

POPULATION STATUS AND EVALUATION OF LANDSCAPE CHANGE FOR
THE LOWER KEYS MARSH RABBIT

A Thesis

by

JASON ALAN SCHMIDT

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

MASTER OF SCIENCE

December 2009

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Population Status and Evaluation of Landscape Change for
the Lower Keys Marsh Rabbit. (December 2009)

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Dr. Nova J. Silvy

Wildlife biologists and land managers tasked with the recovery of the endangered Lower Keys marsh rabbit (LKMR; *Sylvilagus palustris hefneri*) were in need of a current population estimate as well as a method to estimate the LKMR population annually. Habitat loss and fragmentation from population growth and development have threatened the existence of the LKMR. Establishing and understanding long-term habitat availability for the LKMR is important for determining causes of historical population declines as well as designing and implementing successful recovery plans.

I conducted a range-wide pellet survey and a mark-recapture study to estimate the LKMR population. I evaluated the fit of 5 models and considered the variation in behavioral response model the best model. I correlated ($r^2 = 0.913$) this model's rabbit abundance estimates to pellet density in 11 patches and generated a range-wide population estimate of 317, a western clade population of 257, an eastern clade population of 25, and translocated LKMR populations of 35 and 0 on Little Pine and Water keys, respectively. This prediction equation provides managers a quick, efficient, and non-invasive method to estimate LKMR abundance from pellet counts.

To quantify the amount of habitat loss and fragmentation that occurred over the last 50 years, I systematically delineated and compared potential LKMR habitat using 1959 and 2006 aerial photographs. Additionally, I investigated if other factors could have reduced the amount of suitable habitat available for the LKMR with a comparison of habitat loss and fragmentation on a developed island and an undeveloped island. Range-wide, I found that number of habitat patches increased by 38, total class area decreased by 49.0%, and mean patch size decreased by 44.3%. Mean shape index increased by 4.2% and mean proximity index decreased by 13%. Both the 1959 and 2006 connectance indices were low while the 2006 set decreased 12.1%. I observed the same patterns of habitat loss and fragmentation on both the developed and undeveloped islands as I did in the range-wide landscape analysis. I found that LKMR habitat has declined in area and become more fragmented over the last 50 years. Habitat loss and fragmentation by development have directly endangered the LKMR; however, sea level rise and woody encroachment also

could have historically caused habitat loss and fragmentation. Although development in LKMR habitat was halted, sea-level rise and woody encroachment could continue to alter LKMR habitat.

DEDICATION

To Paige McGee

for her humor, devotion, strength, and love

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First I would like to thank both of my co-chairs and both of my committee members. I thank Dr. Robert McCleery for all he did to make this thesis exist. This includes, but is not limited to, visualizing, with the help of my wife, my attendance of graduate school, research ideas, scientific knowledge, supporting my field efforts, editing my writing, and his friendship. I thank Dr. Nova Silvy for his wisdom shared over many hot suppers of chicken wings or lunches at TC. His friendship and knowledge did much to bring this thesis together. I thank Dr. Roel Lopez for giving me the chance to work in the Florida Keys with the wonderful wildlife present in a unique landscape. His guidance and advice have been central in my development as a wildlife biologist. I thank Dr. Rusty Feagin for help envisioning the road forward and encouragement along the way. I also would like to thank the faculty and staff of the Department of Wildlife and Fisheries Sciences for making my time at Texas A&M University a great experience.

I would like to thank all of the previous and current Lower Keys marsh rabbit researchers that have elucidated the particulars of marsh rabbit life; James Lazell, Stephen Howe, Beth Forys, Craig Faulhaber, Neil Perry, David LaFever, Amanda McCleery, and Paige Schmidt.

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CHAPTER I

INTRODUCTION

BACKGROUND

The purpose of this introductory chapter is to provide the reader with general background information on the Lower Keys marsh rabbit (LKMR; *Sylvilagus palustris hefneri*) and provide an outline for this thesis. The chapter begins with a description of the LKMR, its distribution, a description of the study site, conservation issues, and current status. It concludes with a summary of the research objectives for this thesis.

The LKMR is one of 3 subspecies of *Sylvilagus palustris* endemic to the Lower Florida Keys (Fig. 1.1). Lazell described this new sub-species in 1984 as having a shorter molariform tooth row, a higher and more convex frontonasal profile, a broader cranium, and a longer dentary symphysis than the Upper Keys (*S. p. paludicola*) or mainland marsh rabbits (*S. p. paludicola* and *S. p. palustris*) (Lazell 1984). LKMRs historically existed from Key West to Big Pine Key but in recent history their range has decreased as rabbits were extirpated from Key West and Stock Island (de Pourtales 1877, Howe 1988). Additionally, there is a gap in the middle of their range (Gap Islands Complex [Faulhaber 2003]) that divides the metapopulation into 2 genetically distinct management units (Crouse et al. 2009).

The LKMR has been known to occupy patches of saltmarsh-buttonwood (*Conocarpus erectus*) transition zone, brackish and freshwater wetland, and coastal beach berm (Forys and Humphrey 1996, Faulhaber et al. 2008). Within these vegetation types, the LKMR has been associated with dense herbaceous plants such as seashore dropseed (*Sporobolus virginicus*), gulf cord grass (*Spartina spartinae*) and sea daisy (*Borrchia frutescens*) (Forys 1995, Perry 2006, Faulhaber et al. 2008).

Lower Keys marsh rabbits spend most of their lives in 1 patch of suitable vegetation but can move to other patches (Forys and Humphrey 1996). Populations of LKMR in suitable habitat patches co-exist as a metapopulation relying on dispersal for population viability (Forys 1995, Forys and Humphrey 1996). Dispersing subadult LKMRs drive the metapopulation by making one-way movements up to 2 km away from their natal patches (Forys and Humphrey 1996).

The Lower Florida Keys are a group of islands forming the western end of the Florida Keys archipelago, beginning at Big Pine Key on Highway 1 and terminating with the island of Key West (Fig. 1.1). This group of islands is between 23.5° and 25.5° north latitude, several minutes north of the Tropic of Cancer (23° 26' 22" north latitude). Their proximity to the Gulf Stream and the tempering effects of the Gulf of Mexico give the islands their mild, tropical-maritime climate (Chen and Gerber 1990). High

This thesis follows the style of the Journal of Wildlife Management.

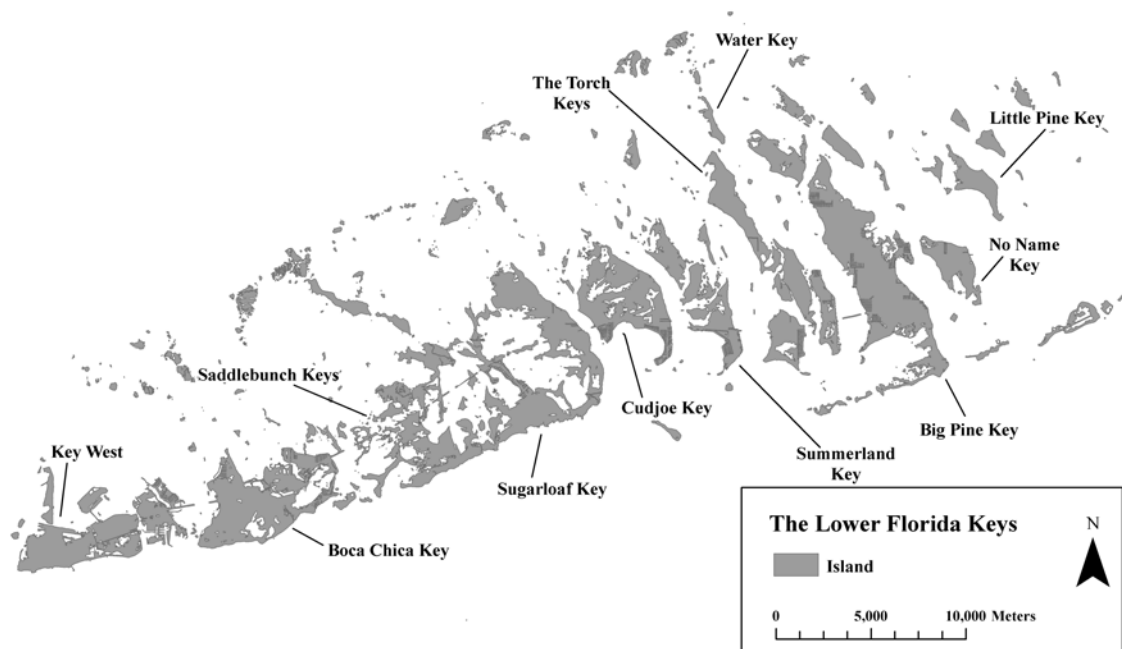


Figure 1.1. The Lower Florida Keys, Florida, USA.

temperatures during the summer averaged 32.2° C and lows averaged 26.1° C. High temperatures during the winter averaged 23.9° C and lows averaged 18.3° C (National Climatic Data Center 2008). Summer rainfall averaged 11.2 cm while winter rainfall averaged 5.3 cm (National Climatic Data Center 2008). As elevation increases in the Florida Keys, vegetation types transitioned from red mangroves (*Rhizophora mangle*), to black mangroves (*Avicennia gerimans*), to white mangroves (*Laguncularia racemosa*), to saltmarsh-buttonwood transition zone, to upland areas of hammocks and pinelands (Faulhaber 2003).

The U.S. Fish and Wildlife Service (USFWS) listed the LKMR as a federally endangered subspecies in 1990, primarily due to habitat loss from human activities (USFWS 1985, USFWS 1990); however, road mortality, predation, and habitat loss from woody encroachment and sea-level rise also were believed to contribute to the species' decline (Forys 1995, USFWS 1999, Perry 2006, Faulhaber et al. 2007). Hurricanes also are a threat to the persistence of the LKMR. They decrease LKMR abundance by direct mortality (i.e., drowning and blunt impact trauma) and indirect mortality (i.e. habitat destruction). Researchers recorded >71% mortality of radio-collared LKMRs due to Hurricane Wilma's storm surge in 2005 (N. D. Perry, Utah Division of Wildlife Resources, Unpublished data).

The last population estimate of 100 adult LKMR was calculated in 1993 (Forys 1995) and recent surveys documented a 27% decline in patch occupancy since 2003 (USFWS 2007). Although development in LKMR habitat was halted (USFWS 2007), it appears that other factors such as predation,

sea-level rise, woody encroachment, and road mortality will continue to threaten the LKMR metapopulation.

RESEARCH OBJECTIVES

The overall study objectives were to estimate the size of the current LKMR metapopulation and quantify changes in LKMR habitat over the longest time period possible. A population estimate was needed for several important reasons. First, continued and timely abundance estimates are vital for the recovery of endangered species. The requirements for downlisting a species (removal from an endangered status to a threatened status) often include target population sizes above which they are unlikely to become extinct in the near future (Foin et al. 1998, USFWS 2002). Second, wildlife managers need current population estimates to measure a population's response to management actions (Sparrow 1994, Foin et al. 1998), such as prescribed fire, translocations, and predator control which have recently been used to increase LKMR populations. Third, a population estimate should include recently discovered LKMR habitat (Faulhaber 2003). Fourth, the populations of genetic distinct clades need to be estimated separately (Crouse et al. 2009). And finally, the long-term success of translocated populations of rabbits should be evaluated (Faulhaber et al. 2006). Chapter II in this thesis addresses these research needs.

Quantifying the change in LKMR habitat over the longest time period possible was imperative for establishing and understanding long-term habitat availability. This understanding also is important for determining causes of historical population declines as well as designing and implementing successful recovery plans (Pringle 2009). Chapter III in this thesis addresses these research needs.

CHAPTER II

POPULATION ESTIMATION AND MONITORING OF THE LOWER KEYS MARSH RABBIT

SYNOPSIS

I conducted a range-wide pellet survey and a mark-recapture study to estimate the endangered Lower Keys marsh rabbit (LKMR; *Sylvilagus palustris hefneri*) population. I trapped 83 rabbits and used Program MARK to evaluate 5 modern closed population models and selected the model that best represented the data. I considered the variation in behavioral response model the best model and correlated ($r^2 = 0.913$) its estimates to pellet densities in patches. From the prediction equation, I generated a range-wide population estimate of 317, a western clade population of 257, an eastern clade population of 25, and translocated LKMR populations of 35 and 0 on Little Pine and Water keys, respectively. Due to the low estimate of the eastern clade population, special effort should be expended to avoid loss of genetic diversity. This study was the most extensive estimate of the LKMR population to date and considering the extent of the survey and the inclusion of all age groups in the estimate, it appears that the LKMR population has declined since the last population estimate in 1991–1993. Translocation sites should be chosen carefully so that translocations will attain long-term success. The prediction equation developed during my study provides managers a quick, efficient, and non-invasive method to estimate LKMR abundance from pellet counts.

