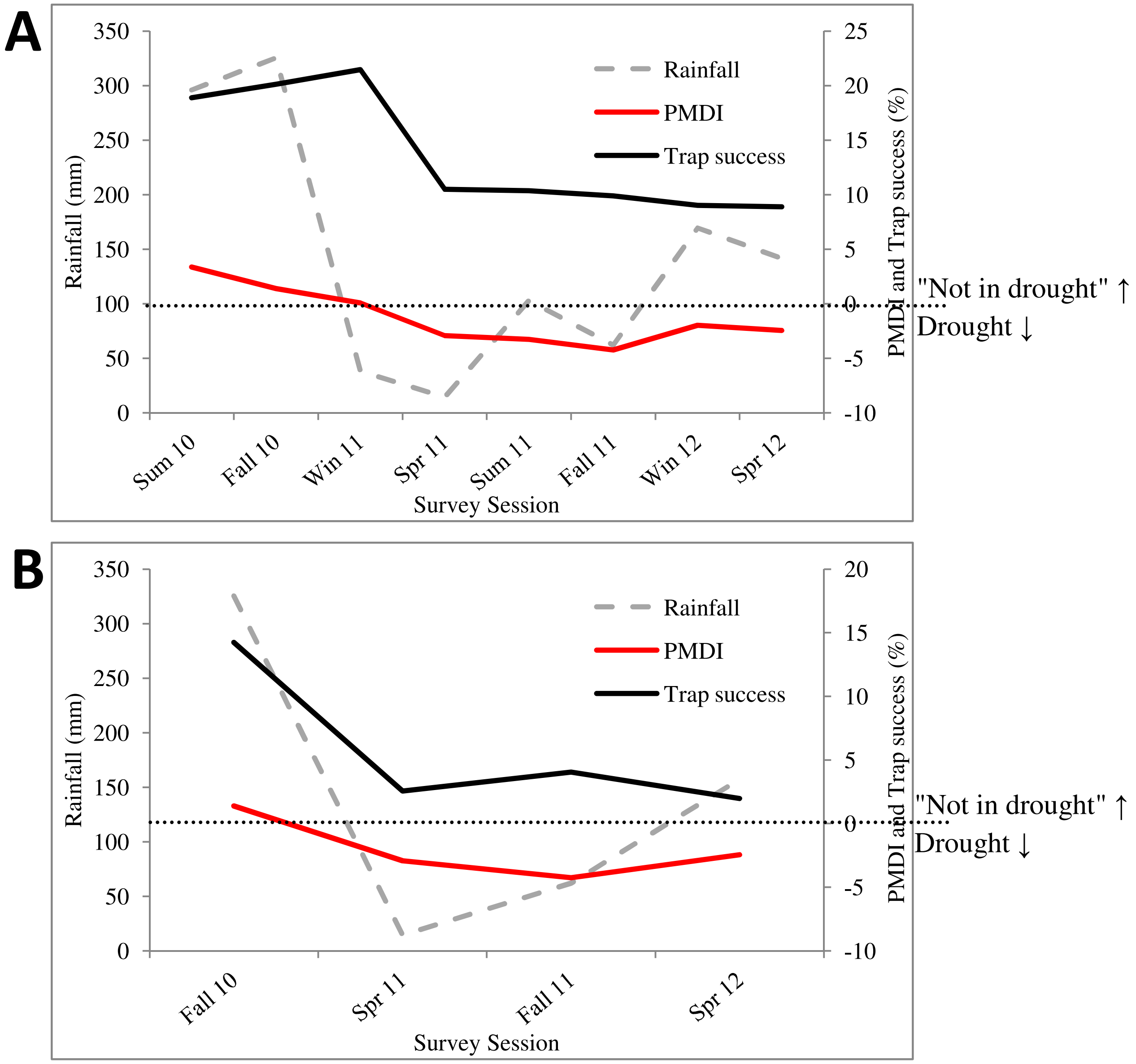

Figure 2.12.—Total rodent trap success (%; right vertical axis) on primary sites (A), and secondary sites (B) at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, from June 2010 to May 2012. Rainfall (mm; grey dashed line) is total precipitation recorded in 3 months prior to survey, and Palmer Modified Drought Index (PMDI; red line) is projected on the right vertical axis. Drought conditions occurred at any value below 0 (below black dotted line), and "not in drought" above 0. Extreme drought and extreme wet conditions occurred at ~ -4.0 and 4.0, respectively.

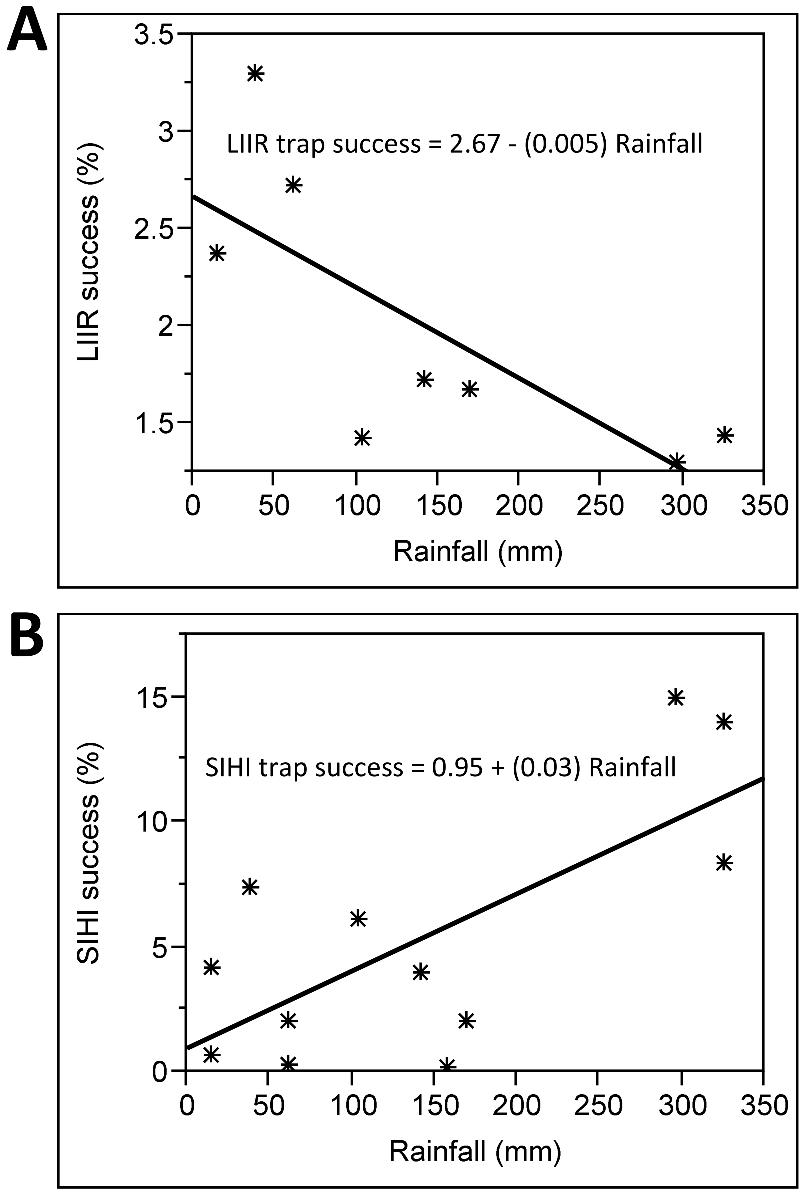

Figure 2.13.—(A) Negative linear correlation (t_6 = -2.76, P = 0.03, R^2 = 0.56) between trap success (%) and rainfall (mm) for Mexican spiny pocket mouse (LIIR) on primary sites at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, from June 2010 to May 2012. For every 1 mm increase in rainfall, there was a 0.005% (*CI* = -0.009 – -0.001) decrease in trap success. (B) Positive linear relationship (t_{10} = 3.22, P = 0.01, R^2 = 0.51) between trap success (%) of hispid cotton rat (SIHI) on primary and secondary sites and rainfall (mm). For every 1 mm increase in rainfall, there was a 0.03% (*CI* = 0.01–0.05) increase in trap success.

between Mexican spiny trap success and PMDI (t_6 = -0.79, P = 0.46), year ($F_{2,9}$ = 1.12, P = 0.37), season ($F_{3,4}$ = 0.75, P= 0.37), or drought presence (t_6 = -0.05, P = 0.96). There were insufficient trap sessions to test relationships between trap success of Mexican spiny on secondary sites with rainfall, PMDI, year, season, or presence of drought.

Trap success of deer mouse did not differ significantly between sites (t_{10} = -1.15, P = 0.28), so primary and secondary trap data were combined. Trap success did not differ significantly by rainfall (t_{10} = -0.21, P = 0.84), PMDI (t_{10} = 0.83, P = 0.43), or year ($F_{2,9}$ = 0.27, P = 0.77), but was significantly different between seasons ($F_{3,8}$ = 6.02, P = 0.02). T-K HSD identified winter trap success as significantly higher than spring and summer, but not different than fall. Deer mouse trap success was not different whether drought was present (t_{10}= -1.8, P = 0.09), but I observed about 2 times higher success when "not in drought".

Trap success of cotton rat did not differ significantly between sites, so primary and secondary sessions were combined. Trap success was positively correlated with increasing rainfall (t_{10} = 3.22, P = 0.009, R^2 = 0.51). For every 1 mm increase in rainfall, trap success of cotton rat increased 0.03% (CI = 0.01–0.05, Fig. 2.13B). There was a positive linear relationship between cotton rat trap success and increasing PMDI values (t_{10} = 6.04, P = 0.0001, R^2 = 0.78). For every 1 unit increase in PMDI, there was a 1.8% (CI = 1.14–2.48, Fig. 2.14) increase in trap success. Trap success was not significantly different between years ($F_{2,9}$ = 12.21, P = 0.003), or season ($F_{3,8}$ = 1.39, P = 0.32), but trended toward higher success in summer sessions followed by fall. Trap success was significantly higher when drought was not present (t_{10} = -5.19, P = 0.0004), and T-K HSD revealed that success was about 5 times higher when "not in drought". June 2010 to May 2012.

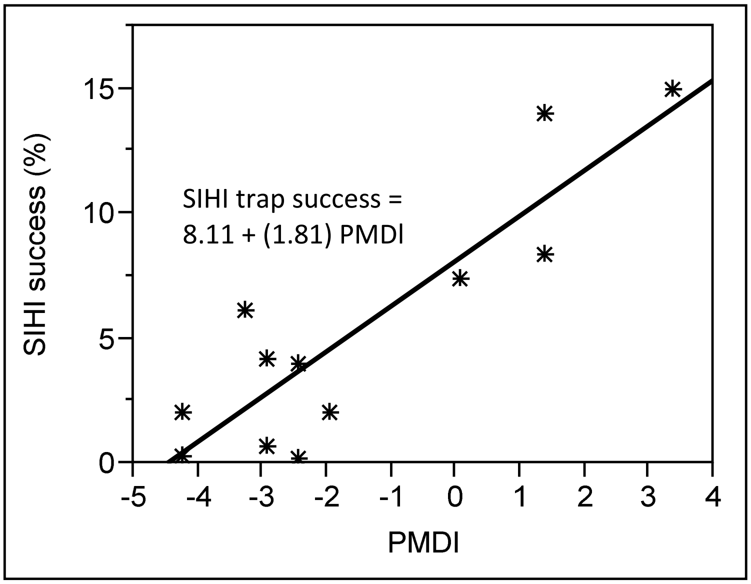

Figure 2.14.—Positive linear correlation ($t_{10} = 6.04$, $P = 0.0001$, $R^2 = 0.78$) between hispid cotton rat (SIHI) trap success and drought (Palmer Modified Drought Index [PMDI]) on primary and secondary sites at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, from June 2010 to May 2012. For every 1 point increase in PMDI, there was a 1.81% (*CI* = 1.14–2.48) increase in SIHI trap success.

Top competing models in multiple logistic regression for cotton rat, Mexican spiny, and deer mouse did not include season, or drought in the previous 3 months (Appendix I). All top models included rainfall, but only cotton rat male, cotton rat reproductively active, Mexican spiny male, deer mouse male, and deer mouse reproductively active individuals included drought (PMDI). There were insufficient captures of Mexican spiny juveniles to create models or coefficient estimates. Primary and secondary site results were reported separately.

The probability ($\hat{P}$) of capturing a male or adult cotton rat on primary sites was lower at the beginning of the study period (summer 2010: male = 48%, adult = 62%), but increased over time and remained relatively stable at ~80%. The probability of capturing a reproductively active individual was highest in summer 2010 (45%), but declined and remained low during the remainder of the study period (~5–9%, Table 2.5). For Mexican spiny, the probability of capture success for males was low in the wet period of 2010, then peaked (83%) during fall surveys in 2011 during a drought period. Few juveniles were captured during the study period, and thus could not be analyzed using logistic regression. The probability of capturing a reproductively active individual did not seem to follow seasonal trends (Table 2.5). It was highest in fall 2010 (68%) during a period of high rainfall, and lowest in spring 2011 during drought (17%), but increased to 40% in winter 2012 even though the area was still experiencing drought conditions (PMDI = -1.98).

Probability of capturing a male deer mouse was lowest in summer 2010 (48%), then increased over time and remained near 80%. For adults, probability of capture success was >90% for every survey session. Probability of capturing a reproductively active deer mouse was highest in summer 2010 (71%), then declined sharply and was between 0 and 3% from winter 2011 to spring 2012 (Table 2.5).

Table 2.5.—Probability ($\hat{P}$) and odds ratio (OR) of capturing a male, or reproductively active (Repro) hispid cotton rat, Mexican spiny pocket mouse, and deer mouse; and adult hispid cotton rat, and deer mouse by season (winter, spring, summer, and fall) and year (2010–2012) on primary and secondary sites at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, from June 2010 to May 2012. Rainfall (mm) is total precipitation from 3 months prior to survey and Palmer Modified Drought Index (PMDI) values are indicated for each survey season. Total estimates across the entire time period for each species are given below.

			Hispid cotton rat						Mexican spiny pocket mouse			
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Repro}$	OR
PRIMARY												
2010												
Summer	295.95	3.37	0.48	0.94	0.62	1.64	0.45	0.81	0.03	0.03	0.63	1.73
Fall	325.35	1.38	0.63	1.67	0.59	1.42	0.27	0.37	0.08	0.09	0.68	2.17
2011												
Winter	38.1	0.07	0.65	1.82	0.85	5.63	0.09	0.10	0.35	0.54	0.19	0.24
Spring	14.48	-2.93	0.80	4.07	0.86	6.31	0.03	0.03	0.74	2.88	0.17	0.20
Summer	102.87	-3.27	0.83	4.87	0.81	4.13	0.03	0.03	0.71	2.43	0.28	0.39
Fall	61.97	-4.25	0.86	6.13	0.83	5.02	0.02	0.02	0.83	4.78	0.22	0.29
2012												
Winter	169.44	-1.98	0.78	3.63	0.75	3.00	0.06	0.06	0.49	0.94	0.40	0.65
Spring	141.48	-2.45	0.80	4.03	0.77	3.43	0.04	0.04	0.57	1.35	0.34	0.53

Table 2.5. (continued)

			Deer mouse					
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
***PRIMARY* (cont.)**								
2010								
Summer	295.95	3.37	0.48	0.94	0.92	12.09	0.71	2.50
Fall	325.35	1.38	0.63	1.67	0.91	9.93	0.39	0.64
2011								
Winter	38.1	0.07	0.65	1.82	0.99	67.49	0.03	0.03
Spring	14.48	-2.93	0.80	4.07	0.99	79.00	0.00	0.00
Summer	102.87	-3.27	0.83	4.87	0.98	43.81	0.00	0.00
Fall	61.97	-4.25	0.86	6.13	0.98	57.55	0.00	0.00
2012								
Winter	169.44	-1.98	0.78	3.63	0.97	28.10	0.01	0.01
Spring	141.48	-2.45	0.80	4.03	0.97	33.86	0.01	0.01

			Hispid cotton rat						Mexican spiny pocket mouse			
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Repro}$	OR
SECONDARY												
2010												
Fall	325.35	1.38	0.63	1.67	0.59	1.42	0.27	0.37	0.08	0.09	0.68	2.17
2011												
Spring	14.48	-2.93	0.80	4.07	0.86	6.31	0.03	0.03	0.74	2.88	0.17	0.20

Table 2.5. (continued)

			Hispid cotton rat						Mexican spiny pocket mouse			
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Repro}$	OR
***SECONDARY* (cont.)**												
2011 (cont.)												
Fall	61.97	-4.25	0.86	6.13	0.83	5.02	0.02	0.02	0.83	4.78	0.22	0.29
Spring	157.25	-2.45	0.80	4.09	0.76	3.18	0.04	0.05	0.56	1.27	0.37	0.59

			Deer mouse					
Season	Rainfall (mm)	PMDI	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
2010								
Fall	325.35	1.38	0.63	1.67	0.91	9.93	0.39	0.64
2011								
Spring	14.48	-2.93	0.80	4.07	0.99	79.00	0.00	0.00
Fall	61.97	-4.25	0.86	6.13	0.98	57.55	0.00	0.00
2012								
Spring	157.25	-2.45	0.80	4.09	0.97	30.48	0.01	0.01

TOTALS BY SPECIES

Hispid cotton rat						Mexican spiny pocket mouse				Deer mouse					
$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Repro}$	OR	$\hat{P}_{Male}$	OR	$\hat{P}_{Adult}$	OR	$\hat{P}_{Repro}$	OR
0.58	1.36	0.87	6.73	0.13	0.14	0.28	0.38	0.15	0.18	0.58	1.36	0.99	86.43	0.05	0.05

On secondary sites, the majority of cotton rat captures were of males ($\hat{P}$ = 63–86%) and adults ($\hat{P}$ = 59–86%). Lowest probability for males (63%) and adults (59%) occurred in fall 2010 after a wet period likely increased breeding, resulting in higher captures of females and juveniles. Probability of capturing a reproductively active individual was highest in fall 2010 (37%), then declined and remained low during the drought period (2–5%, Table 2.5).

Probability of capturing a male Mexican spiny was lowest in fall 2010 (8%) then increased >10-fold to 83% in fall 2011. Though some juveniles were captured, there were not sufficient captures of each age group to estimate probability of adult success. Reproductively active individuals were more likely to be captured in fall 2010 (68%) during the wet period, declined to 17% in spring 2011 after the onset of drought conditions (Table 2.5), then increased over time (fall 2011 = 22%, spring 2012 = 37%) after small rainfall events (fall 2011 = 62 mm, spring 2012 = 157 mm) and decreasing drought conditions (PMDI: fall 2011 = -4.25, spring 2012 = -2.45).

Highest probability of capturing a female or juvenile cotton rat was during periods of highest trap success in summer and fall 2010, correlated to high rainfall (Fig. 2.15). After prolonged severe drought captures were primarily adult males that were not reproductively active. After a small increase in rainfall in winter 2012, captures of reproductively active individuals and overall trap success remained low (spring: primary - 8.9%; secondary - 1.9%).

Demographic variables of Mexican spiny on LANWR had a stronger correlation with rainfall and drought than Yturria Ranch. The wet period of 2010 corresponded to the highest probabilities of capturing females and reproductive individuals (Fig. 2.16). Probability of capturing a reproductively active Mexican spiny increased after each increase in rainfall, and following the highest rainfall, captures consisted of more females. There were insufficient

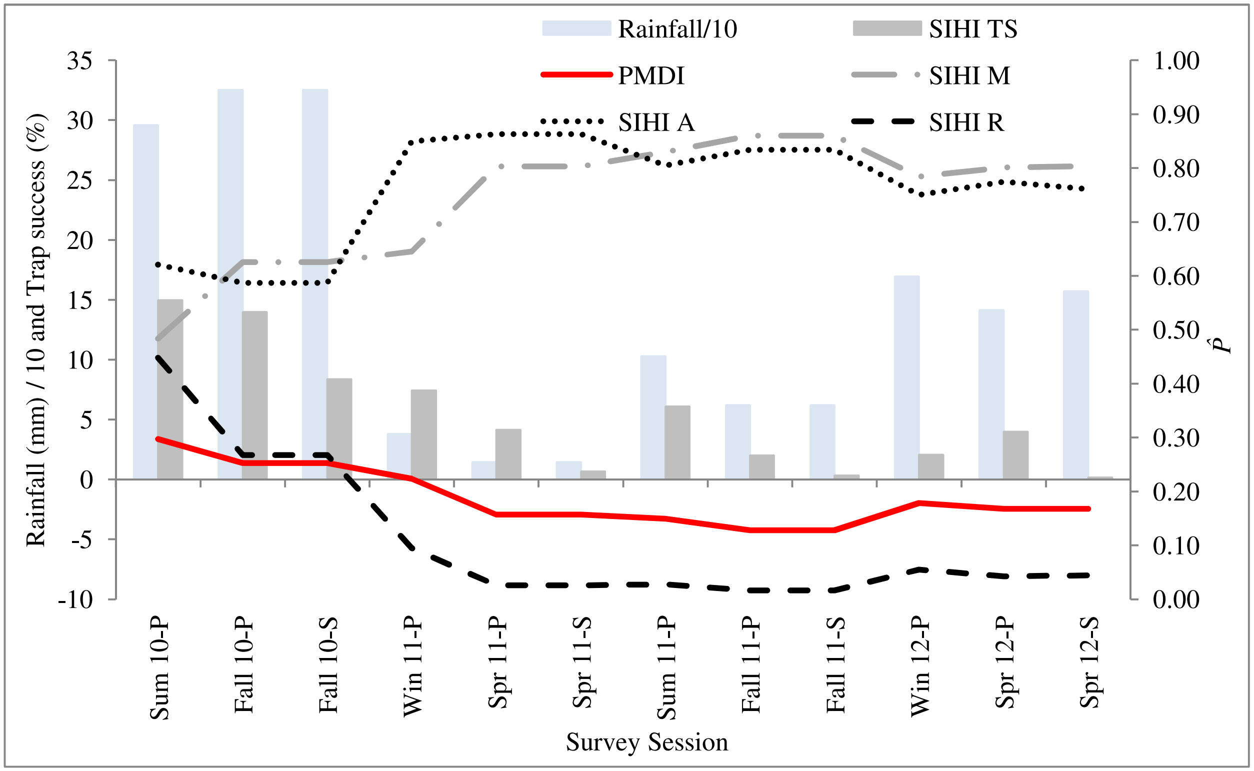

Figure 2.15.—Probability ($\hat{P}$) of capturing (dashed lines; right vertical axis) a male (M), adult (A), or reproductively active (R) hispid cotton rat (SIHI), on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, by survey session from June 2010 to May 2012. Trap success (TS; %), rainfall (mm) as 1/10 of total precipitation recorded in 3 months prior to survey, and PMDI (red line) are projected on the left vertical axis. Primary (P) and secondary (S) sites are as indicated by survey session.

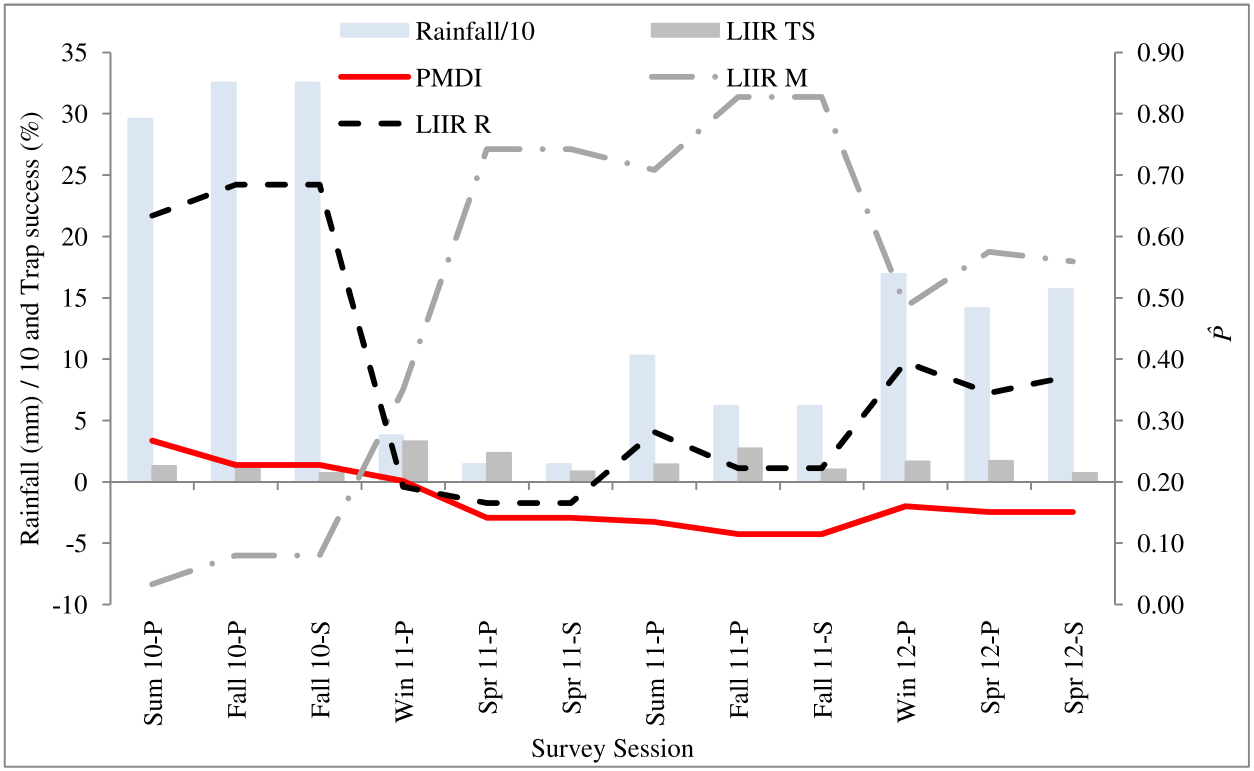

Figure 2.16.—Probability ($\hat{P}$) of capturing (dashed lines; right vertical axis) a male (M), or reproductively active (R) Mexican spiny pocket mouse (LIIR) on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, by survey session from June 2010 to May 2012. Trap success (TS; %), rainfall (mm) as 1/10 of total precipitation recorded in 3 months prior to survey, and PMDI (red line) are projected on left the vertical axis. Primary (P) and secondary (S) sites are as indicated by survey session.

captures of juveniles to estimate probabilities.

The relationship between probabilities of capturing male or reproductive deer mouse was linked to high rainfall. In 2010, I was 2.5 times more likely to capture a reproductive individual, but during drought and below average rainfall I was 850 times more likely to capture individuals that were not reproductive (Fig. 2.17).

DISCUSSION

Schwinning and Sala (2004) proposed that arid and semiarid ecosystem processes are discontinuous and should be modeled in a hierarchical pattern. The magnitude and timing of the rain pulse is important, affecting the ecological response that follows. Additionally, some threshold level may be needed to induce a higher level response (Bradley et al. 2006). For example, a summer rainfall event of ~2 mm may result in an increase in soil microbes (Cui and Caldwell 1997), whereas a higher threshold of >25 mm may be needed to elicit germination of arid plants (Beatley 1974).

Small rainfall events are common in arid and semiarid habitats, and contribute a large part to the total annual precipitation. These rainfall events vary little between years, whereas the quantity of precipitation received from large events (e.g., hurricanes, thunderstorms) is noticeably different between years. Thus, dry and wet year responses will not only vary as expected, but also produce different ecological responses based on the size, duration, and timing of the event. For example, dry periods will lead to reduced reproduction and relative abundance of certain rodent species. In contrast, wet periods should increase these attributes. A drought period following a long wet period with much higher than average precipitation may see a delay in the onset of drought condition responses, such as reduced reproduction or mortality.

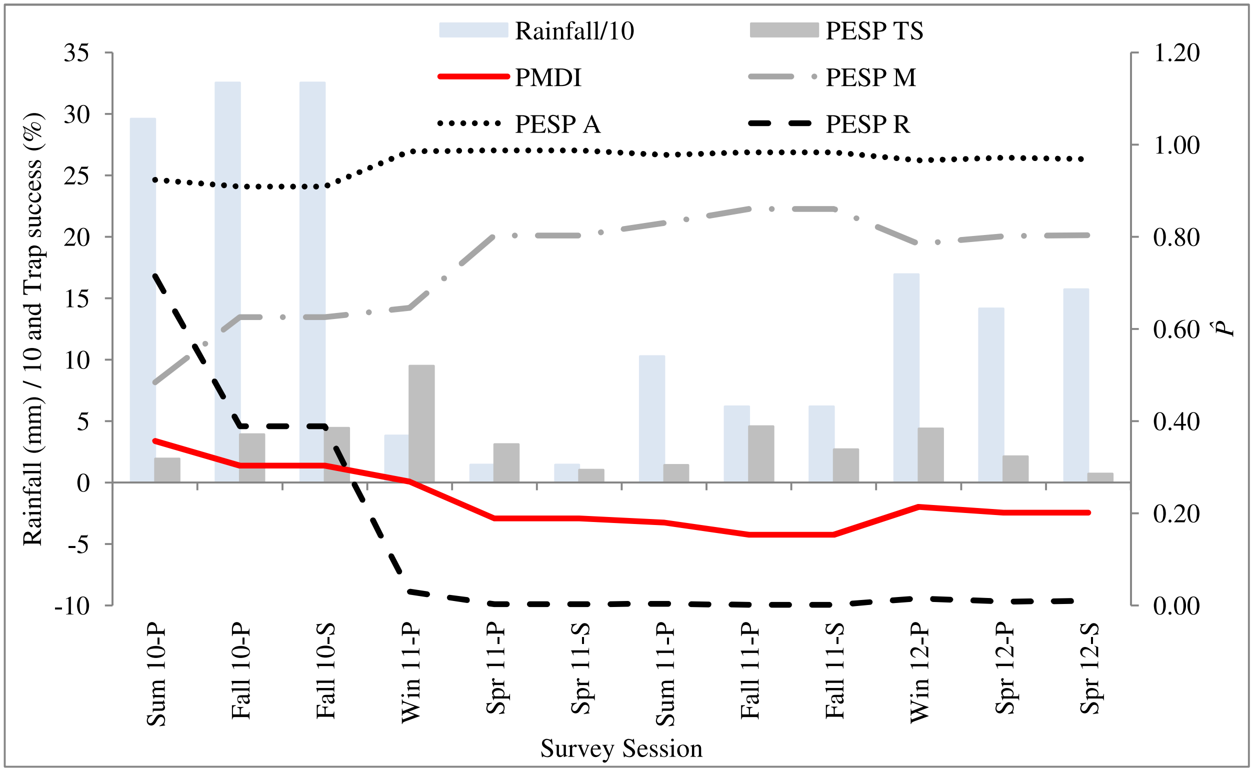

Figure 2.17.—Probability ($\hat{P}$) of capturing (dashed lines; right vertical axis) a male (M), adult (A), or reproductively active (R) deer mouse (PESP), on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, by survey session from June 2010 to May 2012. Trap success (TS; %), rainfall (mm) as 1/10 of total precipitation recorded in 3 months prior to survey, and PMDI (red line) are projected on the left vertical axis. Primary (P) and secondary (S) sites are as indicated by survey session.