INTRODUCTION

The Lower Keys marsh rabbit (LKMR; *Sylvilagus palustris hefneri*) is a subspecies of *S. palustris* endemic to the Lower Florida Keys (Fig. 2.1). The U.S. Fish and Wildlife Service (USFWS) listed the LKMR as a federally endangered subspecies in 1990, primarily due to habitat loss from human activities (USFWS 1985, USFWS 1990); however, road mortality, predation, and habitat loss from woody encroachment and sea-level rise also were believed to contribute to the species' decline (Forys 1995, USFWS 1999, Perry 2006, Faulhaber et al. 2007).

The LKMR has been known to occupy saltmarsh–buttonwood (*Conocarpus erectus*) transition zones, brackish and freshwater wetlands, and coastal beach berms (Forys and Humphrey 1996, Faulhaber et al. 2006, Faulhaber et al. 2008). These areas of suitable vegetation were found in patches ranging in size from <0.1 to 51.2 ha and scattered throughout 29 islands in the Lower Florida Keys (Forys and Humphrey 1996, Faulhaber 2003).

The patchy distribution of their habitat, limited funding, incomplete surveys, lack of rigorous methodologies, and low capture success have restricted the amount and quality of information on the size of the LKMR population. Using unspecified methodologies on a limited number of patches, the

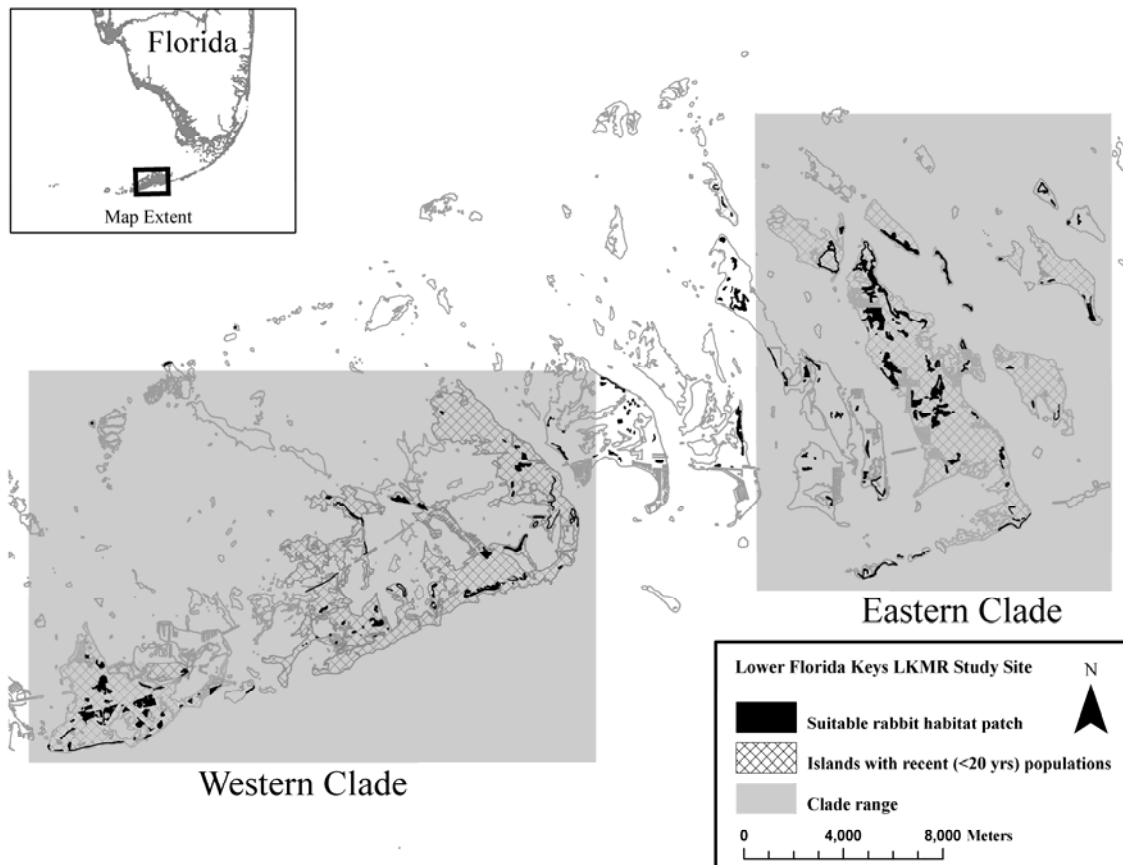


Figure 2.1. Lower Florida Keys Lower Keys marsh rabbit study area showing suitable rabbit habitat patches as well as western and eastern clade boundaries, Lower Florida Keys, USA.

population was loosely estimated to be 500, 259, and 200–400 rabbits in 1976, 1984, and 1988, respectively (Howe 1988). The most recent estimate of the population of 100–300 LKMRs conducted during 1991–1993 on 39 patches was generated using mean number of pellets/area, the time between pellet removal and pellet counting, and rabbit defecation rates (Forys 1995).

Continued and timely abundance estimates are vital for the recovery of endangered species. The requirements for downlisting a species (removal from an endangered status to a threatened status) often include target population sizes above which they are unlikely to become extinct in the near future (Foin et al. 1998, USFWS 2002). Wildlife managers also need current population estimates to measure a population's response to management actions (Sparrow 1994, Foin et al. 1998), such as prescribed fire, translocations, and predator control which have recently been used to increase LKMR populations.

There has been an expressed need for a current range-wide estimate and a method for monitoring the LKMR population. This need has been heightened by the discovery of additional LKMR habitat, a genetic division of the population, recent patch occupancy monitoring, the translocations of rabbits, and

the incidence of hurricanes (Faulhaber 2003, Faulhaber et al. 2006, USFWS 2007, Crouse et al. 2009). During the last effort to estimate the population (1991–1993) there were 59 known LKMR patches (234 ha). Currently >150 patches (>624.7 ha) of habitat have been delineated (Faulhaber 2003). Additionally, Crouse et al. (2009) used mitochondrial DNA analysis to conclude there was a genetic division between eastern and western populations (Crouse et al. 2009) (Fig. 2.1). This was not accounted for in previous population estimates and viability analyses. Furthermore, recent surveys documented a 27% decline in patch occupancy since 2003 (USFWS 2007) and researchers recorded >71% mortality of radio-collared LKMRs due to Hurricane Wilma's storm surge in 2005 (N. D. Perry, Utah Division of Wildlife Resources, Unpublished data). There is also a need to continue to monitor progress of translocations previously deemed successful (Faulhaber et al. 2006).

Several methods have been used to estimate lagomorph populations including: line transects, mark-recapture estimates, and pellet counts (Eberhardt et al. 1963, Krebs et al. 1987, Fa et al. 1999, Palomares 2001, Mills et al. 2005). Pellet counts are noninvasive, efficient, and cheap. They have been repeatedly used to estimate lagomorph populations; however, they give only an index of the population (Krebs et al. 1987, Anderson 2001, Murray et al. 2002). A more rigorous method to monitor lagomorphs is to establish a correlation between lagomorph abundance and lagomorph pellet density (Wood 1988, Krebs et al. 2001, Murray et al. 2002, Homyack et al. 2006, McCann et al. 2008). This methodology has been shown to be effective at estimating populations with low population densities like the LKMR (Murray et al. 2002).

Densities estimated from mark-recapture methods likely provide more accurate population estimates than minimum number alive estimates commonly used to relate pellets to capture estimates (Homyack et al. 2006). When studies have used different methods to estimate rabbit densities from mark-recapture efforts, they did not account for varying capture probabilities (Krebs et al. 1987, Forsy 1995, Forsy and Humphrey 1997, Mills et al. 2005, Homyack et al. 2006). Modern closed-population models, incorporating time variation, behavioral response, and heterogeneity in the capture probabilities are more robust than models in which the capture probabilities are fixed (Chao and Huggins 2005).

My goals for this study were to generate a population estimate for the LKMR metapopulation, develop a low cost monitoring program for this endangered sub-species, and evaluate the long-term success of previous translocations. Specifically, my objectives were to 1) systematically count pellets in every viable habitat patch, 2) generate mark-recapture population estimates for a subset of patches, 3) correlate mark-recapture population estimates to pellet density, 4) use the statistical relationship between pellets and population estimates to generate estimates for the entire population, each of the 2 genetically distinct clades, and the translocated populations, and 5) determine the optimal number of sample units to maximize sampling effort while minimizing sample variance.

STUDY AREA

The Lower Florida Keys are a group of islands forming the western end of the Florida Keys archipelago, beginning at Big Pine Key and terminating with the island of Key West (Fig. 2.1). This group of islands is between 23.5° and 25.5° north latitude, several minutes north of the Tropic of Cancer (23° 26' 22" north latitude). Their proximity to the Gulf Stream and the tempering effects of the Gulf of Mexico give the islands their mild, tropical-maritime climate (Chen and Gerber 1990). High temperatures during the summer averaged 32.2° C and lows averaged 26.1° C. High temperatures during the winter averaged 23.9° C and lows averaged 18.3° C (National Climatic Data Center 2008). Summer rainfall averaged 11.2 cm while winter rainfall averaged 5.3 cm (National Climatic Data Center 2008).

As elevation increases in the Florida Keys, vegetation types transitioned from red mangroves (*Rhizophora mangle*), to black mangroves (*Avicennia gerimans*), to white mangroves (*Laguncularia racemosa*), to saltmarsh–buttonwood transition zone, and to upland areas of hammocks and pinelands (Faulhaber 2003). LKMR habitat was defined by 3 broad land cover types: saltmarsh–buttonwood transition zones, wetlands, and coastal beach berms (Forys and Humphrey 1996, Faulhaber et al. 2007, Faulhaber et al. 2008). The saltmarsh–buttonwood transition zones (at the lowest elevation) included open areas of low halophytic vegetation that are inundated daily with saltwater. Dominant plant species found in this zone included glasswort (*Salicornia spp.*), key grass (*Monanthochloe littoralis*), and saltwort (*Batis maritima*). At slightly higher elevations, salt-tolerant plants such as sea daisy (*Borrichia frutescens*), seashore dropseed (*Sporobolus virginicus*), gulf cord grass (*Spartina spartinae*), saltmarsh fringe-rush (*Fimbristylis castanea*), saltmeadow cordgrass (*Spartina patens*), and saltgrass (*Distichilis spicata*) were present (Faulhaber et al. 2008). Buttonwood was present but not dominant, leaving the mid-elevation saltmarsh fairly free of woody species. At the higher elevations within the saltmarsh–buttonwood transition zones, buttonwood is the dominant woody species and in most LKMR habitat patches only small patches of herbaceous plants composed of seashore dropseed, sea daisy, sea oxeye (*Borrichia arborescens*), and saltgrass were present. Wetlands occurred in relatively low-lying areas where the water table was close to the surface or in depressions that collect precipitation. The understory of wetlands can be composed of open expanses of sedges (Cyperaceae), gulf coast spikerush (*Eleocharis cellulose*), or saw grass (*Cladium jamaicense*) and saw palmetto (*Serenoa repens*) with an overstory of broadleaf trees such as buttonwood, red mangrove, white mangrove, poisonwood (*Metopium toxiferum*), and wax myrtle (*Myrica cerifera*) (Ross et al. 1992). During this study small areas of gulf coast spikerush were the only herbaceous component of these wetlands. Coastal beach berm vegetation was composed of trees, shrubs, and xerophytic plants, growing on accumulations of wind-driven material situated parallel to coastlines (Florida Natural Areas Inventory 1990). Coastal beach berm woody vegetation included seagrape (*Coccoloba uvifera*), Jamaica dogwood (*Piscidia piscipula*), blolly (*Guapira discolor*), gumbo limbo (*Bursera simaruba*), seven year apple (*Casasia clusiifolia*), limber caper (*Capparis flexuosa*), blackbead

(*Pithecellobium guadalupense*), Spanish stopper (*Eugenia foetida*), and Bahama nightshade (*Solanum bahamense*) (Ross et al. 1992). Grasses and sedges also sparsely populated the berms.