Changes in relative abundance (i.e., trap success) and population demographics of rodents in response to fluctuations in rainfall and drought conditions varied between the two study sites. Relationships between rodent trap success and demographic variables on LANWR were more direct, whereas those on Yturria Ranch were highly affected by periodic pulses of localized rainfall, and timing and duration of drought conditions in the absence of rain pulses.

Yturria Ranch.— On Yturria Ranch, increases in rainfall over a long period reduced drought severity as reflected by an increase in regional PMDI. Shorter duration rainfall pulses were not reflected in regional PMDI, but elicited increased trap success of the rodent community and the onset of reproductive activity. Rainfall was significantly higher during "not in drought" periods of this study. Highest rainfall occurred in 2010, the only study year "not in drought". Rainfall amounts did not vary significantly by season, though most precipitation occurred in the summer and fall because of a hurricane and a tropical storm. Rainfall amounts were still not significantly different between seasons when moderate to wet periods occurred,.

Although affected by drought conditions, rodent abundance on Yturria Ranch can remain stable if there is a threshold level of periodic rainfall pulses. The region was in moderate drought during most of 2009, but then experienced a long wet period through 2010 related to tropical disturbances. After the lowest trap success for the study period in winter 2010 (1.6%), success steadily increased during 2010 to 19.5% in fall that year as rainfall remained abundant. Though entering an even more severe drought period in 2011 with almost no rainfall in spring, I recorded the highest trap success for the study period in fall 2011 (27.9%). This was likely a result of two factors: (1) residual deep soil moisture maintained from the wet period of 2010, and (2) localized and episodic rainfall events (i.e., thunderstorms) occurring in summer 2011 that rivaled precipitation quantities of the tropical disturbances of the previous year. This indicates that even with long-term, severe drought conditions in the region, some local habitat patches may be able to maintain stable rodent populations if precipitation does not fall below a certain threshold.

Two peaks in trap success (i.e., rodent abundance) occurred in fall 2009 (23.7%) and fall 2011 (27.9%) when trap success was higher regardless of climatic conditions (Fig. 2.6). The smaller peak in abundance in fall 2010 (19.5%) was likely a result of the wet conditions. After the "boom" in rodent abundance in 2011, populations crashed in 2012 with a rapid decline in trap success. The crash that occurred in winter 2010 (1.6%) was followed with high rainfall and rapid population recovery. This pattern did not occur in 2012 with the region remaining in long-term moderate drought with lower than average rainfall. Rodent abundance had not recovered by the last survey period in March 2013 (4.3%).

Irruptions of rodent populations can increase reproduction of predators (i.e., coyote, bobcat, ocelot, raptors), where predators then do not reach a peak in population size until 2 years after the initial rainfall event (Schwinning and Sala 2004; Tewes and Hornocker 2008). At this same 2-year point, the original pulse of increased plant biomass would be mostly exhausted if subsequent rains did not occur, thus mortality of primary consumers (i.e., rodents) would be high as a result of reduced forage and high predation. This 2-year pattern in high relative abundance of rodents on Yturria Ranch may be exhibiting this phenomenon. The long-duration wet period began in 2009 and rodent abundance peaked 2 years later in fall 2011 (Fig. 2.6).

Concurrent monitoring studies of ocelots on Yturria Ranch revealed 6 new young (kittens and subadults) between January 2011 and October 2011. Estimated birth dates for these individuals corresponded to the period of high rainfall and increasing rodent abundance. Average litter size for ocelots is reported as 1.3 kittens, every 2 years (Murray and Gardner 1997; Emmons 1988; Laack et al. 2005), and less commonly a 1-year interbirth period (Laack et al.

2005). One adult female on Yturria Ranch produced 2 sequential litters of 2 kittens in years when rodent trap success was high, whereas no ocelot reproduction has been detected since rodent populations crashed after fall 2011. Additionally, while cotton rats accounted for more than half of the captures in fall 2011, no individuals were captured on rodent surveys following that period.

Multiple studies report a lag period of 3 months for rodent populations to either decline or increase after onset of drought or high rainfall (Madsen and Shine 1999; Brown and Ernest 2002; Morrison et al. 2002; Bradley et al. 2006). Other studies have reported 2 seasons (Ernest et al. 2000) and a 1-year lag between rodent response and the original increase in plant biomass (Ostfeld and Keesing 2000). Rodent population dynamics on Yturria Ranch do not seem to conform to any one conceptual model. It took almost 2 years (e.g., 21 months) for trap success to approach previous high levels when the area was experiencing drought conditions and low rainfall (January 2009 - 24%, November 2010 - 19%). Regional drought conditions on Yturria Ranch in 2011 were more severe than those that occurred in 2009, but the former did not receive similar periodic high rainfall pulses as the latter. These rainfall pulses maintained the vegetation, and in turn the primary consumers, above some threshold which resulted in peak rodent abundance in fall 2011. In the absence of these pulses, a 3-month lag was observed between the boom in rodent abundance in fall 2011 (28%) that was followed by a decrease in PDMI and low rainfall, resulting in the sharp decline in rodent abundance observed in spring 2012 (5%).

Cotton rat captures were more abundant than harvest mouse, pocket mouse, and Mexican spiny, and similar to deer mouse. Only trap success of pocket mouse was positively correlated with rainfall, increasing with greater rainfall, though the relationship was not strong ($R^2 = 0.28$). Statistically, drought (PMDI) did not significantly affect trap success of any of the 5 species, and only harvest mouse, was affected by drought occurring in the previous 3 months (higher when not present). Trap success of each species did not differ statistically between years, but pocket mice were more abundant in 2010 and 2012, and cotton rat abundance was highest in 2011, dropping to none detected in 2012-13.

Trap success did not differ seasonally for cotton rat or deer mouse, possibly related to their ability to breed throughout the year or to avoid torpor compared to heteromyids. As expected, trap success of pocket mouse was lowest in winter, when individuals undergo torpor in response to cold ambient temperatures (Paulson 1988). Though also a heteromyid, Mexican spiny has a lower temperature tolerance before entering torpor (Dowler and Genoways 1978) thus, were captured more frequently in winter and were most abundant in summer compared to other months. The highest trap success for harvest mouse occurred in dry conditions and winter, as reported in previous studies (Packard 1968; Cameron 1977). This species is omnivorous and known to consume primarily seeds during fall and winter (Gaertner 1968). This trait would explain the tolerance by harvest mouse for dry periods, a period when herbaceous vegetation is less available.

Multiple regression models included rainfall, PMDI, and occurrence of drought in the 3-months prior to surveys, which indicated that the probability of capturing a male, adult, or reproductively active individual for all 5 species (i.e., cotton rat, Mexican spiny, pocket mouse, harvest mouse, and deer mouse) were affected by these covariates. For cotton rat, high rainfall and PMDI corresponded to higher captures of juveniles, which were followed by increasing adult captures with high trap success as the new adults dispersed into the population.

Conversely, only large changes in drought or rainfall elicited a response from Mexican spiny, which otherwise followed normal seasonal fluctuations. In general, juveniles were most likely to be captured in summer and fall, during the peak breeding periods of this species (Dowler and Genoways 1978). The only difference occurred in the wet period of 2010 when captures consisted of mostly adults. This may indicate that reproduction was so rapid, that juveniles matured and dispersed into the population before they could be detected on subsequent surveys 3 months later.

Rainfall and drought seemed to have little effect on trap success or demographics of deer mouse. Trap success remained relatively constant, with small peaks in winter each year after increased reproductive activity in the previous summer. Though the species has been recorded to breed throughout the year in the southern parts of their range, reproduction likely peaks in spring and summer when resources are more abundant. Additionally, deer mice are habitat generalists and omnivores, and this ecological plasticity may support drought tolerance (Lackey et al. 1985).

LANWR.— The relationship between relative abundance of rodents and fluctuations in rainfall and drought was more direct on LANWR than Yturria Ranch. The primary difference was that during the 2-year study period on LANWR, the area did not receive the same localized rainfall pulses as recorded on Yturria Ranch, even though they were ~30 km apart. Overall trap success was significantly higher on primary ocelot translocation release sites, compared to secondary sites, though the vegetation structure appeared similar. Increasing rainfall alleviated the regional drought severity (increased PMDI), but without the periodic rainfall pulses, local responses of primary consumers was brief. Rainfall was highest in 2010, and lowest in 2011, and whereas 2010 was a wet year and significantly "not in drought" compared to 2011 and 2012, rainfall did not differ significantly between drought periods. Rainfall also steadily declined at LANWR throughout the study period, in contrast to Yturria Ranch which recorded the highest trap success in 2011 during regional drought. This highlights the importance of localized rainfall pulses to primary production of plant biomass and small mammals.

More cotton rats were captured on primary sites than Mexican spiny or deer mouse. Increasing rainfall had a negative effect on trap success of Mexican spiny, but abundance did not differ by drought or season. These heteromyid granivores, typically prefer dry, arid habitats, thus extremely wet conditions may be unsuitable if flooding of burrows causes mortality (Williams 1985).

Trap success of cotton rat and deer mouse, did not differ significantly between release sites, so data from the primary and secondary sites were combined for analyses. Abundance of cotton rat was strongly correlated with increasing rainfall and decreasing drought conditions. Trap success was highest in 2010 (though not significant) during a wet period, and generally peaked in summer and fall of each year, as a result of increased breeding in spring and summer. Trap success of cotton rat steadily declined on both sites after rainfall decreased and drought conditions increased. Trap success did not increase again until summer 2011 after an increase in rainfall during the 3 months prior to the survey. Cotton rats on LANWR followed the 3-month lag patterns identified in previous studies (Ernest et al. 2000; Bradley et al. 2006).

Trap success of deer mouse on primary and secondary sites was not correlated with rainfall, drought, or year but was significantly higher in winter. Though not significant, a similar pattern was seen on Yturria Ranch, with small peaks in trap success in winter. Deer mice are likely more resistant to drought as a result of their ability to breed throughout the year, have an omnivorous diet, and to not regularly enter torpor under normal winter temperatures (Lackey et al. 1985).

Multiple regression models did not include covariates for season or drought in the previous 3 months, which indicated that the probability of capturing males, adults, or reproductively active individuals of these 3 species (i.e., cotton rat, Mexican spiny, and deer mouse) on LANWR was not significantly affected by these covariates. The 3 demographic variables (and thus the probability) were significantly affected by changes in rainfall, whereas, drought affected the probability of capturing males and reproductively active individuals, but not adults.

Periods of high trap success for cotton rat were correlated with high rainfall and high probabilities of capturing females and juveniles (Fig. 2.15), which may be a result of increased breeding. During drought, the fewer captures were almost entirely of non-reproductive males, indicating either a severe decrease in population size or cessation of reproduction in this species (Bradley et al. 2006).

In contrast to trap success patterns of Mexican spiny on Yturria Ranch, this species seemed more strongly correlated with drought and rainfall on LANWR (Fig. 2.16). Increasing rainfall resulted in increased probabilities of capturing reproductively active females, as the abundant resources cued breeding activity. Few juveniles were captured on this site, which combined with low trap success, might indicate decreased reproduction. However, it seems more likely that the juvenile group was present but at lower detection, possibly related to "trap shy" behavior, or that individuals matured and were captured as adults before they were detected as a juvenile.

Deer mouse on LANWR exhibited similar patterns to those on Yturria Ranch, only showing a significant increase in abundance after high precipitation amounts. Reproductively active individuals were only detected during high rainfall periods, whereas reproductively active adult males were seldom caught during drought or low rainfall periods. During periods of drought and low rainfall, I was 850 times more likely to capture non-reproductive individuals. Though some precipitation occurred on the area from fall 2011 to spring 2012, it was not enough to alleviate the severe prolonged drought conditions and captures of reproductive individuals remained low.

Yturria Ranch and LANWR.—The dynamics of rodent communities are complex and can rarely be explained by simple relationships between rainfall and drought (Brown and Ernest 2002). In the absence of extreme conditions, cotton rat had the strongest relationship with drought and rainfall fluctuations typical of the semiarid regions of South Texas. Moderate drought conditions reduced reproduction and abundance, which then increased rapidly after the onset of precipitation. After prolonged wet periods, even when the region was in drought, populations of cotton rats irrupted, and local predator communities (i.e., ocelot) may have responded to this peak in prey densities. I recorded multiple cases of ocelot reproduction on Yturria Ranch during the period of high rodent abundance. Previous studies also have shown that cotton rats seem to follow a boom and bust pattern where they apparently cannot maintain extremely high prey densities over long periods (Windberg 1998). Because cotton rats are an important prey item for ocelots in Texas, understanding the pattern and magnitude of their population dynamics in response to drought is crucial for developing management and conservation strategies for this endangered felid.

Regardless of severity of drought or rainfall quantity, rodent abundance peaked in fall throughout the entire monitoring period from July 2009 to March 2013, with the magnitude of the increase impacted by the duration and timing of rainfall or drought. Bobcats in southern latitudes can breed throughout the year but exhibit a peak during December and January (Fritts and Sealander 1978). Bobcats may be using the seasonal high prey densities in fall to store energy reserves in preparation for winter breeding. Laack et al. (2005) recorded ocelots breeding primarily in winter, spring and summer. Reproductive females must expend the greatest energy for lactation and kitten-rearing. Ocelots may breed outside of the fall season so that parturition and kitten-rearing occurs in fall, a period more beneficial for energy demanding lactation when prey are abundant and acquired with less energy expenditure. Recent observations of ocelot reproduction on Yturria Ranch have recorded the presence of several 6 mos–1 yr aged kittens in winter and spring; thereby indicating parturition and lactation of these individuals would have occurred in fall when prey densities were highest. These observations are anecdotal and further research is needed to determine if there is a relationship between increased ocelot reproduction and high prey densities in fall.

Other species such as deer mouse and harvest mouse were more resistant to drought, and although prey items for ocelots, their small size and energetic value are much less than the larger cotton rat. Woodrats and eastern cottontail are even larger prey items, thus similar research should be conducted on these species to determine their population dynamics during drought and changing rainfall. Windberg (1998) recorded a decline in woodrats after high rainfall when other rodent species increased, and postulated it could be a result of mortality induced from flooded burrows: Raun (1966) has expressed a similar view. Long-term remote camera surveys on Yturria Ranch, have recorded ocelots carrying cotton rats, woodrats, and cottontail as prey. During the period of cotton rat decline with no recorded trap success, multiple camera-trap photographs documented ocelots carrying woodrats exclusively. Thus, future research focused on woodrat is needed, in addition to the continued long-term monitoring of rodent populations on Yturria Ranch and LANWR.