METHODS

Pellet Counts and Pellet Density Estimation

I used Faulhaber's (2003) habitat patch delineations for this study. I systematically sampled these patches using a grid with a random start. I created a 42.8 km x 23.5 km grid with 30 m x 30 m node spacing that encompassed the entire lower Florida Keys and contained approximately 1 million nodes in ArcMap 9.1 (Environmental Systems Research Institute ArcMap 9.1, Redlands, California, USA) using Hawth's Analysis Tools ver. 3.27 (Beyer 2006). I uploaded and located grid nodes within LKMR habitat with a *global positioning system* (GPS) unit. I placed a 1-m radius circular plot (Sample Unit [SU]) on each node and recorded the total number of LKMR pellets. Compared to rectangular plots, circular plots can be used with reasonable confidence to predict lagomorph numbers when pellet densities are low (McKelvey et al. 2002, Murray et al. 2002). I used uncleared plots because LKMR pellets have been shown to degrade in 1 rainy season (Howe 1988) and degradation rates <1 year allows for annual estimates from uncleared plots (Murray et al. 2002, Prugh and Krebs 2004). I conducted follow-up counts (± 30 days) of 12 patches used in the mark-recapture study to increase the probability that pellets and density estimates were conducted in a closed system.

I calculated mean fecal pellet density for each habitat patch by dividing the sum of pellets counted in the patch's SUs by the number of SUs sampled within the patch. I then stratified patches into 3 density categories at natural discontinuities in the data (low 0.1–0.9 pellets/SU, medium 1.0–4.9 pellets/SU, and high ≥ 5 pellets/SU). I then randomly selected 12 patches (4 from each of the 3 density categories) for a mark-recapture study to insure that trapping effort was spread over the range of rabbit pellet densities.

Trapping

I trapped for 5 nights in each of 12 randomly selected patches using double-door Tomahawk live traps (Model No. 107, Tomahawk, Wisconsin, USA). I reinforced the sides and doors of the traps with plywood and hardware cloth to protect trapped LKMRs per Faulhaber et al. (2006). Depending on the size of the patch, I preferentially set 17–34 live traps spread throughout each LKMR patch. I set the traps to capture in the evening and checked and closed all traps the following morning as suggested in the American Society of Mammalogists' Guidelines for the Capture, Handling, and Care of Mammals (Animal Care and Use Committee 1989). I restrained LKMRs by wrapping their hindquarters in a thin towel and placed a hood to cover their eyes to reduce stress as approved by the Texas A&M University Institutional Animal Care and Use Committee (Animal Use Protocol No. 2007-76). I recorded weight, sex, right ear length, right hind foot length, total body length, unique markings, and presence or absence of ectoparasites

on each LKMR captured. I photographed each rabbit and marked captured rabbits using fur clipping as a temporary unique marker (Cox and Smith 1990).

Density Estimation

I translated capture occasions into encounter histories and imported them into Program MARK (White and Burnham 1999). Based on rabbit biology, I selected 5 modern closed population models (Table 2.1): 1) behavioral response (M_b) where probability of capture and probability of recapture were different, 2) time (M_t) where probability of capture and recapture were the same but varied by night, 3) behavioral response and time (M_{bt}) where probability of capture and probability of recapture were different and varied by night, 4) trap density and sex (Model $p[\text{trap saturation}] + c[\text{sex}]$) where probability of capture was a function of trap saturation and probability of recapture was a function of sex, and 5) weight (Model p and $c[\text{standard weight}]$), where probability of capture and recapture were a function of weight (Chao and Huggins 2005). I evaluated each model in Program MARK and selected the model with the lowest AICc (Akaike's information criterion with a second order correction for small sample size) values to generate population estimates. Marked rabbits moved across a narrow, overgrown road that divided Patches 1 and 2 so I therefore combined the 2 patches into 1 patch for density estimation and subsequent regression analysis.

Regression Analysis

I correlated rabbit density estimates from the best mark-recapture model to mean patch pellet densities. I evaluated 2 linear regressions, ordinary least-squares regression and regression through the origin. I was interested to see if both methods provided similar results such as those found by Krebs et al. (1987). Regression through the origin can be used if there is a strong *a priori* reason for believing that $Y = 0$ when $X = 0$ (Eisenhauer 2003). In my case, I evaluated regression through the origin because it is intuitive that when there are no rabbits at a patch, there are no pellets. After I obtained both regression equations using Program SPSS 15.0.1.1 (SPSS Inc. Chicago, Illinois, USA), I entered the range-wide pellet data from the 150 patch survey to obtain estimates for the range-wide, the eastern and western, and the tranlocated populations. Using SPSS, I inserted the mean patch pellet densities from the range-wide surveys into both regression equations to generate 95% CIs for each patch.

Sampling effort evaluation

I used PopTools (Hood 2008) to randomly resample pellet totals of all SUs. I used resamples to generate means and standard errors for all plots based on simulated sampling of 1–100 SU for each of the 150 patches. I looked for natural breaks in the standard errors to determine the optimal number of sample units to maximize sampling effort while minimizing sample variance. I changed the sign of the standard errors to visually interpret the plot.

Table 2.1. Modern closed population model descriptions used in Program MARK.

Model name	Description
M_b	variation in behavioral response such as trap-shy or trap-happy individuals in the capture and recapture probabilities
M_{tb}	variation in behavioral response and variation by time in the capture and recapture probabilities
$p(\text{trap saturation})+c(\text{sex})$	trap density influencing capture probability and sex influencing recapture probability
M_t	daily variation in the capture probability
p and $c(\text{standard weight})$	weight of the animal influencing the capture and recapture probability

RESULTS

I searched for pellets at 6,934 SUs located within 150 LKMR habitat patches from December 2007–March 2008. I found pellets in 73 patches with a mean pellet density of 1.6 ($SE = 3.50$) pellets/m². Mean pellet density was initially 2.0 ($SE = 2.18$) pellets/m² for the 12 patches that were trapped for rabbits. My follow-up surveys (June–July 2008) of these 12 patches yielded mean pellet density of 6.7 ($SE = 13.06$) pellets/m². I trapped 12 patches for a total of 1,123 trap nights in May–July 2008. I captured 83 unique rabbits in 9 patches (Table 2.2). I selected model M_b (variation in behavioral response) to estimate rabbit densities in those patches. I considered Model M_b (Table 2.3) the best model and discarded all other models because they had AIC values >2 from the best model and were unlikely representations of the data (Burnham and Anderson 2002, Norman et al. 2004). Model M_b yielded patch population estimates from 6.5–53.7 individuals (Table 2.2).

Table 2.2. Results of follow-up pellet counts, unique Lower Keys marsh rabbit captures per patch, patch area (ha), and model M_b estimates of rabbits per patch based on 11 Lower Keys marsh rabbit habitat patch surveys and trapping, Lower Florida Keys, USA, 2008.

Patch	Mean pellets/m ²	LKMR unique captures/patch	Patch area (ha)	Model M_b estimates of rabbits/patch
1&2	1.8	7	3.49	11.4
5	0.8	4	1.08	6.5
10	44.5	11	0.44	17.9
14	4.7	12	1.38	19.5
36	1.9	5	10.62	8.1
90	0.1	0	4.56	Na*
138	0.1	0	5.01	Na*
140	0	0	1.34	Na*
157	4.3	6	1.91	9.8
160	19.6	33	2.82	53.7
170	1.9	5	0.89	9.4

*Unable to calculate a Huggins model estimate since trap success = 0.

Table 2.3. Results from the 5 Huggins closed population models: M_b , M_{tb} , $p(\text{trap saturation})+c(\text{sex})$, M_t , and $p(\text{standard weight})$.

Model	K	Deviance	AICc	Delta AICc	AICc weight
M_b^a	2	522.1	526.1	0.000	0.7767
M_{tb}^b	8	513.5	529.9	3.723	0.1208
$p(\text{trap saturation})+c(\text{sex})^c$	4	522.1	530.2	4.061	0.1020
M_t^d	5	530.5	540.6	14.50	0.0006
p and $c(\text{standard weight})^e$	2	548.9	552.9	26.79	0.0000

^a Model M_b accounted for variation in behavioral response such as trap-shy or trap-happy individuals in the capture and recapture probabilities

^b Model M_{tb} accounted for variation in behavioral response and variation by time in the capture and recapture probabilities.

^c Model $p(\text{trap saturation})+c(\text{sex})$ accounted for trap density influencing capture probability and sex influencing recapture probability

^d Model M_t accounted for daily variation in the capture probability

^e Model p and $c(\text{standard weight})$ accounted for the weight of the animal and hence the age of the animal in the capture and recapture probability

Mean pellet density and estimates from model M_b were significantly correlated (2-tailed test; $P < 0.001$). I developed 2 predictive equations from regressing pellet density and rabbit abundance estimates; for the ordinary least-squares regression, $\text{Rabbits/ha} = 2.83 + 0.85 * \text{Pellets/m}^2$, with a model fit of $r^2 = 0.907$ (SE of slope = 0.091; Fig. 2.2) and for the regression through the origin, $\text{Rabbits/ha} = 0.95 * \text{Pellets/m}^2$, with a model fit of $r^2 = 0.913$ (SE of slope = 0.092; Fig. 2.3). Using the ordinary least-squares regression, I estimated the range-wide population was 2058 individuals (95% CI , 239–3939) with the 73 occupied patches averaging 4.19 rabbits/ha. Using the regression through the origin, I estimated the range-wide population was 317 individuals (95% CI , 248–383) with the 73 occupied patches averaging 1.53 rabbits/ha, the western clade population was 257 individuals (95% CI , 199–308), the eastern clade population was 25 individuals (95% CI , 22–33), the translocated Little Pine Key population (Faulhaber et al. 2006) was 35 individuals (95% CI , 27–42), and the translocated Water Key population (Faulhaber et al. 2006) to have 0 individuals (95% CI , 0–0).

I randomly resampled pellet totals of all 6,934 SUs and generated means and standard errors for all plots based on hypothetical sampling of 1–100 SU/patch. There was not a distinct pattern to the means, however, the standard errors were highly variable for plots with 1–19 sample units (Fig 2.4) after which they stabilized and began to plateau.

DISCUSSION

My pellet surveys were significantly correlated to LKMR density estimates and my regression through the origin generated LKMR densities that were biologically reasonable. The most appropriate equation for predicting lagomorph numbers via pellet plots should not only have high predictive power but also possess biological relevance and generality and ease of application (Murray et al. 2002). Additionally,

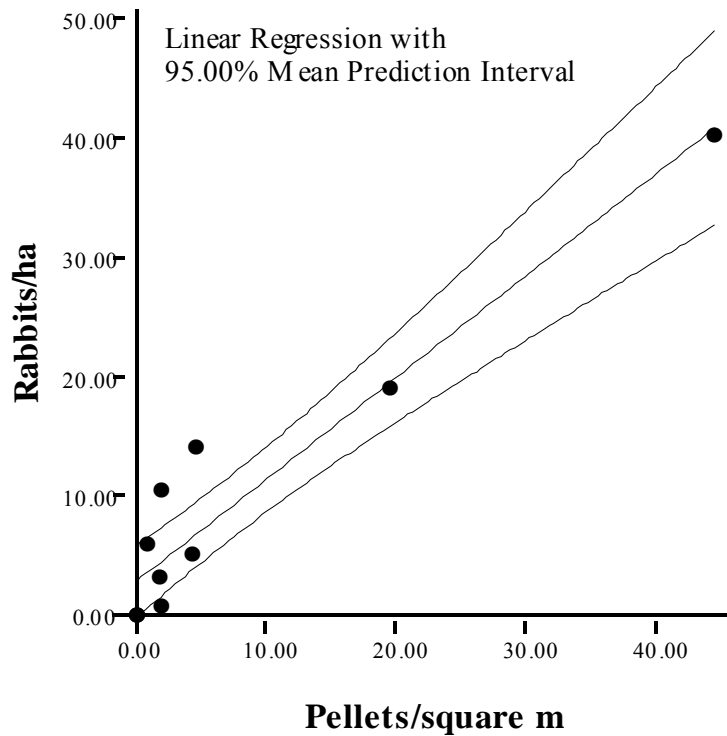


Figure 2.2. Relationship between density of Lower Keys marsh rabbit fecal pellets and density of Lower Keys marsh rabbits with intercept included in the regression. Pellet densities and rabbit densities were estimated within 11 habitat patches during May–July 2008, Lower Florida Keys, USA.

the correlation slope of approximately 1 was comparable to other pellet density rabbit abundance studies (Krebs et al. 1987, Murray et al. 2002). However, regression through the origin does have a drawback as the r^2 value cannot be compared to the r^2 value of an ordinary least-squares model. The square of the sample correlation between observed and predicted values gives an interpretable measure of the quality of a regression through the origin, but does not help in comparing regressions through the origin with ordinary least squares regressions (Eisenhauer 2003).