LITERATURE CITED

BEASOM, S. L., AND R. A. MOORE. 1977. Bobcat food habit response to a change in prey abundance. Southwestern Naturalist 21:451–457.

BEATLEY, J. C. 1974. Phenological events and their environmental triggers in Mojave-desert ecosystems. Ecology 55:856–863.

BLANKENSHIP, T. L. 2000. Ecological response of bobcats to fluctuating prey populations on the Welder Wildlife Foundation Refuge. Ph.D. dissertation. Texas A&M University, College Station; and Texas A&M University-Kingsville, Kingsville.

BRADLEY, R. D. ET AL. 2006. Rapid recovery of rodent populations following severe drought. Southwestern Naturalist 51:87–93.

BROWN, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59:1–20.

BROWN, J. H. , AND E. J. HESKE. 1990. Temporal changes in a Chihuahuan Desert rodent community. Oikos 59:290–302.

BROWN, J. H., AND Z. ZENG. 1989. Comparative population ecology of eleven species of rodents in the Chihuahuan Desert. Ecology 70:1507–1525.

BROWN, J. H., AND S. K. M. ERNEST. 2002. Rain and rodents: complex dynamics of desert consumers. BioScience 52:979–987.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd ed. Springer, New York.

CAMERON, G. N. 1977. Experimental species removal: demographic responses by *Sigmodon hispidus* and *Reithrodontomys fulvescens*. Journal of Mammalogy 58:488–506.

CAMERON, G. N., AND S. R. SPENCER. 1981. *Sigmodon hispidus*. Mammalian Species 158:1–9.

CHEESEMAN, C. L., AND M. J. DELANEY. 1979. The population dynamics of small rodents in a tropical African grassland. Journal of Zoology (London) 188:451–475.

CUI, M., AND M. M. CALDWELL. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. Plant and Soil 191:291–299.

DOWLER, R. C., AND H. H. GENOWYS. 1978. *Liomys irroratus.* Mammalian Species 82:1–6.

EMMONS, L. H. 1987. Comparative feeding ecology of felids in a neotropical rainforest. Behavioral Ecology and Sociobiology 20:271–283.

EMMONS, L. H. 1988. A field study of ocelots (*Felis pardalis*) in Peru. Revue d'Ecologie (la Terre et la Vie) 43:133–157.

ERNEST, S. K. M., J. H. BROWN, AND R. R. PARMENTER. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.

FRITTS, S. H., AND J. A. SEALANDER. 1978. Biology and population characteristics of bobcats (*Lynx rufus*) in Arkansas. Journal of Mammalogy 59:347–353.

GAERTNER, R. A. 1968. Seasonal variations in the energy budgets of the harvest mouse, *Reithrodontomys fulvescens*, and the cotton rat, *Sigmodon hispidus*. Ph.D. Dissertation, University of Arkansas, Fayetteville, Arkansas, United States.

HEDDINGHAUS, T. R., AND P. SABOL. 1991. A review of the Palmer Drought Severity Index and where do we go from here? Seventh Conference on Applied Climatology. pp. 242–246.

HOLMGREN, M. ET AL. 2006. Extreme climate events shape arid and semiarid ecosystems. Frontiers in Ecological Environments 4:87–95.

JAHRSDOERFER, S. E., AND D. M. LESLIE, JR. 1988. Tamaulipan brushland of the Lower Rio Grande Valley of South Texas: description, human impacts, and management options. United States Fish and Wildlife Service, Biological Report 88(36):1–63.

JAKSIC, F. M., AND M. LIMA. 2003. Myths and facts in ratadas: bamboo blooms, rainfall peaks and rodent outbreaks in South America. Australian Ecology 28:237–251..

LAACK, L. L., M. E. TEWES, A. M. HAINES, AND J. H. RAPPOLE. 2005. Reproductive life history of ocelots *Leopardus pardalis* in southern Texas. Acta Theriologica 50:505–514.

LACKEY, J. A., D. G. HUCKABY, AND B. G. ORMISTON. 1985. *Peromyscus leucopus*. Mammalian Species 247:1–10.

LIMA, M., K. E. KEYMER, AND F. M. JAKSIC. 1999. ENSO-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. American Naturalist 153:476–491.

MADSEN, T., AND R. SHINE. 1999. Rainfall and rats: climatically-driven dynamics of a tropical rodent population. Australian Journal of Ecology 24:80–89.

MORRISON, M. L., A. J. KUENZI, C. F. BROWN, AND D. E. SWANN. 2002. Habitat use and abundance of rodents in southeastern Arizona. Southwestern Naturalist 47:519–526.

MURRARY J. L., AND G. L. GARDNER. 1997. *Leopardus pardalis*. Mammalian Species 548:1–10.

NORWINE, J., AND R. BINGHAM. 1985. Frequency and severity of droughts in south Texas: 1900–1983. Pp. 1–19 in Proceedings of a workshop on livestock and wildlife management during drought. (R. D. Brown, ed.) Caesar Kleberg Wildlife Research Institute, Kingsville, Texas, United States.

ODUM, E. P. 1955. An eleven–year history of a *Sigmodon* population. Journal of Mammalogy 36:368–378.

OSTFELD, R. S., AND F. KEESING. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution 15:232–237.

PACKARD, R. L. 1968. An ecological study of the fulvous harvest mouse in eastern Texas. American Midland Naturalist 79:68–88.

PAULSON, D. D. 1988. *Chaetodipus hispidus*. Mammalian Species 320:1–4.

PREDAVEC, M. 1994. Population dynamics and environmental changes during natural irruptions of Australian desert rodents. Australian Wildlife Research 21:569–582.

RAUN, G. G. 1966. A population of woodrats (*Neotoma micropus*) in southern Texas. Bulletin of Texas Memorial Museum 11:1–62.

SCHWINNING, S., AND O. E. SALA. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220.

SHEPPE, W. 1972. The annual cycle of small mammal populations on a Zambian floodplain. Journal of Mammalogy 53:445–460.

SHINDLE, D. B., AND M. E. TEWES. 1998. Woody species composition of habitats used by ocelots (*Leopardus pardalis*) in the Tamaulipan Biotic Province. Southwestern Naturalist 43:273–279

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.

SINGLETON, G. R., S. R. BELMAIN, P. R. BROWN, AND B. HARDY (EDS.). 2010. Rodent outbreaks: ecology and impacts. International Rice Research Institute, Makati City, Philippines.

STRECKER, J. A. 1929. Notes on the Texas cotton and Attwater wood rats in Texas. Journal of Mammalogy 10:216–220.

TEWES, M. E., J. M. MOCK, AND J. H. YOUNG. 2002. Bobcat predation on quail, birds, and mesomammals. Pp. 65–70 in Quail V: Proceedings of the fifth annual national quail symposium. (S. J. DeMaso, W. P. Kuvlesky, Jr., F. Hernández, and M. E. Berger, eds.) Texas Parks and Wildlife Department, Austin, Texas, United States.

TEWES, M. E., AND M. G. HORNOCKER. 2008. Effects of drought on bobcats and ocelots. Pp. 123–138 in Wildlife Science: linking ecological theory and management applications. (T. E. Fulbright and D. G. Hewitt, eds.) CRC Press, Boca Raton, Florida, United States.

U.S. FISH AND WILDLIFE SERVICE. 2010. Draft ocelot (*Leopardus pardalis*) recovery plan, first revision. U.S. Fish and Wildlife Service, Southwest Region, Albuquerque, New Mexico.

WHITFORD, W. G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. Journal of Mammalogy 57:351–369.

WINDBERG, L. A. 1998. Population trends and habitat associations of rodents in southern Texas. American Midland Naturalist 140:153–160.

WILLIAMS, D.F. 1985. A review of the population status of the Tipton kangaroo rat, *Dipodomys nitratoides nitratoides*. U.S. Fish and Wildlife Service, Sacramento, Endangered Species Office, California.

APPENDIX I

Table AI.—Multiple logistic regression top competing models, number of parameters (*K*), $\mathrm{AIC_C}$ score, $\Delta\mathrm{AIC_C}$, model weight (*ω*), and log-likelihood (*LL*). Model averaged coefficients (*β*) from models ($\Delta\mathrm{AIC_C} \leq 2$), and standard errors (*SE*) for hispid cotton rat, Mexican spiny pocket mouse, and deer mouse males, adults, and reproductively active captures on Yturria Ranch, Willacy County, Texas, from January 2009 to March 2013. Covariates are rainfall accumulated in the previous 3 months (Rain), drought (Palmer Modified Drought Index [PMDI]), drought in the previous 3 months (PMDI3), and season (Season).

Model	*K*	$\mathrm{AIC_C}$	$\Delta\mathrm{AIC_C}$	*ω*	*LL*
Hispid cotton rat					
MALE					
Rain + PMDI3 + Season	6	832.68	0.00	0.20	-410.27
PMDI	2	832.77	0.09	0.19	-414.38
Rain	2	833.19	0.50	0.16	-414.58
PMDI3	2	833.34	0.66	0.14	-414.66
PMDI3 + Season	5	833.60	0.92	0.13	-411.75
PMDI + Season	5	833.98	1.30	0.11	-411.94
PMDI + PMDI3	3	834.62	1.94	0.08	-414.29

Covariate	*β*	*SE*
Intercept	0.534	0.997
Rain	-0.003	0.004
PMDI	0.041	0.040
PMDI3	-0.767	1.022
Season (Spring)	0.184	0.374
Season (Summer)	0.152	0.443
Season (Winter)	-1.125	1.111

Table AI (continued)

Model	*K*	AIC_C	ΔAIC_C	*ω*	*LL*
Hispid cotton rat (continued)					
ADULT					
Rain + PMDI + PMDI3 + Season	7	598.48	0.0	0.53	-292.14
Rain + PMDI + Season	6	599.87	1.4	0.26	-293.86
Rain + PMDI3 + Season	6	600.37	1.9	0.21	-294.12

Covariate	*β*	*SE*
Intercept	-2.769	1.539
Rain	0.011	0.004
PMDI	-0.380	0.175
PMDI3	3.047	1.520
Season (Spring)	1.421	0.575
Season (Summer)	-0.657	0.747
Season (Winter)	4.118	1.365

Model	*K*	AIC_C	ΔAIC_C	*ω*	*LL*
REPRODUCTIVE ACTIVE					
Rain + PMDI3 + Season	6	660.95	0.00	0.62	-324.40
Rain + PMDI + PMDI3 + Season	7	661.92	0.97	0.38	-323.87

Covariate	*β*	*SE*
Intercept	-4.561	1.330
Rain	0.010	0.004
PMDI	0.205	0.195
PMDI3	2.798	1.241
Season (Spring)	1.977	0.521
Season (Summer)	0.287	0.535
Season (Winter)	1.446	1.175

Table AI. (continued)

Model	*K*	AIC_C	$\Delta\text{AIC}_\text{C}$	*ω*	*LL*
Mexican spiny pocket mouse					
MALE					
PMDI3	2	226.24	0.00	0.36	-111.09
Rain	2	226.80	0.55	0.27	-111.36
PMDI	2	227.57	1.33	0.19	-111.75
Rain + PMDI3	3	227.65	1.41	0.18	-110.76

Covariate	*β*	*SE*
Intercept	-0.587	0.544
Rain	-0.002	0.001
PMDI	-0.131	0.052
PMDI3	0.792	0.433

Model	*K*	AIC_C	$\Delta\text{AIC}_\text{C}$	*ω*	*LL*
ADULT					
Rain + PMDI + Season	6	75.88	0.00	0.57	-31.69
Rain + PMDI + PMDI3 + Season	7	76.46	0.50	0.43	-30.89

Covariate	*β*	*SE*
Intercept	-2.272	3.539
Rain	0.029	0.013
PMDI	-1.983	1.233
PMDI3	-6.423	6.411
Season (Spring)	4.194	2.105
Season (Summer)	-1.845	1.224
Season (Winter)	6.960	3.757

Model	*K*	AIC_C	$\Delta\text{AIC}_\text{C}$	*ω*	*LL*
REPRODUCTIVE ACTIVE					
Season	4	209.99	0.00	0.42	-100.88
PMDI3 + Season	5	211.33	1.33	0.22	-100.48
PMDI + Season	5	211.44	1.45	0.20	-100.54
Rain + Season	5	211.98	1.99	0.16	-100.81

Table AI. (continued)

Mexican spiny pocket mouse (continued)

Covariate	*β*	*SE*
Intercept	-1.057	0.314
Rain	-0.005	0.001
PMDI	-0.047	0.057
PMDI3	0.310	0.035
Season (Spring)	2.51	0.497
Season (Summer)	1.38	0.406
Season (Winter)	-0.466	0.832

Model	*K*	AIC_C	ΔAIC_C	*ω*	*LL*
Deer mouse					
MALE					
Rain + PMDI3	3	324.45	0.00	0.24	-209.18
Rain	2	424.65	0.20	0.21	-210.30
Rain + PMDI	3	424.89	0.45	0.19	-209.41
Season	4	425.56	1.12	0.14	-208.71
PMDI3	2	425.61	1.16	0.13	-210.78
Rain + PMDI + PMDI3	4	426.43	1.98	0.09	-209.15

Covariate	*β*	*SE*
Intercept	-0.106	0.304
Rain	0.002	0.001
PMDI	-0.059	0.073
PMDI3	0.315	0.284
Season (Spring)	0.128	0.342
Season (Summer)	-0.165	0.397
Season (Winter)	-0.506	0.277

Table AI. (continued)

Model	*K*	AIC$_C$	ΔAIC$_C$	*ω*	*LL*
Deer mouse (continued)					
ADULT					
Rain + PMDI + PMDI3	4	99.56	0.00	0.58	-45.71
PMDI + PMDI3	3	100.19	0.63	0.42	-47.06

Covariate	*β*	*SE*
Intercept	3.613	0.596
Rain	0.005	0.003
PMDI	-0.765	0.242
PMDI3	-2.449	0.984

Model	*K*	AIC$_C$	ΔAIC$_C$	*ω*	*LL*
REPRODUCTIVE ACTIVE					
PMDI + PMDI3 + Season	6	313.81	0.00	0.39	-150.77
Rain + PMDI3 + Season	6	314.25	0.44	0.32	-150.99
Rain + PMDI + PMDI3 + Season	7	314.43	0.61	0.29	-150.03

Covariate	*β*	*SE*
Intercept	-1.228	0.737
Rain	0.004	0.002
PMDI	0.307	0.154
PMDI3	1.612	0.651
Season (Spring)	0.772	0.572
Season(Summer)	1.715	0.544
Season (Winter)	-1.627	0.523

Table AII.—Multiple logistic regression top competing models, number of parameters (*K*), AIC_C score, ΔAIC_C, model weight (ω), and log-likelihood (*LL*). Model averaged coefficients (β) from models ($\Delta AIC_C \leq 2$), and standard errors (*SE*) for hispid cotton rat, Mexican spiny pocket mouse, and deer mouse males, adults, and reproductively active captures on primary and secondary sites at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, from June 2010 to May 2012. Covariates are rainfall accumulated in the previous 3 months (Rain), drought (Palmer Modified Drought Index [PMDI]), drought in the previous 3 months (PMDI3), and season (Season).

Model	*K*	AIC_C	ΔAIC_C	ω	*LL*
Hispid cotton rat					
MALE					
PMDI	2	183.77	0.00	0.46	-89.84
Rain + PMDI	3	184.80	1.02	0.28	-89.31
Rain	2	184.96	1.18	0.26	-90.43

Covariates	β	*SE*
Intercept	0.581	0.278
Rain	0.001	0.002
PMDI	-0.276	0.245

Model	*K*	AIC_C	ΔAIC_C	ω	*LL*
ADULT					
Rain	2	389.09	0.00	0.73	-192.53

Covariates	β	*SE*
Intercept	1.911	0.432
Rain	-0.005	0.001

Table AII. (continued)

Model	*K*	AIC$_C$	ΔAIC$_C$	*ω*	*LL*
Hispid cotton rat (continued)					
REPRODUCTIVE ACTIVE					
Rain + PMDI	3	354.79	0.00	0.99	-174.35
Rain	2	365.21	10.42	0.01	-180.59

Covariates	*β*	*SE*
Rain	0.002	0.002
PMDI	0.436	0.124

Model	*K*	AIC$_C$	ΔAIC$_C$	*ω*	*LL*
Mexican spiny pocket mouse					
MALE					
PMDI	2	53.60	0.00	0.54	-24.65
Rain	2	53.95	0.36	0.46	-24.83

Covariates	*β*	*SE*
Intercept	-0.430	0.483
Rain	-0.004	0.003
PMDI	-0.527	0.343

Model	*K*	AIC$_C$	ΔAIC$_C$	*ω*	*LL*
REPRODUCTIVE ACTIVE					
Rain	2	55.35	0.00	1.00	-25.53

Covariates	*β*	*SE*
Intercept	-1.731	0.632
Rain	0.008	0.003

Table AII. (continued)

Model	K	AIC_C	ΔAIC_C	ω	LL
Deer mouse					
MALE					
PMDI	2	183.77	0.00	0.46	-89.84
Rain + PMDI	3	184.80	1.02	0.28	-89.31
Rain	2	184.96	1.18	0.26	-90.43

Covariates	β	SE
Intercept	0.581	0.278
Rain	0.001	0.002
PMDI	-0.276	0.245

Model	K	AIC_C	ΔAIC_C	ω	LL
ADULT					
Rain	2	55.04	0.00	0.61	-25.48

Covariates	β	SE
Intercept	4.467	1.144
Rain	-0.007	0.004

Model	K	AIC_C	ΔAIC_C	ω	LL
REPRODUCTIVE ACTIVE					
Rain + PMDI	3	113.15	0.00	1.00	-53.48

Covariates	β	SE
Intercept	-3.818	0.811
Rain	0.007	0.003
PMDI	0.791	0.304

CHAPTER III

FINE-SCALE MOVEMENT PATTERNS OF BOBCATS (*LYNX RUFUS*) USING FRACTAL ANALYSIS

Bobcats (*Lynx rufus*) are an important predator in the ecosystems of Texas, likely acting in top-down processes aiding in the regulation of animal populations (Navarrete and Menge 1996, Sinclair 2003). By altering habitat use because of overharvest or disturbance (e.g., brush management, urbanization), bobcats may affect the diversity of animals and plants in an area. Changing land uses in Texas have increased urbanization and modified habitats through application of brush management. Brush manipulation is a common management practice used to optimize livestock production and produce income from hunting of game species (Whitson et al. 1977), such as white-tailed deer (*Odocoileus virginianus*) and northern bobwhite (*Colinus virginianus*). Understanding predator responses within these shifting environments is important for wildlife biologists and ranch managers seeking to manage these lands.

Additionally, bobcats are a common species often used as a model for the endangered ocelot (*Leopardu*s *pardalis*), which are less abundant and difficult to monitor. Bobcats have adapted extremely well to the presence of humans and can be found in areas of extensive urbanization. This felid has been recorded in every county in Texas, showing an affinity for diverse habitats (Schmidly 2004).

Bobcats maintain territories and home ranges based on prior residence and occupancy maintained through scent marking (Anderson 1988, Bailey 1974, Lovallo and Anderson 1995). Home range size varies by geographic region and is usually smaller in southern latitudes (Anderson and Lovallo 2003). Home range sizes for males in southern environments may be as

---

Chapter 3 of this dissertation follows the style of the *Journal of Wildlife Management.*

small as 3.5 km^2 (Bradley and Fagre 1988) but usually average around 15 km^2, whereas ranges in northern regions may be as large as 100-300 km^2 (Hansen 2007). This spatial disparity may be related to higher prey densities in southern regions and the need to greater travel distances to find prey in the northern ranges.

Home range size is influenced by many factors including food availability, body mass, and population density (Benson et al. 2006). Blankenship (2000) found bobcats increased their home ranges by 100% when prey populations were reduced. Male home ranges often are considerably larger than females and can increase during the breeding season (Anderson 1987, Chamberlain et al. 2003, Hansen 2007). It was previously believed that male bobcats exhibit high levels of home range overlap, and more territoriality and exclusion existed between female bobcats (Marshall and Jenkins 1966, Bailey 1974, Lembeck and Gould 1979, Hamilton 1982). However, recent studies have shown extensive intrasexual home range overlap, while maintaining separate core areas (Chamberlain and Leopold 2001, Nielson and Woolf 2001).

In general, male home ranges overlap or encompass one to a few female home ranges. Adult female home ranges tend to overlap with their female offspring for a short duration after weaning, but not with unrelated females (Bailey 1974, Lawhead 1984, Hansen 2007). Young males disperse longer distances from their mothers compared to young females and seldom overlap with their mothers when they claim a resident home range (Janečka et al. 2007). Additionally, occupation of a large home range by a male may result in greater fitness (Conner et al. 1999).

Habitat use is commonly measured at 2 scales: home range and core area, and without regard to movement patterns of the animal. Traditionally, movement of wild felids has been measured by calculating movement rate; usually the distance between consecutive locations divided by time (Beier et al. 1995, Lovallo and Anderson 1996, Chamberlain et al. 1999, Chamberlain et al. 2003). Recent advances in movement analyses may provide an increased understanding of habitat use and movement of wild felids.

Animal movements through home ranges may be examined using analyses such as correlated random walk (Renshaw and Henderson 1981), Brownian bridge (Horne et al. 2007), or fractal dimensions (Nams and Bourgeois 2004). These methods are more robust when animal location data may not be independent, which often occurs with data collected by Global Positioning System (GPS) collars using short duration location schedules. Fractal analysis is a measure of movement path tortuosity and is typically evaluated using fractal dimensions (D) (Mandlebrot 1967, Nams 1996). When movement paths are straight, D is closer to 1; when they are highly tortuous (i.e., twisted) and therefore cover a plane at a high level, D can reach up to 2 in value. In some cases D can be >2, which occurs when the movement path is so tortuous that it crosses over itself many times and creates an additional dimension (Mandlebrot 1984).

Fractals have been used to analyze movement patterns of white-tailed deer (Webb et al. 2009), songbirds (Doerr and Doerr 2004), sharks (Barnett et al. 2010), small mammals (Nams 2005), mesocarnivores (Nams and Bourgeois 2004), and wolves (Bascompte and Vilá 1997). Straight-line movements may indicate a bobcat is traveling across its home range with a specific purpose, such as scent marking, searching for mates, or visiting a known resource patch or water source. More tortuous movements may indicate search patterns for prey or denning periods for females. Additionally, fractals can aid in determining the scale at which animals perceive habitat or patches and resource assessments (Nams 2006; Nams et al. 2006). Mechanically-manipulated brush strips result in artificial patch habitats on the study site, which may cause bobcats to use them differently than the remainder of their home range. Tortuosity is scale-dependent, where D

may appear different when viewed at a smaller scale. Thus, caution should be used when estimating an overall value of *D*, ensuring that it is estimated over the same range of scales for each animal to reduce this bias.

The first objective of this study was to determine how fine-scale movement patterns of bobcats, measured through fractal analyses varied in response to brush manipulation (measured as proportion of brush strips in a home range) and differences in demographic (e.g., sex) or ecological factors (e.g., season). Second, I determined if home range size was influenced by tortuosity. As home ranges become larger, a pattern often observed for male bobcats (Kitchings and Story 1984), the value of *D* may decrease, as the bobcat must make longer, straight-line movements to cross its home range. Third, I determined if home range or core area size varied between sexes. My last objective was to test if use of brush strips varied by time period (e.g., diurnal, nocturnal, and crepuscular).

It has been well documented that male bobcats have larger home ranges than females (Hansen 2007); therefore I hypothesized that the larger size of male home ranges would have more straight-line movement paths and lower *D* values. Bobcats spend more time searching small patches for resources (Smith 1974), therefore movements within home ranges with a larger proportion of brush strips (i.e., patchy habitat) should exhibit increased tortuosity. Thus, I hypothesized that bobcat home ranges with a greater proportion of brush strips would have increased values of *D.* Additionally, I predicted that tortuosity would vary with season. Males move over larger areas in the breeding season to encounter potential mates, and therefore *D* should be lower for males during that period. Conversely, kitten-rearing season should lead to increased *D* for females when they remain primarily at den sites, making only short and more tortuous forays for hunting. Finally, I predicted that bobcats primarily would use brush strips as travel or hunting paths when they are most active during nocturnal and crepuscular periods (Anderson 1990; McCord and Cordoza 1982).

STUDY AREA

This study occurred on the Santa Gertrudis Division of King Ranch, about 21 km west of Kingsville, Texas, USA (Fig. 3.1). The Division is approximately 800 km^2 located in Kleberg and Jim Wells counties. The research was focused on 3 pastures: Patricio, East Conchas, and West Conchas. The Patricio pasture (22.6 km^2) and East Conchas pasture (15.9 km^2) had received mechanical brush management that produced north-south linear brush strips measuring 91-137 m in width, alternating with unaltered vegetation (e.g., grassland) measuring 137-183 m in width. Brush treatment occurred on the Patricio pasture in 1997 and included 2-way chaining which was then stacked, rootplowed, and raked. Two-way chaining consisted of bulldozers dragging a large anchor chain twice across the treatment area to uproot vegetation. Rootplowing is an effective method to remove most vegetation, except prickly pear cactus (*Opuntia engelmannii*), which can root from severed parts. Thus, it was followed by stacking and raking to aid in removal of small brush and prickly pear cactus.

In 1999, 2001, 2003, and 2010, grass strips were chemically treated to inhibit mesquite regrowth. A 3.2 km^2 trap (e.g., small fenced area for enclosing cattle) at the eastern portion of the pasture did not receive any brush treatment. The East Conchas pasture received similar treatment, but had human-created brush mottes of the same size left intact at various intervals between brush strips. Strips in the eastern portion of the pasture were oriented north-south and created in 2006-2007 with mottes 91-183 m apart. Strips in the western portion were oriented northwest-southeast and were created in 2009 with mottes about 45 m apart. Portions of the

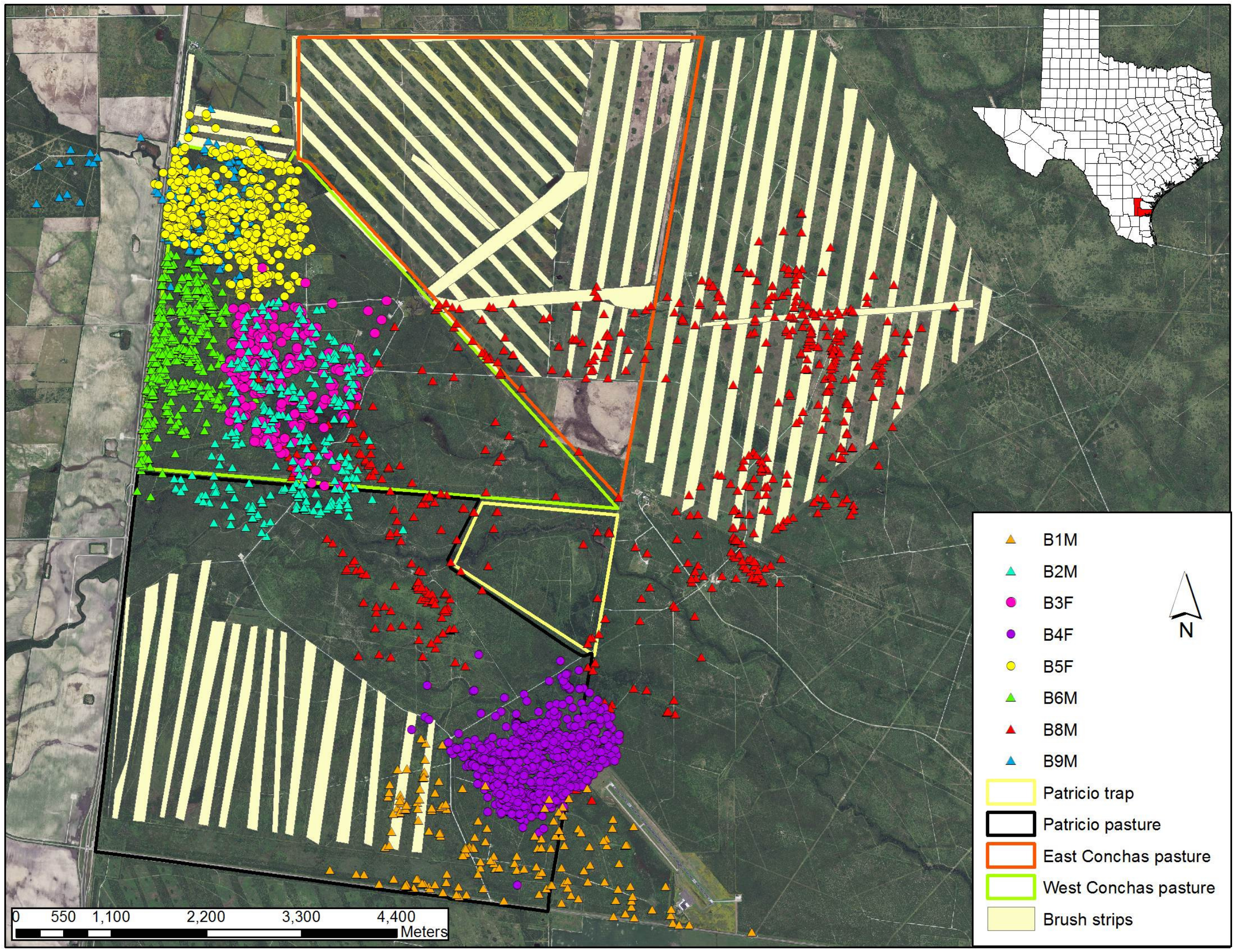

Figure 3.1. Aerial view of the Patricio trap (untreated), Patricio pasture (treated), East Conchas pasture (treated), and the West Conchas pasture (untreated) located in the Santa Gertrudis Division of King Ranch, Kleberg and Jim Wells counties, Texas. GPS locations of 8 collared bobcats (male = triangle; female = circle) from June 2011 to May 2012 are indicated in relation to brush strips (light yellow).

pasture received aerial chemical treatment to prevent brush regrowth; the eastern area was treated in 2011 and the western area was treated in 2012. The control was the untreated West Conchas pasture (12.9 km^2) which had not received any mechanical or chemical brush management within the past 50 years. The West Conchas pasture was bordered on the west by a 4-lane, divided state highway; and the Patricio pasture was bordered on the south by a 2-lane state farm road. Both roads had maximum speed limits of 113 kph.