The ordinary least-squares regression and the regression through the origin did not produce the same results. Without setting the intercept to 0, I predicted rabbits in patches that did not contain pellets. If a patch did not contain pellets, the predicted rabbit population was 2.83 multiplied by the patch size (ha) which certainly overestimated patch and overall rabbit densities. I therefore rejected the ordinary least-squares regression and I used the regression through the origin equation to estimate the LKMR range-wide population. My mean rabbit density of 1.53 rabbits/ha for occupied patches is larger than the most recent estimate (average 1.3 rabbits/ha, range from 0.86 to 2.26 rabbits/ha) but well under normal *Sylvilagus* population densities (Edwards and Eberhardt 1967, Forys 1995). Nonetheless, my range-wide estimate (317 individuals [95% CI, 248–383]) was relatively close to previous estimates. However, this does not

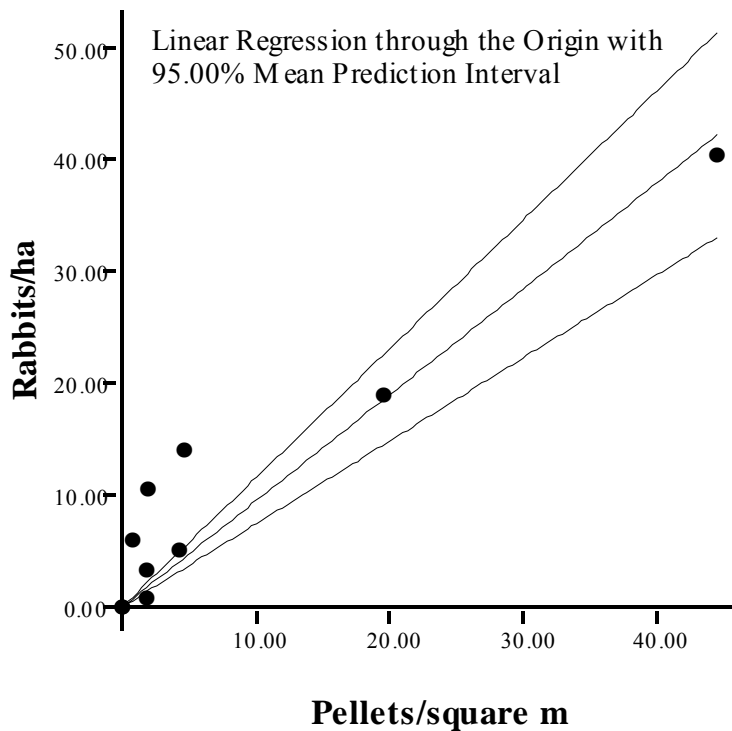


Figure 2.3. Relationship between density of Lower Keys marsh rabbit fecal pellets and density of Lower Keys marsh rabbits with intercept set through the origin. Pellet densities and rabbit densities were estimated within 11 habitat patches during May–July 2008, Lower Florida Keys, USA.

suggest the LKMR population is stable. Instead, my estimate was a function of the breadth of the survey. This study was the most extensive estimate of the LKMR population to date. My estimate was based upon on a sampling area >260% any previous estimate. Additionally, my range-wide population estimate was larger than the most recent estimate (100–300 individuals [Forys 1995]) because I included all rabbit age groups whereas the previous survey includes only adults. Considering the population estimate, the extent of the survey, the inclusion of all age groups in the estimate, and the results from USFWS occupancy surveys, a case can be made that the LKMR population has declined since the last population estimate in 1993.

My results indicated large disparities between western (257 individuals) and eastern clade (25 individuals) LKMR populations. Crouse et al. (2009) suggested these clades had the possibility of possessing distinct evolutionary potential so effort should be placed on recovering the eastern clade. I noticed during my range-wide surveys that patches in the eastern clade contained virtually no herbaceous material. Within the saltmarsh habitat, this was likely due to the woody encroachment of buttonwood trees (Perry 2006). Within the freshwater marsh habitat, it is possible that standing storm surge water and salinification of the soil as well as mosquito ditches, which drained fresh water and allowed for greater

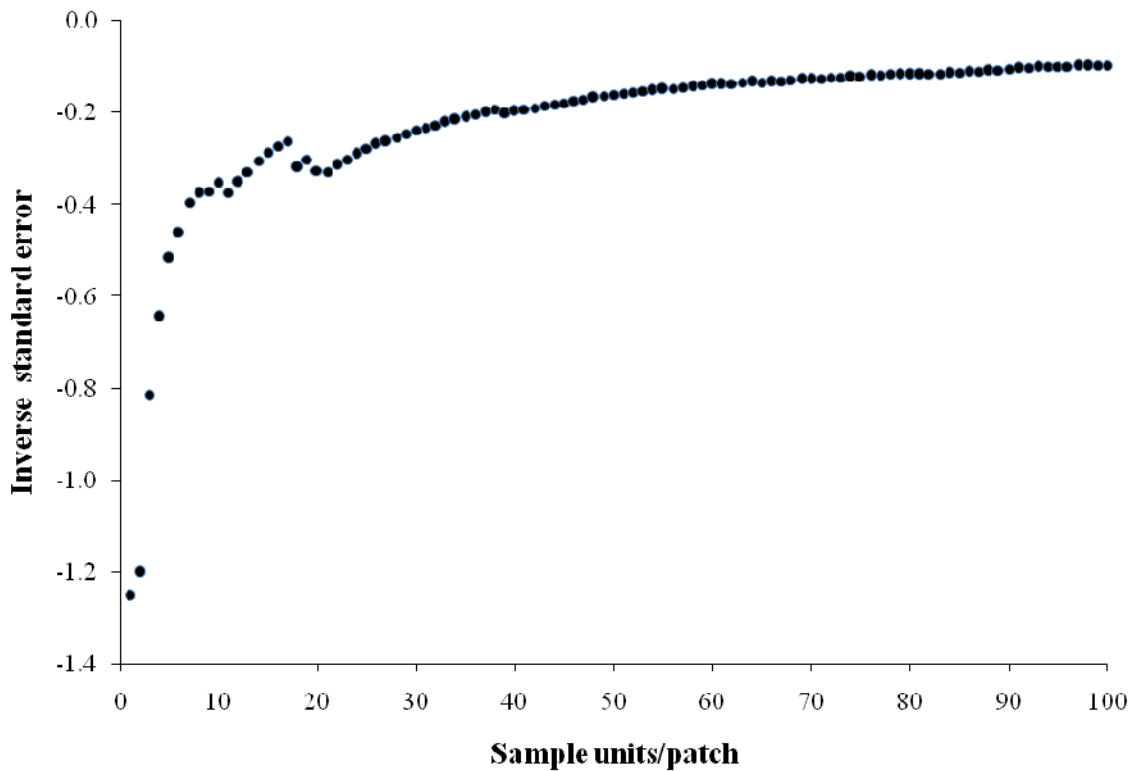


Figure 2.4. Plot of inverse standard error of mean pellets/SU for hypothetical patches with 1–100 sample units sampled 150 times from 6,934 sample units.

saltwater intrusion during hurricanes, have reduced herbaceous vegetation (Bradley 2006, USFWS 2006, USFWS 2007). The range of the eastern clade includes islands of higher elevation and more freshwater habitat types (approximately 38%) than the western clade (approximately 3%) for LKMRs, possibly explaining the lower population of the eastern clade. Regardless of the reason for its low abundance, special effort should be placed on recovering the eastern clade population if genetic diversity is to be maintained.

I estimated the western clade's Boca Chica population at 211 individuals (95% *CI*, 163–253); almost 67% of the entire LKMR population and 82% of the western clade's population. Because the majority of both the western clade and the entire LKMR population are located on the single island of Boca Chica, any event which impacts this island should be of concern.

The translocated LKMR population on Little Pine Key (Faulhaber et al. 2006) appeared to be successful. Faulhaber et al. (2006) released 11 western clade LKMRs (5M, 6F) on Little Pine Key in early 2002 and later released an eastern clade female in October of the same year. From this founder population, I estimated 35 rabbits. Unfortunately, translocations have not all been successful. Faulhaber et al. (2006) also released 7 western clade LKMRs (3M, 4F) on Water Key in 2004. I did not find

evidence of LKMRs on Water Key during my surveys. Although preliminary results of the Water Key translocation were deemed successful based on high survivorship, release-site fidelity, and successful reproduction, I did not find evidence of a population (Faulhaber et al. 2006). Water Key is smaller (92 ha) than Little Pine Key (325 ha), contains no uplands, and during high tides, only a portion of the island (<1 ha) is not submerged (unpublished data). This fact could have been exacerbated by Hurricane Wilma (24 October 2005) which could have reduced the number of rabbits on Water Key below a sustainable level.

The plot of the standard error against the increasing number of SUs within a hypothetical patch suggests that the standard error stabilizes when sample effort is 20–40 SU/patch. This suggests that patches with less than 20 SU were undersampled while patches with more than 40 sample units were oversampled.

MANAGEMENT RECOMMENDATIONS

My regression through the origin equation provides managers with an easily applied, highly predictive tool for estimating LKMR densities from pellet counts in the Lower Florida Keys. My regression equation does not depend upon defecation rates, which not only vary by particular rabbit but can vary from day to day for the same rabbit (Cochran and Stains 1961). I recommend this survey method be implemented each year with 2 modifications. I suggest that patches be sampled using a variable number of SUs dependent upon the area of the patch. If 20 SUs are randomly placed in patches <1ha, 20 SUs are randomly placed in 1–2 ha patches, and 40 SUs are randomly placed in patches >2 ha, sample effort will not be wasted on large patches and small patches will be sampled intensively, thereby reducing the variation inherent in small sample sizes. I also recommend that LKMR surveys be conducted in both patches delineated from the 2006 data (see Chapter III) as well as in the currently surveyed patches (Faulhaber 2003). Using both delineations will improve the probability that all potential LKMR habitat patches will be surveyed and the LKMR population will be accurately monitored. This method can be completed with approximately 500 hours of work, giving managers yearly population estimates of the LKMR. Additionally, I recommend that special effort should be expended on the eastern clade, if extinction is to be avoided. Finally, Water Key should not be viewed as a viable translocation site and future translocation sites should be chosen carefully and prepared for translocations (habitat enhancement/predator removal) so that translocations will attain long-term success.

CHAPTER III
QUANTITATIVE ASSESSMENT OF CURRENT AND HISTORIC LOWER KEYS MARSH RABBIT
HABITAT

SYNOPSIS

Habitat loss and fragmentation from human population growth and development has threatened the existence of the endangered Lower Keys marsh rabbit (LKMR; *Sylvilagus palustris hefneri*). Fragmentation affects landscape composition, structure, and function and therefore it is vitally important to quantify its effect on LKMR habitat. I systematically delineated and compared potential LKMR habitat using 1959 and 2006 aerial photographs, as well as compared habitat loss and fragmentation on a developed island and an undeveloped island. Comparing 1959 to 2006 I found 38 more habitat patches, class area decreased by 49.0%, and mean patch size decreased by 44.3%. Mean shape index increased by 4.2% and mean proximity index decreased by 13%. Both the 1959 and 2006 connectance indices were low while the 2006 set decreased 12.1%. I observed the same patterns of habitat loss and fragmentation on both the developed and undeveloped islands as I did in the range-wide landscape analysis. Habitat loss and fragmentation by development have directly endangered the LKMR; however, sea level rise and woody encroachment also could have historically caused habitat loss and fragmentation. Although development in LKMR habitat was halted, sea-level rise and woody encroachment could continue to alter LKMR habitat.

INTRODUCTION

Habitat loss and fragmentation is the prevalent trajectory of landscape change in human-dominated regions of the world, and is increasingly being recognized as a major cause of declining biodiversity (Wilcox and Murphy 1985, Noss and Cooperrider 1994, Czech et al. 2000, Sole 2004, Hanski 2005). Habitat loss and fragmentation from human population growth and development has threatened the existence of several of the 31 federally endangered, threatened, or candidate species that occur in the Lower Florida Keys (U.S. Fish and Wildlife Service [USFWS] 2008).

One particular species of interest in this region, the Lower Keys marsh rabbit (LKMR; *Sylvilagus palustris hefneri*), a subspecies of *S. palustris*, was listed as federally endangered by the USFWS in 1990 (USFWS 1990). LKMRs historically ranged from Key West to Big Pine Key and in recent history a decline in rabbit numbers was reported (de Pourtales 1877, Howe 1988). At the time of its listing, habitat loss due to human development was the primary factor for the decline of this subspecies (USFWS 1985, USFWS 1990). Between 1979 and 1999, it is believed that more than half of suitable LKMR habitat was lost due to human modification of the landscape (USFWS 1999). Road mortality and predation have been

cited as additional factors contributing to the species' decline (Howe 1988, Forys 1995, USFWS 1999, Perry 2006).

Habitat degradation due to woody encroachment and sea-level rise also has changed the frequency of vegetation types that are an important component of LKMR habitat. There have been drastic changes in the distribution of vegetative communities, as shown by comparing historic accounts and aerial photographs to current satellite images (Gallagher 1991). This is in part due to the fragmentation of natural vegetation communities by dredging and filling operations that proliferated in the Lower Florida Keys during the mid-20th century to create ocean front property. Additionally, an increase in sea-level also could have changed the vegetative structure of the Lower Florida Keys and hastened the decline of the LKMR. In fact, population modeling has suggested that future sea-level rise will continue to decrease the amount of potential rabbit habitat and in turn the LKMR population (LaFever 2006, LaFever et al. 2007).

The LKMR has been known to occupy patches of saltmarsh-buttonwood (*Conocarpus erectus*) transition zone, brackish and freshwater wetland, and coastal beach berm (Forys and Humphrey 1996, Faulhaber et al. 2008). Within these vegetation types, the LKMR has been associated with dense herbaceous plants such as seashore dropseed (*Sporobolus virginicus*), gulf cord grass (*Spartina spartinae*) and sea daisy (*Borrchia frutescens*) (Forys 1995, Perry 2006, Faulhaber et al. 2008).

Lower Keys marsh rabbits spend most of their lives in 1 patch of suitable vegetation but can move to other patches (Forys and Humphrey 1996). Populations of LKMR in suitable habitat patches co-exist as a metapopulation relying on dispersal for population viability (Forys 1995, Forys and Humphrey 1996). Metapopulations can be defined as a group of populations existing in discrete areas with some demographic or genetic connection among them (Wells and Richmond 1995). The spatial configuration of habitat is important for a metapopulation as local extinctions are offset by colonizations from nearby patches. Dispersing subadult LKMRs drive the metapopulation by making one-way movements up to 2 km away from their natal patches (Forys and Humphrey 1996). Eleven (11 M, 6 F) of 17 radiomarked subadult LKMRs made movements greater than the average diameter of the home range of adult rabbits (Forys and Humphrey 1996). Only 1 male and 5 females did not exceed this distance (Forys and Humphrey 1996). As the distance between patches increases, the probability that an animal can successfully traverse the less favorable landscape between the two decreases. Indeed, distance between patches has been shown to be the best predictor of whether a patch will receive LKMR emigrants, regardless of the composition of the surroundings areas (Forys and Humphrey 1999).

Habitat fragmentation is a landscape-level process in which contiguous habitat is progressively sub-divided into smaller and more isolated habitat fragments as a result of both natural processes and human land-use activities (McGarigal and McComb 1995). Fragmentation affects landscape composition, structure, and function and therefore it is vitally important to quantify its effect on LKMR habitat. Landscape metrics can be used to understand how patches relate to each other spatially and aspects of

landscape structure (Hargis et al. 1998, McGarigal et al. 2002). Class-level metrics are a sub-set of landscape metrics which are either averaged values or weighted-averaged values integrated over a collective group (a class) of habitat patches. Class-level metrics are primarily concerned with the amount and distribution of a particular patch type, as the aggregated properties at the class level result from the unique configuration of patches across the landscape (McGarigal et al. 2002).

LKMR habitat patches have been delineated several times, most recently by Faulhaber (2003) with patches sized from <0.1 to 51.2 ha. Faulhaber (2003) used a variety of data to delineate the patches including published surveys (Howe 1988, Forsy 1995, Forsy et al. 1996), unpublished data, 1994–1995 digital orthophoto quarter quads, 1999 United States Geological Survey aerial photographs, 2001 satellite photographs of Boca Chica Key, and the Advanced Identification of Wetlands Geographic Information System coverage (Faulhaber et al. 2007). Nonetheless, no systematic study has been undertaken to objectively identify LKMR habitat in the Lower Florida Keys using high-resolution imagery, which can improve delineation of suitable LKMR habitat (Fensham and Fairfax 2002). Nor has an attempt been made to estimate historic land area and configuration of habitat available for the LKMR. Establishing and understanding long-term habitat availability for the LKMR is important for determining causes of historical population declines as well as designing and implementing successful recovery plans (Pringle 2009). In addition, the effect of processes other than development by humans on LKMR habitat has not been studied as it pertains to past habitat loss.

My goals for this study were to spatially describe and compare LKMR habitat from 1959 to 2006 and relate changes in habitat size and structure to the declining LKMR population. Additionally, I wanted to evaluate the role that processes such as sea-level rise and woody encroachment could have had on patch alteration and the LKMR decline. Specifically, my objectives were to: 1) systematically delineate and compare potential LKMR habitat using 1959 and 2006 aerial photographs, 2) compare habitat change on an island mostly unaffected by human development with an island greatly affected by human development, to assess the role of sea-level rise and woody encroachment on potential LKMR habitat, and 3) relate landscape changes to the decline of the LKMR metapopulation.

STUDY AREA

The Lower Florida Keys are a group of islands forming the western end of the Florida Keys archipelago, beginning at Big Pine Key and terminating with the island of Key West (Fig. 3.1). This group of islands is between 23.5° and 25.5° north latitude, several minutes north of the Tropic of Cancer (23° 26' 22" north latitude). Their proximity to the Gulf Stream and the tempering effects of the Gulf of Mexico give the islands their mild, tropical-maritime climate (Chen and Gerber 1990). High temperatures during the summer averaged 32.2° C and lows averaged 26.1° C. High temperatures during the winter averaged 23.9° C and lows averaged 18.3° C (National Climatic Data Center 2008). Summer rainfall

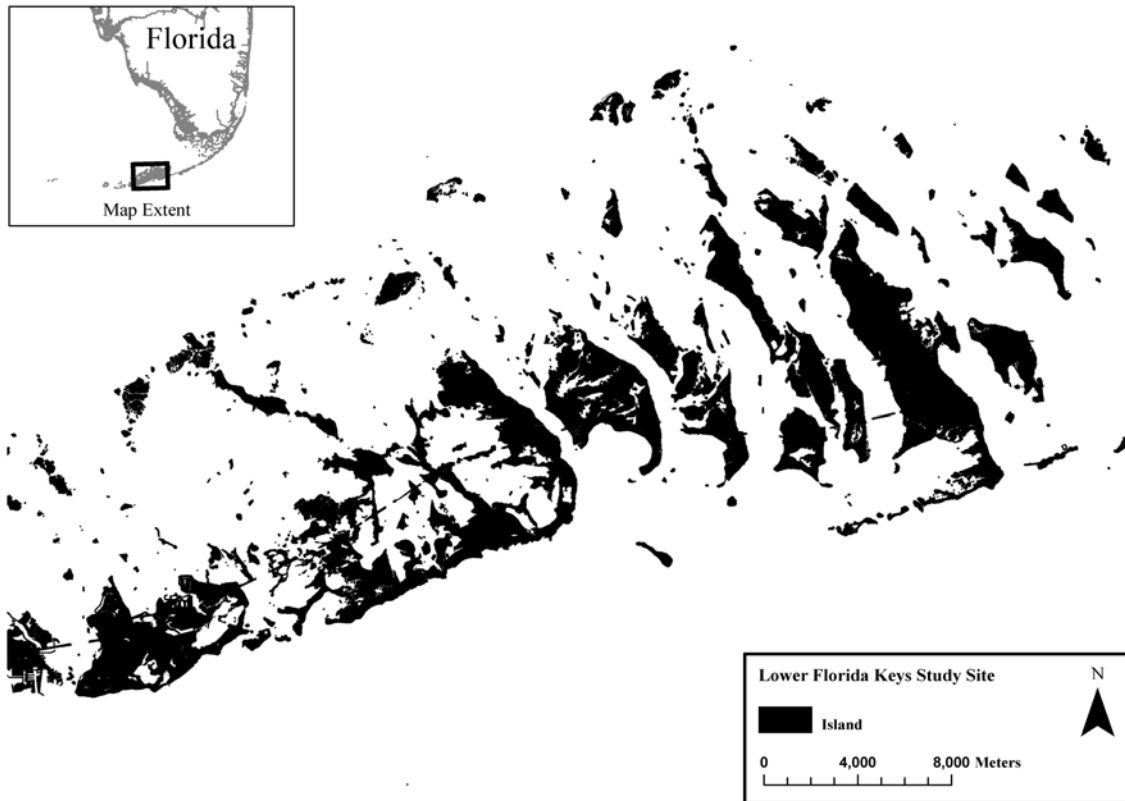


Figure 3.1. Lower Florida Keys study area showing distribution of islands, Lower Florida Keys, USA.

averaged 11.2 cm while winter rainfall averaged 5.3 cm (National Climatic Data Center 2008). As elevation increases in the Florida Keys, vegetation types transitioned from red mangroves (*Rhizophora mangle*), to black mangroves (*Avicennia gerimans*), to white mangroves (*Laguncularia racemosa*), to saltmarsh-buttonwood transition zone, and to upland areas of hammocks and pinelands (Faulhaber 2003).

The saltmarsh-buttonwood transition zone has been subdivided by some authors (McNeese and Taylor 1998, USFWS 1999) into 3 sub-zones resulting from slight elevational changes: intertidal marsh, grassy saltmarsh, and buttonwood transitional. The intertidal marsh occupies the lowest elevations and includes open areas of low halophytic vegetation that are inundated daily with saltwater. Dominant species of this sub-zone include glasswort (*Salicornia spp.*), key grass (*Monanthochloe littoralis*), and saltwort (*Batis maritima*). The grassy saltmarsh occurs at slightly higher elevations and contains salt-tolerant plants such as sea daisy (*Borrchia frutescens*), seashore dropseed, gulf cord grass, saltmarsh fringe-rush (*Fimbristylis castanea*), saltmeadow cordgrass (*Spartina patens*), and saltgrass (*Distichilis spicata*) (Faulhaber et al. 2008). Buttonwood is present but not dominant, leaving the grassy saltmarsh relatively free of woody species. Buttonwood transitional areas occur at the highest elevations within the saltmarsh-buttonwood transition zone, often adjacent to hammocks. Dominated by buttonwood trees,

these areas historically had a relatively open canopy that allowed sunlight to penetrate to the ground but in most LKMR habitat patches only small patches of herbaceous plants composed of seashore dropseed, sea daisy, sea oxeye (*Borrchia arborescens*), and saltgrass were present.

There are 3 types of freshwater wetlands in the Lower Keys: freshwater pine flats, freshwater hardwood forest, and freshwater marsh (McGarry MacAulay et al. 1994). These wetlands occur in low-lying areas where the water table is close to the surface or in depressions that collect precipitation. The amount of freshwater in these wetlands is controlled by precipitation and thus varies seasonally (Ross et al. 1992). Freshwater pine flats are dominated by slash pines in the upper story and by saw grass (*Cladium jamaicense*) and saw palmetto (*Serenoa repens*) in the understory (McGarry MacAulay et al. 1994). During my study, a majority of the slash pines and saw grass had been killed in several of these freshwater pine flats by standing storm surge water associated with Hurricane Wilma (24 Oct 2005). Freshwater hardwood forests are composed of broadleaf trees such as buttonwood, red mangrove, white mangrove, poisonwood, and wax myrtle (*Myrica cerifera*) with an understory of saw grass. Freshwater marshes are open expanses of sedges (Cyperaceae), saw grass, and gulf coast spikerush (*Eleocharis cellulosa*) (Ross et al. 1992). During my study, small areas of gulf coast spikerush were the only herbaceous component of these wetlands. Trees, such as buttonwood and red mangrove, are present but occur in low densities.