Vegetation on the study site was typical of the Tamaulipan Biotic Province consisting of thornshrub dominated by mesquite (*Prosopis glandulosa*), huisache (*Acacia farnesiana*), and prickly pear cactus, and grasslands consisting primarily of Kleberg bluestem (*Dichanthium annulatum*), buffelgrass (*Pennisetum ciliare*), and a diverse forb community. The untreated pastures had a greater percent of woody canopy cover than treated pastures. Climate is semi-arid with highly variable rainfall patterns. Average annual temperature was 23° C and annual rainfall averaged 68 cm (Norwine and Bingham 1985).

METHODS

Bobcat capture

Bobcats were live-trapped intermittently from June 2011 to January 2012 with modified Tomahawk® traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA). A 51 x 38 x 51 cm extension reinforced with hardware cloth was attached to the trap and contained a live chicken or pigeon that was provided food and water *ad libitum*. Between 20 and 40 box traps were placed in selected locations spread across the 3 pastures in an attempt to catch bobcats using brush treatments. Bobcats were sedated using a sedation pole that contained an intramuscular injection of either a mixture of 20 mg/kg of ketamine hydrochloride (Fort Dodge

Laboratories, Fort Dodge, Iowa, USA) and 0.05 mg/kg of xylazine hydrochloride (Vedco, Inc., St. Joseph, Missouri, USA; n = 5) or Telazol (tiletamine hydrochloride and zolazepam hydrochloride, Fort Dodge Laboratories) at 5 mg/kg (n = 4). Standard body measurements (Boitani and Powell 2012) were recorded from each bobcat in addition to collections of blood, hair, and ectoparasites. Approximately 1-2 cc of blood was added to 3-5 cc of lysis buffer (Longmire et al. 1997). Adult bobcats were fitted with a 215 g GPS radio collar (Sirtrack, Ltd., New Zealand). Bobcats were monitored during recovery inside a pet carrier in a shaded location near point of capture, and then released following recovery from sedation. Bobcats were captured and handled following Texas A&M University-Kingsville Institutional Care and Use Committee guidelines under approved protocol 2009-08-4A-01.

Spatial data collection

The GPS collars were programmed to obtain locations once every 2 hours (n = 7) or once every 4 hours (n = 1). Collars released on a specified date 125-150 days after placement which was determined by battery life of the collars. Collars also were fitted with VHF transmitters that were on continuously. Collared bobcats were located every few weeks to check for mortality or dispersal from the study area using triangulation (White and Garrott 1990). Between 2 and 4 bearings were taken using a Suunto Precision Compass® (Suunto, Vantaa, Finland), Yagi antenna, and an Advanced Telemetry Systems® R2000 receiver. Locations were determined using program LOAS 4.0 (Ecological Software Solutions LLC, Hegymagas, Hungary). Only GPS locations were used for analyses, whereas VHF locations were used for monitoring. After the programmed release occurred, collars emitted a mortality signal and were recovered using the homing technique (White and Garrott 1990).

Spatial data analysis

The GPS locations of bobcats were downloaded and converted to Universal Transverse Mercator (UTM) and local time (Central Standard Time [CST]) with correction for Daylight Savings Time [DST]). Locations with low positional accuracy (Horizontal Dilution of Precision [HDOP] ≤ 4) were not evaluated. To test for differences in bobcat use of brush strips during different time periods, I separated the location data into 3 non-overlapping periods: diurnal (beginning the second hour after sunrise and ending the second hour before sunset, $n = 10$ h), crepuscular (1 hour before and after sunrise, and 1 hour before and after sunset, $n = 4$ h), and nocturnal (beginning the second hour after sunset and ending the second hour before sunrise, $n = 10$ h). Diel periods were adjusted for seasonal changes in sunrise and sunset over time and during daylight savings. Bobcat locations also were placed into 3 seasonal periods to test for differences in D by season. In southern latitudes, breeding occurs earlier and sometimes throughout the year, when conditions are favorable (Hansen 2007). Therefore, I delineated ecological seasons as breeding (January 1 - April 30), kitten-rearing (May 1 - August 31), and fall/winter (September 1 - December 31). These were offset one month earlier to periods defined by Chamberlain et al. (2003) to account for the lower latitudes of this region.

Brush strips were hand-digitized as a polygon layer in ArcMap 10.1 and the total area calculated. For each bobcat home range, the number of locations occupying brush strips for each time period was calculated using Hawth's Tools (Hawth's Analysis Tools for GIS, www.spatialecology.com) extension. Total area (km^2) of brush strips in the home range of each individual was calculated using the "Clip" function in ArcCatalog, then expressed as a proportion of the total home range.

Home ranges were created for each individual using kernel density estimators (KDE). This type of estimation includes less unused space and provides better space-use analyses than minimum convex polygon (MCP) methods (Barg et al. 2005). Additionally, GPS locations with frequent fix rates (location rates < 24 h) are not considered independent and kernel estimators can be less sensitive to these violations of serial independence (Swihart and Slade 1997). Worton (1995) and Seaman and Powell (1996) recommended use of fixed kernel estimation methods after finding they produced unbiased home range estimates. I used adaptive KDE with either the reference bandwidth smoothing parameter (h_{ref}) or Least Cost Squares Validation (LCSV) in Home Range Extension (HRE: The Home Range Extension for ArcView, Centre for Northern Forest Ecosystem Research, Ontario, Canada) for ArcView 9.3. I calculated 95% home ranges and 50% core use area (Kaufman 1962) polygons, then transferred them to ArcMap 10.1 for visualization and additional analyses.

Fractal D

Fractal dimensions (*D)* were calculated for the movements of each individual, and for each season in program Fractal 5.2 (Nova Scotia Agricultural College, Truro, Nova Scotia, Canada). I used the Fractal Mean estimator which uses the traditional dividers method (Mandelbrot 1967), beginning at random points along the path and measuring it multiple times forward and backward at each divider size (Nams 2006). This method was applied at the same range of spatial scales for each individual and season from 1/20th of the mean home range diameter size to 5 times the mean home range diameter size (Webb et al. 2009). The VFractal also was calculated because it estimates error in the form of confidence intervals (*CI*). Movement paths were combined by sex so that Vfractal considered each path a replicate. Thus, error estimates were based on among-path variation and allowed for inferences to be extrapolated (Nams 1996). The movement paths were weighted by the number of sampling intervals for each path length (N). Fractal analyses are scale-variant (Turchin 1996), so I plotted scale versus D, variances of tortuosity, and correlations of tortuosity to detect bobcat movement pattern differences in response to habitat patches (Doerr and Doerr 2004). Plots of variances should show a decline when movement paths are larger than the patch sizes, but remain high when path lengths are at or below patch size (Nams 2005). Plots of correlation values should be 0 when movement paths are larger than patch size, negative when paths are equal to patch size, and positive when paths are smaller than patch size (Nams 2005). Estimates of fractal D were normalized by transformation to $\log(D\text{-}1)$ for statistical analyses (Nams and Bourgeois 2004).

Statistical analyses

I determined if variances were equal among home range size, core area size, and D estimates for male and female bobcats using a Fisher's F-test. A 2-sample t-test was used to test for differences in home range size, core area size, and D between sexes. A simple linear regression was used to determine if D was related to proportion of brush strips in the home range. Two separate simple linear regressions were used to determine if D (response variable) was influenced by size of home range (explanatory variable) or core area (explanatory variable). To account for differences in length of diel period (diurnal = 10 h, nocturnal = 10 h, crepuscular = 4 h), I calculated the proportions of the day (diurnal = 42%, nocturnal = 42%, and crepuscular = 16%). A Chi-squared goodness-of-fit test (GOF) was used to determine if number of locations in brush strips differed by period for each bobcat individually. For example, if a bobcat had 100 locations in brush strips, the expected number of locations for diurnal, nocturnal, and crepuscular would be 42, 42, and 16, respectively. The GOF was used to test whether the observed number of locations in brush strips differed from the calculated expected number of locations in brush strips. Analyses were conducted in program R 2.15.2 (The R Foundation for Statistical Computing 2012), with means ± SE reported and statistical significance set as $P = 0.05$.

RESULTS

Trapping and collar success

I captured 9 bobcats (5 M, 4 F) during 1,745 trap nights for a success rate of 1 bobcat during 194 trap nights. One female bobcat (7F) was a kitten (<5 kg) and not fitted with a collar during sedation. Male (6M) was a sub-adult (~1.5 years old), and male (8M) was >12 years old, but the remaining 6 captured bobcats were adults about 4-8 years old, and these 8 individuals received GPS collars. Bobcat collars had a fix rate every 2 h except for the last male collared (9M) which had a fix rate every 4 h. I collected 4,372 locations (after removal of low-accuracy locations) for the 8 bobcats (5 M, 3 F) with GPS collars. Mean number of locations collected were 547 ± 116 points over 81 ± 11 days. High variation in locations obtained were in part due to one collar (1M) that malfunctioned and dropped early after 28 days and another collar (4F) that missed few locations yielding 1,262 GPS points over 142 days. Excluding these 2 outliers, collars averaged 488 ± 56 locations over 80 ± 2 days. Success rate for locations for the 8 collars was 54 ± 5%. Seven collars did not perform over the predicted 125 days of battery life, but instead lasted an average 65% of the expected duration.

Home range and core area

Home-range size averaged 4.9 ± 0.5 km^2 and 2.9 ± 0.3 km^2 for adult male and female bobcats, respectively. Core-area size averaged 1.4 ± 0.5 km^2 and 0.7 ± 0.1 km^2 for adult male and female bobcats, respectively. One male bobcat (8M) with a large home range of 35 km^2 and core area of 10 km^2 was excluded from average estimations. A sub-adult male (6M) was excluded from the adult bobcat estimations (Table 3.1). Variances were equal between adult home range sizes ($F_{2,2} = 4.85$, $P = 0.34$) and core areas ($F_{2,2} = 14.08$, $P = 0.13$). Home range sizes for adult male bobcats were larger than adult females ($t_4 = -3.50$, $P = 0.01$), but did not differ for core areas ($t_4 = -1.57$, $P = 0.10$). Though not statistically different, core areas of adult male bobcats on this site were generally larger than females (Table 3.1). Adult home range ($t_4 = 0.2$, $P = 0.85$) or core area ($t_4 = 0.41$, $P = 0.71$) sizes did not differ between treated or untreated pastures.

Use of brush strips by period

Only 2 bobcats were captured in pastures treated with brush strips. Of the 6 other collared bobcats that were captured in the control pasture, 3 had home ranges that overlapped brush strips in adjacent treated pastures. A male bobcat (8M) that was captured in the control pasture had a home range that covered 35 km^2, which encompassed almost an entire treated pasture. Even though the bobcat was old (>12 years) and covered a large area, this individual returned multiple times to the capture location and to other portions of its home range and, thus did not seem to be exhibiting transient behavior. This male was the only bobcat to maintain a large proportion of brush strips within a home range (Table 3.2). Individually, 2 bobcats had locations in brush strips different than expected and 2 had locations as expected among time periods. Locations in brush strips for bobcats 5F and 9M differed by time

Table 3.1. Male and female bobcat 95% home range (km^2) size and 50% core area sizes (km^2) estimated from GPS locations using kernel density estimators in ArcMap 9.3. Bobcats were residents of the Santa Gertrudis Division of King Ranch, Kleberg and Jim Wells counties, Texas, from June 2011 to May 2012. Individual estimates and averages ± standard errors for each sex and age range are indicated.

ID	Age	Sex	Home Range	Core Area
1M	Adult	M	537	1.9
2M	Adult	M	5.1	1.8
3F	Adult	F	3.2	0.6
4F	Adult	F	2.4	0.5
5F	Adult	F	3.0	0.9
6M[1]	Sub-adult	M	2.3	0.6
8M[2]	Adult	M	34.8	10.0
9M	Adult	M	3.9	0.5
AVERAGE MALE (*n* = 5)			4.2 ± 0.8	1.2 ± 0.4
AVERAGE ADULT MALE (*n* = 4)			4.9 ± 0.5	1.4 ± 0.5
AVERAGE ADULT FEMALE (*n* = 3)			2.9 ± 0.3	0.8 ± 0.1

[1] Home range estimate used in overall average male estimations but not in the average of adult males.

[2] Home range estimate not used in overall male or adult male average home range estimations.

Table 3.2. Number of locations in brush strips (observed and expected) per diel period (diurnal, nocturnal, and crepuscular) for 4 bobcats (1M, 5F, 8M, and 9M) with GPS locations in brush strips on King Ranch, Kleberg and Jim Wells counties, Texas, from June 2011 to May 2012. Differences between observed and expected locations in brush strips tested using a Chi-squared goodness of fit test. Test statistic (χ^2), degrees of freedom (*df*) and significance (*P*-value) are indicated for each bobcat.

	Bobcat ID			
	1M	5F	8M	9M
Diurnal				
Observed	11	1	96	5
Expected	8.4	5.46	106.68	4.2
Nocturnal				
Observed	6	12	112	1
Expected	8.4	5.46	106.68	4.2
Crepuscular				
Observed	3	0	46	4
Expected	3.2	2.08	40.64	1.6
Total in brush strips	20	13	254	10
χ^2	1.54	13.8	1.59	5.84
df	2	2	2	2
P	0.46	0.0001[1]	0.45	0.05[1]

[1] Bobcats with observed locations in brush strips significantly different than expected.

period ($\chi^2 = 13.8$, $df = 2$, $P = 0.001$, and $\chi^2 = 5.84$, $df = 2$, $P = 0.05$, respectively). Locations in brush strips for Female bobcat (5F) had fewer locations in brush strips than expected for diurnal and crepuscular periods, and more locations than expected for the nocturnal period. Male bobcat (9M) had locations in brush strips as expected for the diurnal period, fewer locations than expected for the nocturnal period and more locations than expected for the crepuscular period. Locations for 2 male bobcats, 1M and 8M, were distributed between time periods as expected ($\chi^2 = 1.54$, $df = 2$, $P = 0.46$, and $\chi^2 = 1.59$, $df = 2$, $P = 0.45$, respectively). Forty percent of locations by male bobcat (8M) were within brush strips. Of 254 locations within brush strips, 38% were diurnal, 44% were nocturnal, and 18% were crepuscular hours, which was not significantly different than expected (i.e., diurnal = 42%, nocturnal = 42%, and crepuscular = 16%).

Fractal D

Fractal *D* did not differ by sex ($t_4 = 0.58$, $P = 0.60$) or season ($F_8 = 0.44$, $P = 0.66$). After pooling data by sex and removing the large outlier (8M), tortuosity increased as home range size ($t_5 = 5.11$, $P < 0.01$, $R^2 = 0.81$) and core area size ($t_5 = -6.59$, $P < 0.01$, $R^2 = 0.88$) decreased (Fig. 3.2). Male and female bobcats showed different scale-variant movement patterns over varying path lengths. Females showed changes in tortuosity at 2 different path lengths, with the first at approximately 403 m and the second at approximately 621 m (Fig. 3.3 top). Variance dropped at path length 621 m (Fig. 3.3 middle), indicating that path lengths greater than this length were larger than patch size. The correlation plot was less clear for females, though they were negative for path lengths <439 m (Fig. 3.3 bottom). This result suggests that optimal patch size perceived

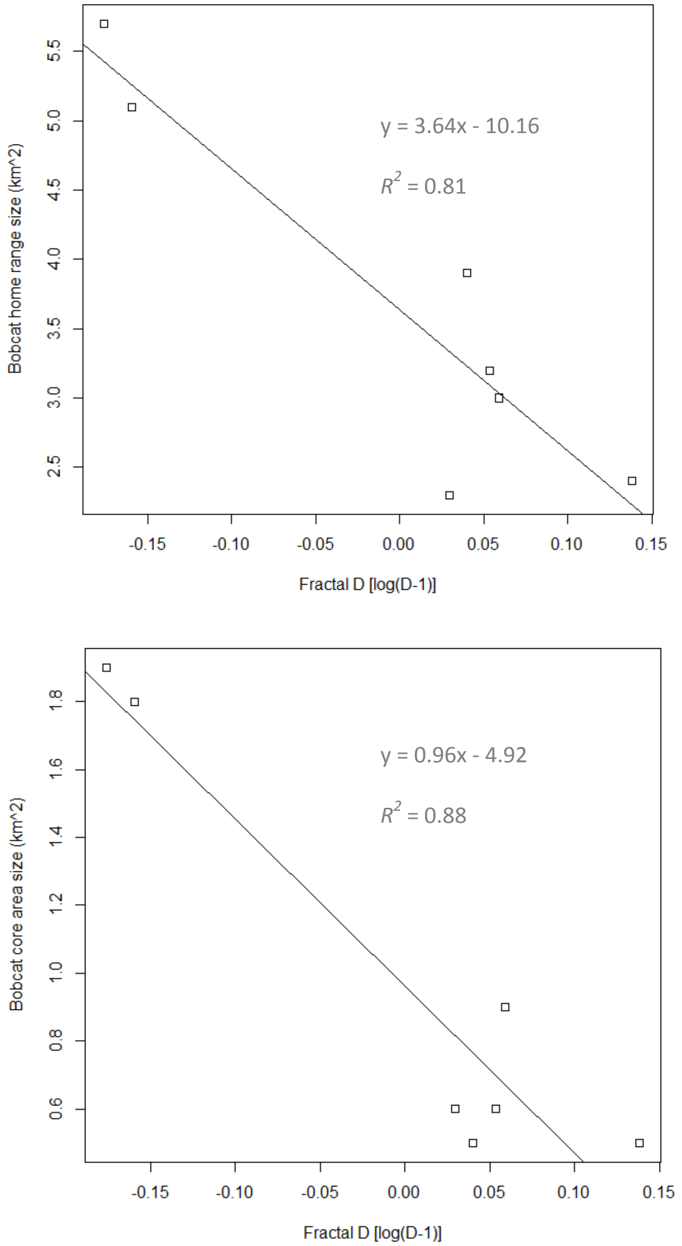

Figure 3.2. Linear regression plot showing negative correlation between fractal *D* [log(*D*-1)] and home range (top) and core area size (bottom) of bobcats on King Ranch, Kleberg and Jim Wells counties, Texas, from June 2011 to May 2012. This figure does not include the outlier home range from bobcat 8M.

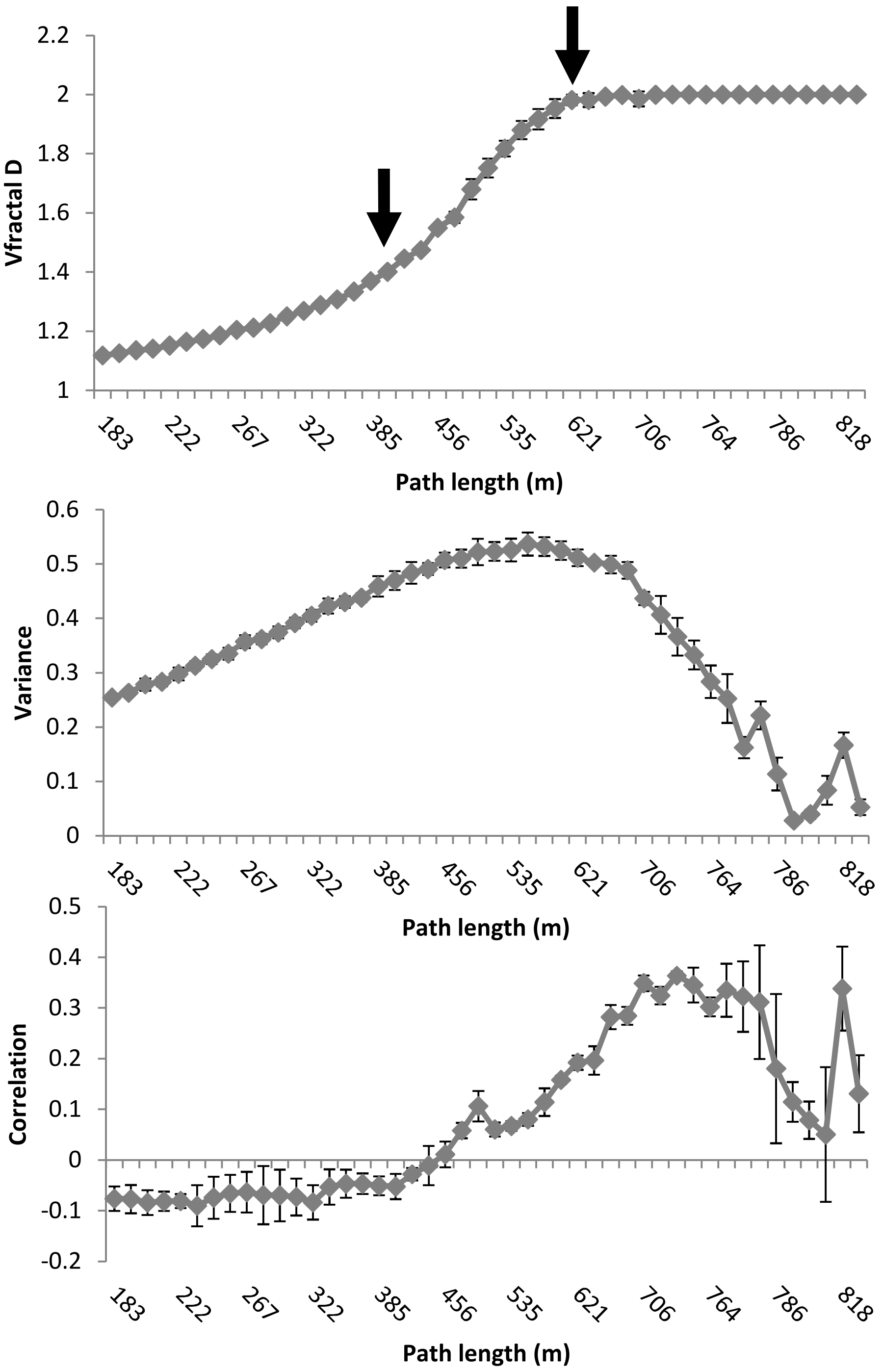

Figure 3.3. Plots of scale versus: VFractal *D* (top), variance in *D* (middle) and correlation of *D* (bottom) with 95% confidence intervals for female bobcats (*n* = 3) on King Ranch, Kleberg and Jim Wells counties, Texas, from July 2011 to May 2012. Black arrows at 403 m and 578 m indicate path lengths where tortuosity changed.

by female bobcats was between ~400-650 m. Results for male bobcats were more variable, as evidenced by wider confidence intervals, but in general they appeared to have only one small change in movement patterns in relation to path length for the plot of *D*. A slight increase in the curve occurred at 344 m, but this did not correspond to a drop in variance or change in correlation of adjacent path segments (Fig 3.4 top). A small drop in variance occured at 901 m (Fig. 3.4 middle) and correlation was negative at path lengths below 473 m (Fig. 3.4 bottom). Male bobcats appeared to have a wider perceived patch size than females occurring between ~400-900 m.

Four bobcats had home ranges that contained treated brush strips, and one home range had a major brush strip presence, so the strength of the statistical comparison of proportion of brush strips in home range in relation to changing tortuosity was likely low. A negative linear correlation occurred between proportion of brush strips and *D*, but it was not statistically significant ($t_2 = -1.56$, $P = 0.26$, $R_2 = 0.32$). Of the 4 bobcat home ranges with brush strips, 8M had the largest home range with the greatest proportion of brush strips (26%) and the smallest *D* (1.55).

DISCUSSION

Home range estimates were similar to those reported for bobcats in southern latitudes (Miller and Speake 1979, Chamberlain et al. 2003) and areas of fragmented habitat (Riley et al. 2003). Bradley and Fagre (1988) reported unusually small bobcat home ranges (males = 3.46 km^2, $n = 3$; female = 1.16 km^2, $n = 1$) on a research area with cattle, located <10 km from this study site. Extensive predator overlap and tolerance could have been attributed to abundant resources such as prey and habitat (Bradley and Fagre 1988).

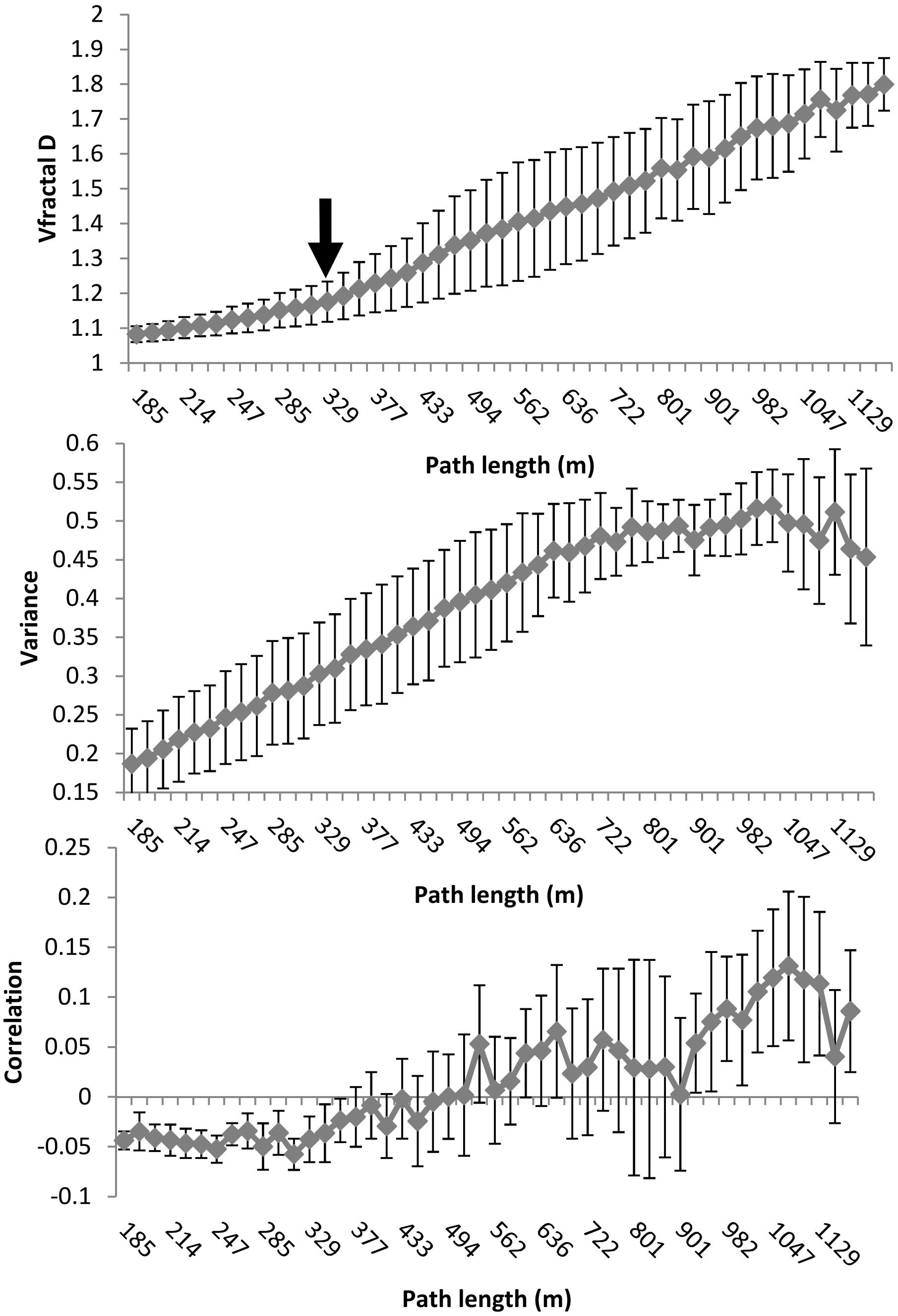

Figure 3.4. Plots of scale versus VFractal *D* (top), variance in *D* (middle) and correlation of *D* (bottom) with 95% confidence intervals for male bobcats (*n* = 5) on King Ranch, Kleberg and Jim Wells counties, Texas, from June 2011 to May 2012. Black arrow at 344 m indicates path length where tortuosity changed.

Male bobcats on this study site had larger home ranges (4.9 ± 0.5 km^2) than females (2.9± 0.8 km^2). Male core areas also were larger (1.4 ± 0.5 km^2) than females (0.7 ± 0.1 km^2), though not statistically significant. Five of the collared bobcats occurred almost exclusively within one 12.9 km^2 pasture (untreated), with extensive overlap among individuals. Overlap may reflect tolerance related to abundant resources such as prey, or because bobcat core areas remained exclusive (Nielson and Woolf 2001). Tucker et al. (2008) suspected that the fragmented farm landscape of Iowa would cause bobcats to maintain larger home range sizes, but instead found home ranges with similar sizes to others in the region. Differences were not detected in adult home range or core area sizes between pastures with brush strips (i.e., fragmented) and those with contiguous habitat. Adult home ranges were relatively small compared to other studies (Miller and Speake 1979, Chamberlain et al. 2003) and could indicate high habitat quality and abundant prey resources. Home range size is partly influenced by food availability (Litvaitis et al. 1986, Knick 1990) and typically decreases with greater food availability (Harestad and Bunnell 1979). Brush strips were used to create edge habitat for game species such as white-tailed deer and northern bobwhite. Edge habitat may have higher prey diversity (Harris 1988), and should create hunting opportunities for predators.

I predicted that brush strips would be most useful for bobcats during nocturnal and crepuscular periods when bobcats were hunting or traveling within their territory. Two male bobcats did not show a preference for using brush strips in a particular diel period. One female and 1 male bobcat used brush strips more than expected during nocturnal period and crepuscular periods, respectively, which may indicate a preference for using strips for hunting or travel. Three bobcats did not have home ranges that encompassed or overlapped adjacent brush strip habitat and thus had no locations in brush strips. A larger sample size is needed to determine whether brush strips are preferred in a particular diel period. Furthermore, prey surveys in both habitat types could delineate whether brush strips provide greater hunting opportunities.