Coastal beach berm vegetation is composed of trees, shrubs, and xerophytic plants, growing on accumulations of wind-driven material situated parallel to coastlines (Florida Natural Areas Inventory 1990). Coastal beach berm woody vegetation included seagrape (*Coccoloba uvifera*), Jamaica dogwood (*Piscidia piscipula*), blolly (*Guapira discolor*), gumbo limbo (*Bursera simaruba*), seven year apple (*Casasia clusiifolia*), limber caper (*Capparis flexuosa*), blackbead (*Pithecellobium guadalupense*), Spanish stopper (*Eugenia foetida*), and Bahama nightshade (*Solanum bahamense*) (Ross et al. 1992). Grasses and sedges also sparsely populated the berms.

METHODS

Habitat Delineation 2006

I obtained the most recent, highest resolution remotely sensed data set available for the study area from the Monroe County GIS Department collected between the dates of 5 February 2006 and 8 March 2006 using a Leica ADS40 sensor serial #30028. This data set was received georeferenced by the Monroe County GIS Department and contained 5 SID files with an average size of 20 gigabytes. The images were 3-band true color images with a spatial resolution of 0.15 m. I used major roads, bodies of water, and non-habitat to divide patches. I delineated patches using the land cover types shown to be used by the LKMR; including, saltmarsh-buttonwood (*Conocarpus erectus*) transition zones (intertidal marsh, grassy saltmarsh, and buttonwood transitional), freshwater wetlands (freshwater pine flats, freshwater hardwood

forest, and freshwater marsh), and coastal beach berms, (Forys and Humphrey 1996, Faulhaber et al. 2008). Whereas Forys (1995) and Forys and Humphrey (1999) did not consider patches <0.5 because this size is smaller than the smallest LKMR home range, I followed Faulhaber et al. (2007) and delineated patches <0.5 ha. This scheme is biologically more feasible because smaller patches have been shown to be occupied by LKMRs and these patches can be used to disperse throughout the landscape (Faulhaber et al. 2007).

I began delineating habitat at the most northwestern position in the image and moved south until the bottom of the image was encountered. I then shifted my view east until I encountered uninvestigated imagery and then moved in a northern direction. In this way, I covered each image entirely. I used photo-interpretation to identify target land cover types and used ArcMap 9.3 to digitize the boundary of specific patches (Fensham and Fairfax 2002).

Accuracy Assessment

I assessed the accuracy of the classification of the 2006 data set by using ground-truthed GPS points. These points were classified as either habitat or non-habitat from data taken in the field in January–April 2008 (Schmidt 2009). I divided the number of correctly classified points in each category (habitat and non-habitat) by the total number of points in each category to calculate the producer's accuracy, a measure of the probability of a reference point being correctly classified (measure of omission errors) (Jensen 2005). I then divided the total number of correct points in each category (habitat and non-habitat) by the total number of points that were actually classified in that category. This gives the user's accuracy (measure of commission errors) and is the probability that a point classified in the data set actually represents that category on the ground (Jensen 2005). Additionally, I divided the total number of correctly identified points by the total number of points to arrive at the overall accuracy of the classification. Finally, I calculated the K_{hat} coefficient which is a measure of accuracy between the remote sensing-derived classification and the reference data and can be used to determine whether the results of the classification are significantly better than a random classification (Rosenfield and Fitzpatrick-Lins 1986, Congalton 1991, Paine and Kiser 2003). K_{hat} values >80% represent strong agreement between the classification map and the ground reference information. K_{hat} values between 40 and 80% represent moderate agreement. K_{hat} values below 40% represent poor agreement (Landis and Koch 1977).

Habitat Delineation 1959

I obtained the oldest, most complete set of aerial photographs available for the study area from the Florida Department of Transportation collected on 24 February 1959. This data set contained approximately 300 individual aerial photographs in the SID file format. Each image contained 1 panchromatic black-and-white band and was approximately 350 megabytes in size. I was able to decrease the size of the data set due to the overlap of the spatial extent of each image. I geometrically corrected the images using image-to-image registration (Jensen 2005). I georeferenced the remaining images and

cropped each image to remove the black border as well as most of the unfocused imagery from the borders using ArcMap 9.3 (Environmental Systems Research Institute 2008). After I cropped an image, the pixel values decreased throughout the image. This was due to the removal of the pixels with low values (the black border) and the subsequent histogram stretch performed by ArcMap to display the image. I utilized the “Blend” option in ArcMap 9.3 to mosaic the images as it produced the best results; “Blend” refers to the fact that output cell value of the overlapping areas will be a blend of the values of the overlap which uses a algorithm that is weight based and dependent on the distance from the pixel to the edge within the overlapped area: The mosaic of the 53 images produced a file that was 51 gigabytes in size. I used the same methods to delineate the 1959 habitat patches used for the 2006 delineation.

Landscape Analysis

I converted each of the habitat delineations into raster format using ArcMap 9.3 before importing into Fragstats 3.3 (McGarigal et al. 2002) and Patch Analyst 4 (Ontario Ministry of Natural Resources 2008) for the calculation of class-level metrics for my 2 habitat delineations (1959, 2006). I included in the analysis only patches that occurred on islands in which habitat could have possibly been delineated in each data set. I compared the total number of patches, total class area (LKMR habitat area), mean patch size, mean shape index, mean proximity index, and connectance index of the data sets.

The shape index metric is the simplest measure of patch shape complexity. It is equal to the patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the same size as the patch under examination (McGarigal et al. 2002). The simplest shape (a square for raster data, a circle for vector data) results in a shape index of 1.

The proximity index metric accounts for the size and proximity of all patches whose edges are within a specified search radius of the focal patch (Gustafson and Parker 1994). Proximity index is useful when applied to low density patches with varying degrees of isolation or the spatial pattern of metapopulations (Hargis et al. 1998). I used 2 km for the search radius as this is the maximum dispersal distance a LKMR has been observed to travel (Forys and Humphrey 1996). The proximity index distinguishes sparse distributions of small habitat patches from clusters of large patches (Gustafson and Parker 1994). The index was calculated in Fragstats 3.3 by dividing the patch area of each patch within the search radius of the focal patch by the squared edge-to-edge distance between that patch and the focal patch, and summing the quotients. This index can be useful for describing habitat patch density and accessibility across a fragmented landscape, especially for a metapopulation (Gustafson and Parker 1994). Finally, the connectance index is a measure of overall landscape patch connectance expressed as a percentage of the maximum possible connectance given the number of patches. It is calculated by summing the number of functional joining (in this case patches ≤ 2 km apart), dividing by the total number of possible joining, and multiplying by 100 to convert to a percentage.

I also used the methods and metrics described above to compare habitat change on the island of Little Torch Key to the island of Middle Torch Key to investigate the influence of sea-level rise/woody encroachment with different degrees of anthropogenic development. The islands were similar in size and were adjacent to one another but had very different levels of human development. Little Torch Key is an island of approximately 272 ha in size and contained at least 6 subdivisions and 600 residences situated throughout the island in 2006. A network of parallel and perpendicular roads connected the subdivisions to one another and to US1, a major road which divided the island into a northern and a southern section. A major canal ran across 80% of the island's width dividing the upper one-third of the island from the lower two-thirds. On the other hand, Middle Torch Key, an island approximately 338 ha in size, had only 13 residences with an asphalt road running the length of the island.

RESULTS

From digital imagery collected in 2006, I delineated 403 LKMR habitat patches for a total patch area of 867.1 ha, of which 133 patches were <0.5 ha (Fig. 3.2). The overall accuracy of the 2006 classification was 93.2% and the K_{hat} coefficient was 0.69 which represented moderate agreement (Table 3.1). The producer's accuracy of habitat and non-habitat were 98.9% and 61.0%, respectively and the user's accuracy for habitat and non-habitat were 93.6 and 90.4%, respectively. Using aerial photographs from 1959, I successfully georeferenced 53 images during pre-processing using image to image registration. After an image was georeferenced, the spatial resolution became approximately 0.2 m. From the 1959 data, I delineated 366 habitat patches for a total patch area of 1,772.2 ha, of which 57 were <0.5 ha (Fig. 3.3).

I delineated 38 more habitat patches in the 2006 data than I delineated for the 1959 data (Table 3.2). Comparing class level metrics from 1959 to 2006, I found total class area decreased by 49.0%, and mean patch size decreased by 44.3% between the 1959 and 2006 data sets (Table 3.2). Mean shape index increased by 4.2% in the 2006 data set. Mean proximity index decreased by 13% in the 2006 data set. Both the 1959 and 2006 connectance indices were low with the 2006 set 12.1% lower than the 1959 set.

Table 3.1. Error matrix of the habitat delineation map derived from 2006 multispectral data of the Lower Florida Keys.

		Reference Data		
		Habitat	Non-habitat	Row total
Digitized Data	Habitat	436	30	466
	Non-habitat	5	47	52
	Column total	441	77	518

Table 3.2. Class metrics for the 1959 and 2006 data sets.

	1959	2006
Number of Patches	366	403
Total Class Area (ha)	1,772.2	867.1
Mean Patch Size (ha)	4.85	2.15
Mean Shape Index	2.06	2.15
Mean Proximity Index	281.15	244.57
Connectance Index	6.26	5.50

Table 3.3. Class metrics for the Little Torch Key and Middle Torch Key 1959 and 2006 data sets.

	Little Torch Key		Middle Torch Key	
	1959	2006	1959	2006
Number of Patches	23	18	11	11
Total Class Area (ha)	58.50	15.56	55.05	16.40
Mean Patch Size (ha)	2.54	0.86	5.00	1.49
Mean Shape Index	1.93	2.30	2.15	2.78
Mean Proximity Index	253.47	165.98	22.46	189.10
Connectance Index	96.05	71.32	100.00	87.27

My analysis of the changes in patch metrics between a highly developed and a minimally developed island yielded interesting results (Table 3.3). I delineated 22 habitat patches from the Little Torch Key 1959 data set, 5 more than I delineated for the 2006 data set (Fig. 3.4). On the other hand, I delineated the same number of patches ($n = 11$) for Middle Torch Key on each data set. I found total class area decreased by 73.4% and 70.2% between the 1959 and 2006 data sets for Little Torch Key and Middle Torch Key, respectively. Mean patch size decreased by 66.0% and 70.2% between the 1959 and 2006 data sets for Little Torch Key and Middle Torch Key, respectively. Mean shape index increased by 15.8% and 22.7% between the 1959 and 2006 data sets for Little Torch Key and Middle Torch Key, respectively. Mean proximity index decreased by 34.5% between the 1959 and 2006 Little Torch Key data sets and yet increased by 88.1% between the 1959 and 2006 Middle Torch Key data sets. The connectance index decreased by 25.7% and 12.7% between the 1959 and 2006 data sets for Little Torch Key and Middle Torch Key, respectively.

DISCUSSION

When comparing patch metrics from 1959 to 2006, I found the number of habitat patches increased while the total area of habitat had decreased by almost half (49%). An increase in the number of patches often signifies an increase in fragmentation as seen when roads or forest clearing cut large contiguous areas into smaller disjointed patches (Reed et al. 1996, Lui et al. 2001). In terms of the amount of area lost, my results were similar to USFWS (1999) which estimated that more than half of the suitable

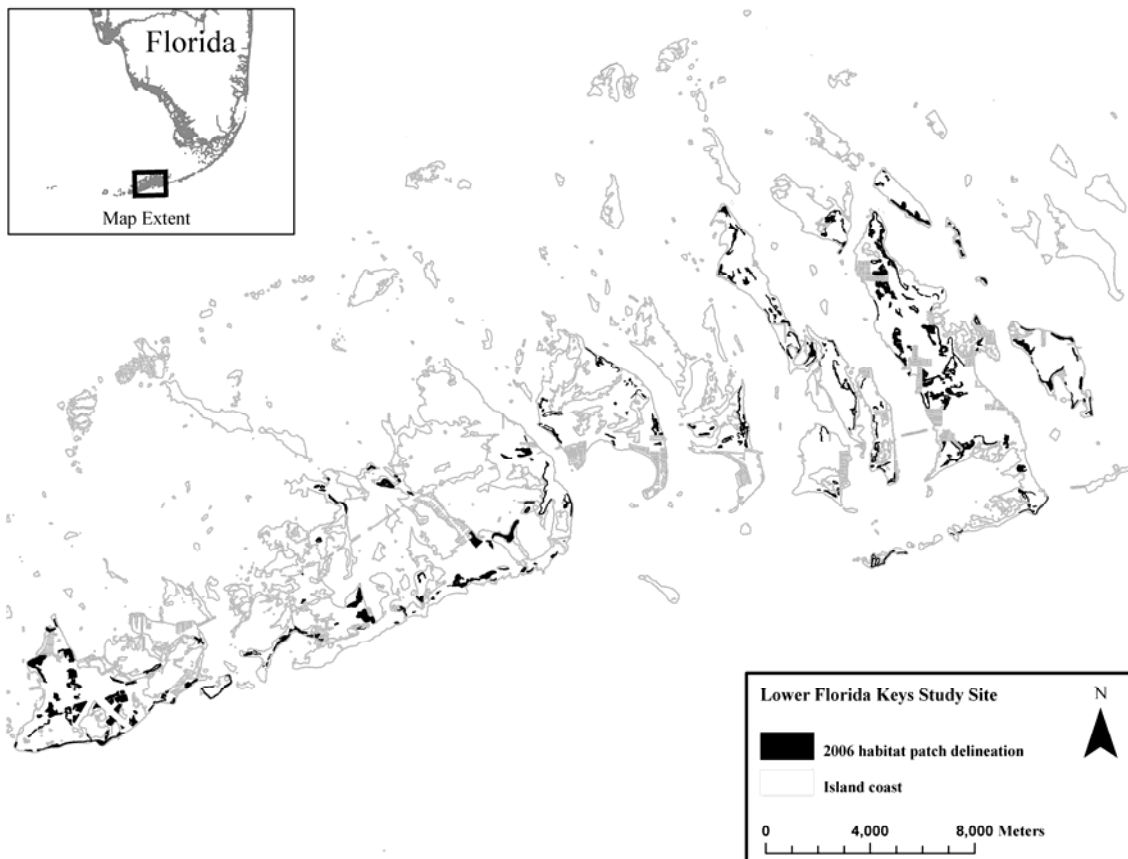


Figure 3.2. Lower Florida Keys study area showing Lower Keys marsh rabbit habitat patches delineated from 2006 aerial photographs, Lower Florida Keys, USA.

LKMR habitat was lost to human activities from 1979–1999. The time period for the present study was considerable longer; however, the 2 estimates certainly agree that a large amount of LKMR habitat has been lost. The mean size of habitat patches that existed in 2006 had decreased 44%. This indicates that not only had the total area of LKMR habitat decreased, but the size of individual patches had contracted. I found that mean patch shape became more complex, implying habitat fragmentation; likely due to canals, roads, and subdivisions that cut into the natural, less complex shape of patches.

Several of the smaller, lower elevation islands in the 1959 data appeared to support saltmarsh-buttonwood transition zone vegetation across the entirety of the island. These islands appeared to support more mangrove communities in the 2006 data while the open, herbaceous areas, characteristic of the saltmarsh-buttonwood transition zone, decreased in size or were altogether absent. This suggested that sea-level rise had converted the majority of these small, lower elevation islands to vegetation types that were not beneficial to the LKMR. The increase in the number of patches and mean shape index, and the

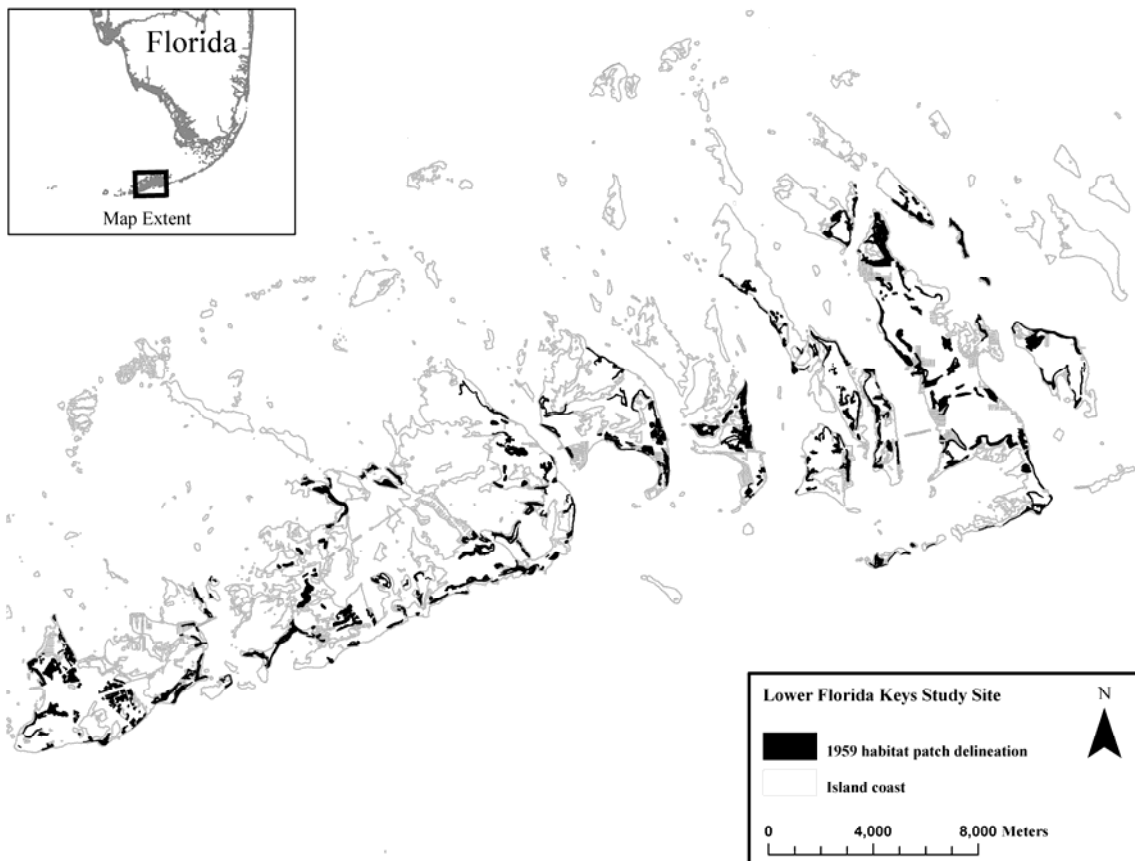


Figure 3.3. Lower Florida Keys study area showing Lower Keys marsh rabbit habitat patches delineated from 1959 aerial photographs, Lower Florida Keys, USA.

decrease in patch size, mean proximity index, and connectance index all suggested that LKMR habitat patches had become more fragmented during the 1959–2006 study period.

An interesting finding was the low values of the connectance index for both the 1959 and 2006 data sets. The connectance index provided evidence that LKMR habitat has always been disconnected. The connectance index is expressed as a percentage of the amount of habitat patches that are functionally joined. Only 6.3% and 5.5% of the habitat patches delineated from the 1959 and 2006 data, respectively, were functionally joined. The low connectance index of both delineations are most likely the result of the linear arrangement of the Lower Florida Keys and therefore the linear arrangement of the LKMR habitat patches stretching from No Name Key to Boca Chica Key. The east-west distance of the study area (the current range of the LKMR) is approximately 43 km while the north-south distance is approximately 14 km. With the patches dispersed over this distance and with the LKMR's maximum known dispersal distance of 2 km, functional connectance was necessarily quite low.

Although the USFWS (USFWS 1985) listed human development as the major cause of LKMR

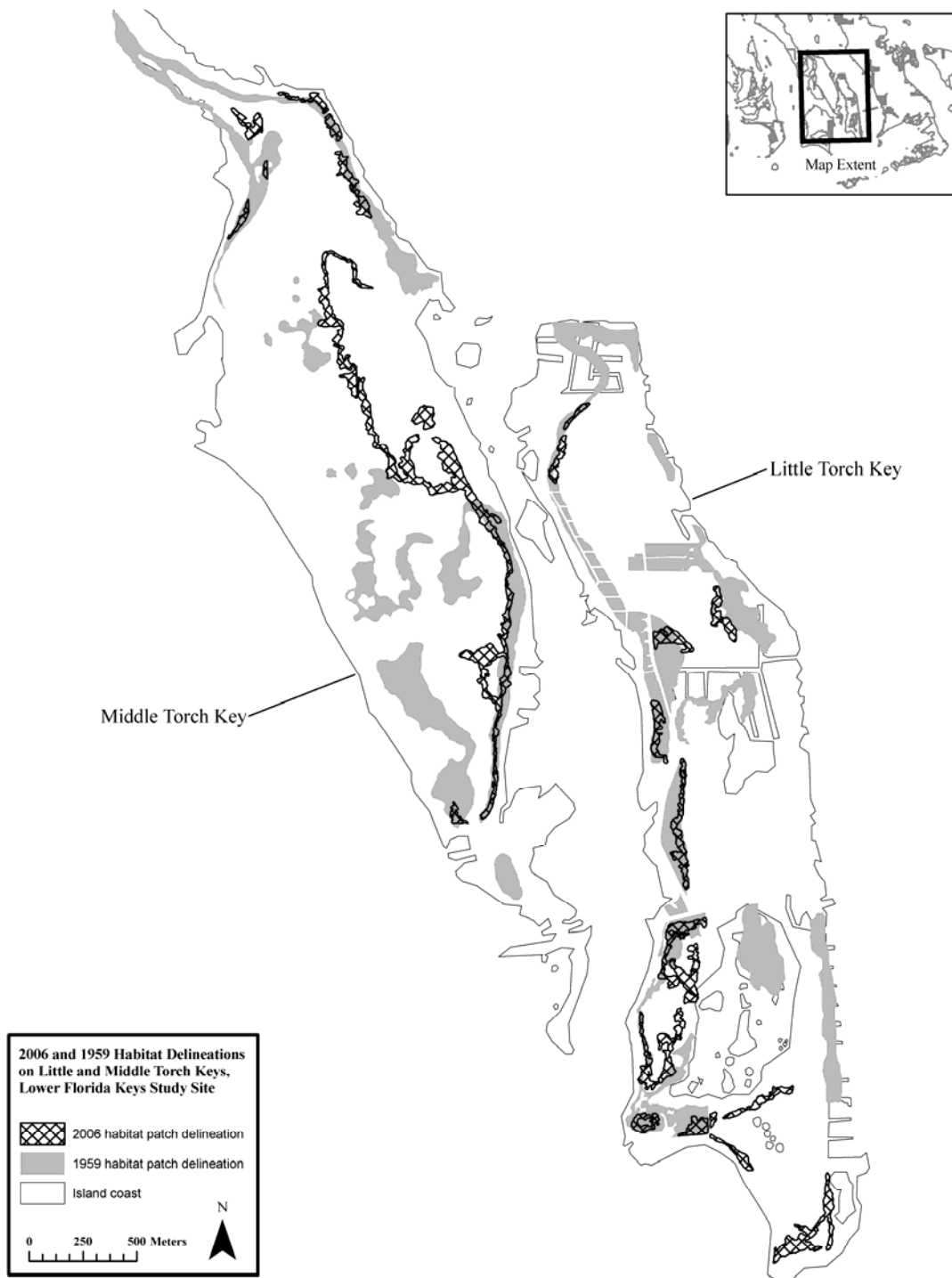


Figure 3.4. Little and Middle Torch keys showing Lower Keys marsh rabbit habitat patches delineated from 1959 and 2006 aerial photographs, Lower Florida Keys, USA.

habitat destruction, my analysis appears to indicate that LKMR habitat also has been reduced by other factors, possibly sea-level rise and woody encroachment. I observed the same patterns on both the developed and undeveloped islands as I did in the range-wide landscape analysis; total area of habitat, mean patch size, and connectance decreased. Proximity index did not follow the landscape pattern and was a result of island-specific patterns and as such, a result of the limitation of this analysis. This analysis was limited to 2 small islands and cannot be used to extrapolate to all of the islands of the Lower Florida Keys. Proximity index for Middle Torch Key increased whereas the index for the range-wide analysis decreased. The second largest patch in the 2006 data set was centrally located among the rest of the patches and had a proximity index of 1,515.7 which increased the mean proximity index for this data set. Using only this index would lead one to believe that the LKMR habitat on Middle Torch Key had become more connected so care should be taken when interpreting results and all metrics should be interpreted in concert. Unfortunately I could not find clear patterns to distinguish habitat loss due to development from loss due to sea-level rise/woody encroachment. However, it is apparent that development is not the only factor that has decreased and fragmented LKMR habitat.