No statistical difference occurred for *D* between sexes or seasons. Males exhibited less tortuosity (1.82 ± 0.24) in their movement paths compared to females (2.22 ± 0.14). One female tracked during kitten-rearing season had a fractal *D* of 2.22, larger than that of males in the same season (1.64 ± 0.03). Bobcat kittens are altricial and born blind. The mother will only leave the den for short durations until kittens are about 3-5 months old and can follow on hunts. If resources are abundant, the female should only need to make brief forays to acquire prey and thus will increase tortuosity in movement paths and increase *D* values. Female Iberian wolves (*Canis lupis signatus*) exhibited the same pattern with increased tortuosity when caring for cubs (Bascompte and Vilá 1997).

In fall-winter, female bobcats (2.05 ± 0.16) had more tortuous movements than 1 male bobcat (1.47) tracked at that time. Bobcat offspring may remain with the mother from 9 months to 1.5 years before dispersing (Hansen 2007). If a female bobcat had kittens in fall-winter, movement patterns would likely be shorter and more tortuous. Furthermore, male movements tend to be more frequent and at longer distances in winter (Chamberlain et al. 1999). Adult bobcats had similar *D* values (males = 1.92 ± 0.25, females = 1.92 ± 0.14) during breeding season, when bobcats make longer (and straighter) movements in search of mates (Anderson 1987, Sandell 1989). One sub-adult male bobcat of non-breeding age tracked during breeding season exhibited more tortuous movements (2.23).

Tortuosity was inversely related to home range and core area size for all bobcats collared on this study site. Home range and core area size decreased as movement paths became more tortuous. Because fractal analyses can indicate the intensity that an area is searched, the smaller home range and core areas recorded on this study site, which may also have more abundant resources (Harestad and Bunnell 1979, Benson et al. 2006), may be more thoroughly traversed or searched. Additional research is needed to determine if prey abundance differs between brush strips and other habitat types on this study site.

Fractal patterns of bobcats on this site seemed to be scale-variant and sex-specific, where males and females had varying values of *D* at different scales that were masked when estimating one overall mean value of tortuosity. Sex-dependent factors were likely related to differences in foraging activity, energetic requirements (Benson et al. 2006), and seasonal reproduction. The plot of *D* versus path lengths for females clearly shows 2 breaks, indicating that they had 3 separate domains; female bobcats were moving differently at 3 spatial scales: 183-403 m, 403-621 m, and 621-822 m. Plots of variances between adjacent path segments also measure path heterogeneity and highlight segments where *D* may change. Female bobcats had a decrease in variance at 621 m, confirming one of these thresholds. The plot of *D* for males was less distinctive, revealing no clear thresholds and possibly indicating they moved through all patch sizes in a similar pattern. There was a slight drop in variance at path lengths of 901 m, which may reveal that males were using larger patches than females.

The plot of correlation between adjacent path lengths is generally easier to interpret. When correlations are: positive, path lengths are smaller than patch size; negative, paths are the same as patch size; and at zero, scale of path lengths is larger than patch size (Nams 2005). Male correlations were negative up to 473 m, whereas females were negative to only about 439 m, indicating that females used slightly smaller patch sizes. Plots of *D* and variance for males indicated use of 1 domain, but the negative correlation values indicated a threshold and showed 2 domains: 185-473 m and 473-1,119 m. The small decrease in variance at 901 m, coupled with the near zero value in correlation at the same path length, suggests there was another threshold, and therefore males were using 3 domains: 185-473 m, 473-901 m, and 901-1,119 m. Male bobcat *D* values, variance, and correlation plotted with scale were more variable than those for females, as indicated by the wider confidence intervals. Male movements varied widely between seasons, with longer paths occurring during breeding season. This pattern could have resulted in more variability and larger confidence intervals when estimating overall *D* values (Nams et al. 2006).

Male and female bobcats on this study site seem to be moving through home ranges at 3 separate scales of varying patch size, with females using smaller sizes. The size of manipulated brush strips were well within the patch sizes used by males and females, but the 8 bobcats did not appear to select for use of brush strips. Although 2 bobcats used brush strips in greater proportion to availability there was no other support that bobcats on this site were either positively affected or negatively affected by the presence of brush strips.

Female bobcat movements and home ranges are particularly influenced by habitat quality (Anderson 1987), whereas male patterns are influenced by breeding opportunities (Anderson 1987, Sandell 1989). These ecological factors may account for the differences in male and female patch sizes and tortuosity on this site. Males used larger patches and covered longer distances (Kitchings and Story 1979, Lawhead 1984), whereas females traveled shorter distances and used smaller core areas during kitten-rearing periods.

Many of the statistical analyses were not significant, most likely related to small sample sizes. Application of these methods to medium-sized carnivores is not common, and although previous studies also have had problems with low sample size (e.g., Iberian wolves, Bascompte and Vilá 1997), they still revealed important insights into carnivore ecology. My conclusions corroborate with previous studies on bobcats, including patterns where males exhibited larger home ranges, core areas, and traveled more straight-line movements than females.

Bobcats are an integral part of an ecologically healthy and productive ecosystem, but are often overlooked in management strategies and planning. Male and female bobcats on this site moved through habitat at different spatial scales but within patch size of manipulated brush strips. Although these results do not indicate a positive or negative response to brush strip management, further research is needed. Additional research may indicate some brush management strategies negatively affect carnivore communities. Through bottom-down processes, a declining carnivore population could lead to degraded vegetative conditions important for game management and economic opportunities.

Although this study examined fine-scale movement patterns of bobcats, these methods can be applied to endangered ocelots, which exist in an extremely fragmented landscape and may aid in developing conservation strategies for this sympatric felid.

LITERATURE CITED

Anderson, E. M. 1987. A critical review and annotated bibliography of literature on the bobcat. Colorado Division of Wildlife Special Report 62.

———. 1988. Effects of male removal on spatial distribution of bobcats. Journal of Mammalogy 69:637–641.

———. 1990. Bobcat diurnal loafing sites in southeastern Colorado. Journal of Wildlife Management 54:600–602.

———, and M. J. Lovallo. 2003. Bobcat and lynx. Pages 758–782 *in* G.A. Feldhammer, B.C. Thompson and J.A. Chapman, editors. Wild mammals of North America: biology, management, and conservation (2nd Edition). John Hopkins Press, Baltimore, Maryland, USA.

Bailey, T. N. 1974. Social organization in a bobcat population. Journal of Wildlife Management 38:435–446.

Barg, J. J., J. Jones, and R. J. Robertson. 2005. Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. Journal of Animal Ecology 74:139–149.

Barnett, A., K. G. Abrantes, J. D. Stevens, B. D. Bruce, and J. M. Semmens. 2010. Fine-scale movements of the broadnose sevengill shark and its main prey, the gummy shark. PLOS One 5(12):e15464.

Bascompte, J., and C. Vilá. 1997. Fractals and search paths in mammals. Landscape Ecology 12:213–221.

Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. Journal of Mammalogy 76:1056–1070.

Benson, J. F., M. J. Chamberlain, and B. D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? Animal Behavior 71:685–693.

Blankenship, T. L. 2000. Ecological response of bobcats to fluctuating prey populations on the Welder Wildlife Foundation Refuge. Ph.D. Dissertation, Texas A&M University-Kingsville, Kingsville, USA.

Boitani, L., and R. A. Powell (eds.). 2012. Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, New York, USA.

Bradley, L. C., and D. B. Fagre. 1988. Coyote and bobcat responses to integrated ranch management practices in south Texas. Journal of Range Management 41:322–327.

Chamberlain, M. J., B. D. Leopold, L. W. Burger, B. D. Plowman, and L. M. Conner. 1999. Survival and cause-specific mortality of adult bobcats in central Mississippi. Journal of Wildlife Management 63:613–620.

———, and ———. 2001. Spatio-temporal relationships among adult bobcats in central Mississippi. Pages 45–55 *in* A. Woolf, C. K. Nielsen and R. D. Bluett, editors. Proceedings of a symposium on current bobcat research and implications for management. The Wildlife Society Conference 2000, Nashville, Tennessee, USA.

———, ———, and L. M. Conner. 2003. Space use, movements and habitat selection of adult bobcats (*Lynx rufus*) in central Mississippi. American Midland Naturalist 149:395–405.

Conner, M., B. Plowman, B. Leopold, and C. Lovell. 1999. Influence of time-in-residence on home range and habitat use of bobcats. Journal of Wildlife Management 63:261–269.

Doerr, V. A. J., and E. D. Doerr. 2004. Fractal analysis can explain individual variation in dispersal search paths. Ecology 85:1428–1438.

Hamilton, D. A. 1982. Ecology of the bobcat in Missouri. M.S. thesis, University of Missouri.

Hansen, K. 2007. Bobcat: master of survival. Oxford University Press, New York, USA.

Harestad, A. S., and F. L. Bunnell. 1979. Home range and body weight: a reevaluation. Ecology 60:389–402.

Harris, L. 1988. Effects and conservation of biotic diversity. Conservation Biology 2:330-332.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology 88:2354–2363.

Janečka, J. E., T. L. Blankenship, D. H. Hirth, C. W. Kilpatrick, M. E. Tewes, and L. I. Grassman. 2007. Evidence for male-biased dispersal in bobcats *Lynx rufus* using relatedness analysis. Journal of Wildlife Biology 13:38–47.

Kaufman, J. 1962. Ecology and social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. Zoologica 60:95–222.

Kitchings, J. T., and J. D. Story. 1979. Home range studies of bobcats in eastern Tennessee. Pages 47–52 *in* L. Blum and P. C. Escherich, editors. Proceedings of the 1979 bobcat research conference: current research on biology and management of *Lynx rufus*. Scientific and Technical Series 6. National Wildlife Federation, Washington, D.C., USA.

———, and ———. 1984. Movements and dispersal of bobcats in East Tennessee. Journal of Wildlife Management 48:957–961.

Knick, S. T. 1990. Ecology of bobcats relative to exploitation and prey decline in southeastern Idaho. Wildlife Monographs 108:1–42.

Lawhead, D. N. 1984. Bobcat (*Lynx rufus*) home range, density and habitat preference in south-central Arizona. The Southwestern Naturalist 29:10–113.

Lembeck, M., and G. I. Gould, Jr. 1979. Dynamics of harvested and unharvested bobcat populations in California. Pages 53–54 *in* L. Blum and P. C. Escherich, editors. Proceedings of the 1979 bobcat research conference: current research on biology and management of *Lynx rufus*. Scientific and Technical Series 6. National Wildlife Federation, Washington, D.C., USA.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110–117.

Longmire, J. L., M. Maltbie, and R. J. Baker. 1997. Use of lysis buffer in isolation and its implications for museum collections. Occasional Papers, The Museum of Texas Tech University, Lubbock, 163:1–3.

Lovallo, M. J. and E. M. Anderson. 1995. Range shift by a female bobcat (*Lynx rufus*) after removal of a neighboring female. American Midland Naturalist 134:409–412.

———, and ———. 1996. Bobcat movements and home ranges relative to roads in Wisconsin. Wildlife Society Bulletin 24:71–76.

Mandelbrot, B. B. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. Science 156:636–638.

———. 1984. Fractals in physics: squig clusters, diffusions, fractal measures, and the unicity of fractal dimensionality. Journal of Statistical Physics 34:895–930.

Marshall, A. D., and J. H. Jenkins. 1966. Movements and home ranges of bobcats as determined by radio-tracking in the upper coastal plain of west-central South Carolina. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 20:206–214.

McCord, C. M., and J. E. Cordoza. 1982. Bobcat and lynx (*Felis rufus* and *Felis lynx*). Pages 728–766 *in* J. A. Chapman and G. A. Feldhammer, editors. Wild mammals of North America: biology, management, and economics. Johns Hopkins University Press, Baltimore, Maryland, USA.

Miller, S. D., and D. W. Speake. 1979. Progress report: demography and home range of the bobcat in south Alabama. Pages 123–124 *in* L. Blum and P. C. Escherich, editors. Proceedings of the 1979 bobcat research conference: current research on biology and management of *Lynx rufus*. Scientific and Technical Series 6. National Wildlife Federation, Washington, D.C., USA.

Nams, V. O. 1996. The VFractal: a new estimator for fractal dimension of animal movement paths. Landscape Ecology 11:289–297.

———. 2005. Using animal movement paths to measure response to scale. Oecologia 143:179–188.

———. 2006. Improving accuracy and precision in estimating fractal dimension of animal movement paths. Acta Biotheoretica 54:1–11.

———., and M. Bourgeois. 2004. Fractal analysis measures habitat use at different spatial scales: an example with American marten. Canadian Journal of Zoology 82:1738–1747.

______., G. Mowat, and M. A. Panian. 2006. Determining the spatial scale for conservation purposes: an example with grizzly bears. Biological Conservation 128:109–119.

Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. Ecological Monographs 66:409–429.

Nielson, C. K., and A. Woolf. 2001. Spatial organization of bobcats (*Lynx rufus*) in southern Illinois. American Midland Naturalist 146:43–52.

Norwine J., and R. Bingham R. 1985. Frequency and severity of drought in south Texas. Pages 1–19 *in* R. Brown, editor. Livestock and Wildlife Management During Drought. Caesar Kleberg Wildlife Research Institute Press, Kingsville, Texas.

Renshaw, E., and R. Henderson. 1981. The correlated random walk. Journal of Applied Probability 18:403–414.

Riley, S. P. D., R. M. Sauvajoet, T. K. Fuller, E. C. York, D. A. Kamraldt, C. Bromley, and R. K. Wayne. 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17:566–576.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pages 164–182 *in* J. L. Gittleman, editor. Carnivore behavior, ecology, and evolution. Cornell University Press, Ithaca, New York, USA.

Schmidly, D. J. 2004. The mammals of Texas. Revised edition. University of Texas Press, Austin, USA.

Seaman, D. E. and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085.

Sinclair, A. R. E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. Philosophical Transactions of the Royal Society of London 358:1729–1740.

Smith, J. N. M. 1974. The food searching behavior of two European thrushes. 1: Description and analysis of search paths. Behaviour 48:276–302.

Swihart, R. K., and N. A. Slade. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2:48–63.

Tucker, S. A., W. R. Clark, and T. E. Gosselink. 2008. Space use and habitat selection by bobcats in the fragmented landscape of south-central Iowa. Journal of Wildlife Management 72:1114–1124.

Turchin, P. 1996. Fractal analyses of animal movement: a critique. Ecology 77:2086-2090.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demarais. 2009. Using fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210–1217.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, Michigan, USA.

Whitson, R. E., S. L. Beasom, and C. J. Scifres. 1977. Economic evaluation of cattle and white-tailed deer response to aerial spraying of mixed brush. Journal of Range Management 30:214–217.

Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel based home range estimators. Journal of Wildlife Management, 59:794–800.

VITA

Name: Jennifer Marie Korn

Education: B.S., Biology and Anthropology, University of Texas at Arlington

M.S., Wildlife Ecology, Texas State University–San Marcos

Address: 108 Lemon Rd NE, Lake Placid, Florida 33852

Professional Experience:

2013–present	Florida Panther Specialist, Florida Fish and Wildlife Conservation Commission, Venus, Florida
2008–2013	Doctoral Research Assistant, Caesar Kleberg Wildlife Research Institute, Texas A&M University–Kingsville, Kingsville, Texas
2008	Staff Biologist, Loomis Austin, Inc., Austin, Texas
2008	Contract Biologist, Plateau Land and Wildlife, Austin, Texas
2006–2008	Certified Wildland Firefighter/Seasonal Researcher, Texas Forest Service, Bastrop, Texas
2006–2008	Instructional Assistant, Texas State University–San Marcos, Texas