My analysis clearly illustrated that LKMR habitat has decreased in size and connectivity over time. Development of the Lower Florida Keys was originally concentrated on the perimeter of islands as these offered the best views of the ocean and gulf. These perimeter developments fragmented beach berms, saltmarsh-buttonwood transition zones, and freshwater wetlands. Much of exterior development had either already occurred or was in progress in 1959. Development moved to the interior of islands as dredging and filling operations were disallowed by law. These interior developments also fragmented or destroyed saltmarsh-buttonwood transition zones and freshwater wetlands.

Faulhaber's (2003) delineation contained fewer patches ($n = 213$) with less total area (781.2 ha) than both the 1959 and 2006 delineations. This should not be interpreted to mean LKMR habitat increased from 2003–2006. Faulhaber used different delineation methods, so while comparisons can be made, direct quantification of differences should not be attempted. Mean patch size was higher than the 2006 delineation, likely a result of the higher resolution 2006 data set. Small areas of LKMR habitat could have been more discernable on high resolution imagery. Mean shape index should not be compared as higher resolution imagery depicts complex edges not seen in lower resolution data. The mean proximity index lent evidence that the 2003 patch delineation was less connected than the 1959 and 2006 delineations. However, the connectance index was higher for the 2001 data set, most likely because of the linear arrangement of the lower keys. Since the 2001 delineation contained less patches but the overall range of the patches was the same as the other data sets, a larger proportion of those patches would have been functionally connected (i.e., within 2 km).

Since LKMRs spend most of their lives in 1 patch but rely upon one-way immigration movements for metapopulation persistence, patch connectivity is vital for their survival. This analysis

demonstrated that LKMR habitat has decreased in amount since 1959, but I believe an equally important factor directing their decline is the loss of patch connectivity. I found that even in 1959 the connectance index was quite low, only 6.2% of the patches were functionally joined. The connectance analysis did not consider barriers to LKMR movements such as major roads, canals, and buildings. If these factors were accounted for, I believe that connectance of LKMR patches would be lower than that observed.

LKMRs historically existed from Key West to Big Pine Key and in recent history a decline in rabbit numbers was reported (de Pourtales 1877, Howe 1988). Although there are no known population estimates earlier than the 1976 D. Holle estimate of 500 rabbits (Howe 1988), the population of the LKMR has declined to the point of being listed as a federally endangered species. Decreasing patch size and patch connectivity, such as in this analysis, have been shown to decrease populations and increase the probability of local extinctions (Fahrig and Merriam 1985, Bender et al. 1998, Fahrig 2002). Habitat loss and fragmentation by development have directly endangered the LKMR; however, sea level rise and woody encroachment also could have historically caused habitat loss and fragmentation. Although development in LKMR habitat was halted, sea-level rise and woody encroachment could continue to alter LKMR habitat.

MANAGEMENT RECOMMENDATIONS

I recommend that LKMR surveys be conducted in both patches delineated from the 2006 data as well as in the currently surveyed patches (Faulhaber 2003). Using both delineations will improve the probability that all potential LKMR habitat patches will be surveyed and the LKMR population will be accurately monitored. Although development in LKMR habitat was halted (USFWS 2007), factors such as sea-level rise and woody encroachment will continue to alter LKMR habitat. The spatial alteration will be unpredictable but it appears that the trajectory will be one-directional in the case of sea-level rise (LaFever et al. 2007). My results suggest that simply acquiring habitat and designating it protected may not increase the LKMR metapopulation. Effective management of protected land is one of the greatest challenges faced by managers today (Duncan et al. 1999). Without well planned habitat enhancement and restoration, we can expect to see a decrease in both overall LKMR habitat area and high quality LKMR habitat which will result in further decline of the LKMR metapopulation.

CHAPTER IV

CONCLUSIONS AND IMPLICATIONS

The purpose of this chapter is to summarize the findings of my thesis and the implications of these results. It begins with research highlights from the above chapters and proceeds to the implications for management and conservation of the Lower Keys marsh rabbit in the Lower Florida Keys.

RESEARCH HIGHLIGHTS

I conducted a range-wide pellet survey and a mark-recapture study to estimate the endangered Lower Keys marsh rabbit (LKMR; *Sylvilagus palustris hefneri*) population. My pellet surveys were significantly correlated to LKMR density estimates and my regression through the origin possessed a slope of approximately 1 which was comparable to other pellet density rabbit abundance correlations (Krebs et al. 1987, Murray et al. 2002). In addition, my prediction equation produced LKMR densities that were biologically reasonable. However, the r^2 value of my regression through the origin cannot be compared to the r^2 value of an ordinary least-squares model. The square of the sample correlation between observed and predicted values gives an interpretable measure of the quality of a regression through the origin, but does not help in comparing regressions through the origin with ordinary least squares regressions (Eisenhauer 2003).

The ordinary least-squares regression and the regression through the origin correlating rabbit abundance estimates from model M_b and pellet densities did not produce the same results. Without setting the intercept to 0, I would predict rabbits in patches that did not contain pellets which would certainly overestimate patch and overall rabbit densities. I therefore rejected the ordinary least-squares regression and I used the regression through the origin equation to estimate the LKMR range-wide population. I found mean rabbit density to be 1.53 rabbits/ha for occupied patches which was larger than the most recent estimate in 1991–1993 (average 1.3 rabbits/ha, range from 0.86 to 2.26 rabbits/ha) but well under normal *Sylvilagus* population densities (Edwards and Eberhardt 1967, Forys 1995).

Nonetheless, my range-wide estimate (317 individuals [95% CI, 248–383]) was relatively close to previous estimates. However, this does not suggest the LKMR population is stable. Instead, my estimate was a function of the breadth of the survey. This study was the most extensive estimate of the LKMR population to date. My estimate was based upon on a sampling area >260% any previous estimate. Additionally, my range-wide population estimate was larger than the most recent estimate (100–300 individuals [Forys 1995]) because I included all rabbit age groups whereas the previous survey includes only adults. Considering the population estimate, the extent of the survey, the inclusion of all age groups in the estimate, and the results from USFWS occupancy surveys, a case can be made that the LKMR population has declined since the last population estimate in 1991–1993.

My results indicated large disparities between western (257 individuals) and eastern clade (25 individuals) LKMR populations. Crouse et al. (2009) suggested these clades had the possibility of possessing distinct evolutionary potential so effort should be placed on recovering the eastern clade if genetic diversity is to be maintained.

I estimated the western clade's Boca Chica population at 211 individuals (95% *CI*, 163–253); almost 67% of the entire LKMR population and 82% of the western clade's population. Because the majority of both the western clade and the entire LKMR population are located on the single island of Boca Chica, any event which impacts this island should be of concern.

The LKMR population translocated to Little Pine Key in 2002 (Faulhaber et al. 2006) appeared to be successful. From a founder population of 12 LKMR, I estimated 35 rabbits existed. Unfortunately, translocations have not all been successful. I could not find evidence of the 7 LKMRs Faulhaber et al. (2006) released on Water Key in 2004. Water Key is smaller (92 ha) than Little Pine Key (325 ha), contains no uplands, and during high tides, only a portion of the island (<1 ha) is not submerged (unpublished data). This fact could have been exacerbated by Hurricane Wilma (24 October 2005) which could have reduced the number of rabbits on Water Key below a sustainable level.

The plot of the standard error against the increasing number of sample units within a hypothetical patch suggests that the standard error stabilizes when sample effort is between 20–40 sample units/patch. This suggests that patches with less than 20 sample units were undersampled while patches with more than 40 sample units were oversampled.

When comparing range-wide patch metrics from 1959 to 2006, I found the number of habitat patches increased while the total area of habitat had decreased by 49%. An increase in the number of patches often signifies an increase in fragmentation as seen when roads or forest clearing cut large contiguous areas into smaller disjointed patches (Reed et al. 1996, Lui et al. 2001). In terms of the amount of area lost, my results were similar to USFWS (1999) which estimated that more than half of the suitable LKMR habitat was lost to human activities from 1979–1999. The time period for the present study was considerable longer; however, the 2 estimates certainly agree that a large amount of LKMR habitat has been lost. The mean size of habitat patches that existed in 2006 had decreased 44%. This indicates that not only had the total area of LKMR habitat decreased, but the size of individual patches had contracted. I found that mean patch shape became more complex, implying habitat fragmentation; likely due to canals, roads, and subdivisions that cut into the natural, less complex shape of patches.

Several of the smaller, lower elevation islands in the 1959 data appeared to support saltmarsh-buttonwood transition zone vegetation across the entirety of the island. These islands appeared to support more mangrove communities in the 2006 data while the open, herbaceous areas, characteristic of the saltmarsh-buttonwood transition zone, decreased in size or were altogether absent. This suggested that sea-level rise had converted the majority of these small, lower elevation islands to vegetation types that

were not beneficial to the LKMR. The increase in the number of patches and mean shape index, and the decrease in patch size, mean proximity index, and connectance index all suggest that LKMR habitat patches had become more fragmented during the 1959–2006 study period.

The connectance index was low for both the 1959 and 2006 data sets. Only 6.3% and 5.5% of the habitat patches delineated from the 1959 and 2006 data, respectively, were functionally joined. The connectance index provided evidence that LKMR habitat has always been disconnected, most likely the result of the linear arrangement of the Lower Florida Keys and therefore the linear arrangement of the LKMR habitat patches stretching from No Name Key to Boca Chica Key.

Although the USFWS (USFWS 1985) listed human development as the major cause of LKMR habitat destruction, my analysis appears to indicate that LKMR habitat also has been reduced by other factors, possibly sea-level rise and woody encroachment. I observed the same patterns on both the developed and undeveloped islands as I did in the range-wide landscape analysis; total area of habitat, mean patch size, and connectance decreased. However, island-specific patterns were seen to overshadow range-wide patterns on these 2 small islands. A limitation of this analysis is that the results pertained to 2 small islands and cannot be used to extrapolate to all of the islands of the Lower Florida Keys. Unfortunately, I could not find clear patterns to distinguish habitat loss due to development from loss due to sea-level rise/woody encroachment. However, it is apparent that development is not the only factor that has decreased and fragmented LKMR habitat.

LKMRs historically existed from Key West to Big Pine Key and in recent history a decline in rabbit numbers was reported (de Pourtales 1877, Howe 1988). Although there are no known population estimates earlier than the 1976 D. Holle estimate of 500 rabbits (Howe 1988), the population of the LKMR has declined to the point of being listed as a federally endangered species. Decreasing patch size and patch connectivity, such as in this analysis, have been shown to decrease populations and increase the probability of local extinctions (Fahrig and Merriam 1985, Bender et al. 1998, Fahrig 2002). The endangerment of the LKMR has been the direct effect of habitat loss and fragmentation, caused by development, but just as importantly, by non-anthropogenic factors such as eustatic sea-level rise and woody encroachment.

MANAGEMENT AND CONSERVATION IMPLICATIONS

My regression through the origin equation provides managers with an easily applied, highly predictive tool for estimating LKMR densities from pellet counts in the Lower Florida Keys. I recommend this survey method be implemented each year with 2 modifications. I suggest that patches be sampled using a variable number of SUs dependent upon the area of the patch. If 20 SUs are randomly placed in patches < 1ha, 20 SUs are randomly placed in 1–2 ha patches, and 40 SUs are randomly placed in patches > 2 ha, sample effort will not be wasted on large patches and small patches will be sampled

intensively, thereby reducing the variation inherent in small sample sizes. I also recommend that LKMR surveys be conducted in both patches delineated from the 2006 data as well as in the currently surveyed patches (Faulhaber 2003). Using both delineations will improve the probability that all potential LKMR habitat patches will be surveyed and the LKMR population will be accurately monitored. This method can be completed with approximately 500 hours of work, giving managers yearly population estimates of the LKMR. Additionally, I recommend that special effort should be expended on restoring the eastern clade, if extinction is to be avoided. Finally, Water Key should not be viewed as a viable translocation site and future translocation sites should be chosen carefully and prepared for translocations to attain long-term success.

Although development in LKMR habitat was halted (USFWS 2007), factors such as sea-level rise and woody encroachment could and most likely will continue to alter LKMR habitat. The spatial alteration will be unpredictable but it appears that the trajectory will be one-directional in the case of sea-level rise (LaFever et al. 2007). My results suggest that simply acquiring habitat and designating it protected may not increase the LKMR metapopulation. Effective management of protected land is one of the greatest challenges faced by managers today (Duncan et al. 1999). Without well planned habitat enhancement and restoration, we can expect to see a decrease in both overall LKMR habitat area and high quality LKMR habitat which will result in further decline of the LKMR metapopulation.

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