METAPOPULATION ECOLOGY AND RECOVERY OF THE ENDANGERED LOWER KEYS MARSH RABBIT

A Dissertation

by

PAIGE MCGEE SCHMIDT

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

DOCTOR OF PHILOSOPHY

December 2009

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Co-Chairs of Committee,	Roel R. Lopez
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ABSTRACT

Metapopulation Ecology and Recovery of the Endangered Lower Keys Marsh Rabbit.

(December 2009)

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Co-Chairs of Advisory Committee: Dr. Roel R. Lopez
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The Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*), a subspecies of marsh rabbit endemic to the Lower Keys, Florida, is threatened with extinction due to extensive coastal development of salt marsh habitats. LKMR recovery is limited by habitat loss and degradation from brush encroachment, predation by free-roaming cats (*Felis catus*) and raccoons (*Procyon lotor*), sea-level rise, and hurricanes. This study sought to determine local and landscape factors that influence LKMR metapopulation ecology and dynamics and to evaluate strategies for their recovery. I evaluated the influence of patch and landscape characteristics on LKMR densities, extinction, and colonization rates following Hurricane Wilma, and the response of LKMRs and salt marsh habitats to prescribed fire. I used estimates of population change based on annual monitoring data to validate vital rates, constructed a spatially explicit demographic model to evaluate various levels and spatial configurations of recovery scenarios implemented throughout the LKMRs range, and validated expected changes in parameter estimates using measures of habitat degradation and raccoon activity from known LKMR populations.

I found LKMR densities were higher in patches with greater numbers of bunchgrasses and forbs and less edge and lower in patches with higher measures of raccoon activity. In response to a hurricane, I found the distance between LKMR patches and the coast had a negative influence on extinction probability; the distance between an extirpated and occupied LKMR patch had a negative influence on colonization probability and patch size had a positive influence. Adult LKMRs increased as woody cover <0.5 m decreased, herbaceous cover <0.5 m increased, and food availability increased in at least one site following prescribed fire. Model results indicated habitat management actions that improve carrying capacity of local rabbit populations and juvenile survival and control raccoon populations to increase rabbit reproductive rates are effective population recovery strategies. In total, my results provide a conservation planning tool that can be used to select recovery strategies and locations that will maximize benefits to LKMRs, thus improving their viability and recovery.

DEDICATION

For the people of the Citizen Potawatomi Nation and the Lower Keys marsh rabbit;

2 shining examples of perseverance in the face of annihilation.

ACKNOWLEDGEMENTS

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I would like to conclude with an expression of my immense gratitude to my family and to my husband Jason. Without their love and support, I would not have had the courage to attempt this opportunity, nor strength, to see it through to completion.

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CHAPTER I

INTRODUCTION

The Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*) is a subspecies of marsh rabbit endemic to the Lower Keys, Florida that was listed as endangered by the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission in 1990 (Lazell 1984, USFWS 1990). Historically, LKMRs were abundant and found throughout the Lower Keys but development has limited their distribution to 4 main islands (Boca Chica, Saddlebunch, Sugarloaf, and Big Pine keys) and several smaller, outlying islands (de Pourtales 1877, Faulhaber et al. 2007). Remaining LKMR habitats are small, averaging ≈ 4 ha, and distributed in discrete patches or sites that function as a classic metapopulation with interaction between local populations limited to dispersal of individuals outside their natal patch (Levins 1970, Forys 1995, Forys and Humphrey 1996, USFWS 1999). LKMR recovery has been limited by habitat loss and degradation from brush encroachment, predation by free-roaming cats (*Felis catus*) and raccoons (*Procyon lotor*), sea-level rise and hurricanes (USFWS 1999, 2007).

In my study, I sought to determine local and landscape factors that influence LKMR metapopulation ecology and dynamics, to apply those findings by building and validating a metapopulation model, and to evaluate strategies for LKMR recovery. My objectives were 1) to evaluate the effect of patch attributes, raccoon activity, and habitat attributes on adult and juvenile LKMRs, 2) to quantify extinction and colonization of

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This dissertation follows the style of Journal of Wildlife Management.

local patches after Hurricane Wilma and determine if patch configuration and habitat composition affect local population dynamics, 3) to evaluate the use of prescribed fire in maintaining and restoring coastal salt marsh prairies important to LKMRs, and finally 4) to evaluate translocations, habitat management and raccoon control using a population viability analysis of the Lower Keys marsh rabbit.

Here, I have presented an outline of the dissertation and my research objectives. The dissertation is divided into chapters that have been prepared as independent, stand-alone manuscripts with a distinct research focus. While each chapter has unique research objectives, the overall objective of the dissertation was to increase our understanding of the metapopulation ecology of the endangered Lower Keys marsh rabbit and to evaluate strategies for its recovery. Thus, some information is repeated among chapters (i.e., species and study area description).

CHAPTER II

HARDWOOD ENCROACHMENT AND RACCOONS AS LIMITING FACTORS FOR LOWER KEYS MARSH RABBITS

SYNOPSIS

The Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*), a marsh rabbit subspecies endemic to the Lower Keys, Florida was protected in 1990 due to habitat loss, predation by cats, and vehicle mortality. Populations of LKMR continue to decline despite recovery efforts thus necessitating re-evaluation of threats, including previously unrecognized threats such as hardwood encroachment and predation by native species such as raccoons (*Procyon lotor*). I surveyed 150 LKMR patches in 2008 tallying adult and juvenile rabbit pellets, woody and herbaceous ground cover, number of herbaceous species, and number of raccoon signs. I calculated each patches' shape index (perimeter to area ratio) using ArcGIS and evaluated the relationship between patch shape index and habitat variables on LKMR using regression analysis and model selection. I found both adult and juvenile LKMR densities were higher in patches with greater numbers of herbaceous species present and lower in patches with higher shape indices. I also found adult LKMR densities were lower in patches with higher measures of raccoon activity. My results suggest habitat succession and raccoons pose a threat to the persistence and recovery of LKMR populations. Recovery efforts should focus on reducing patch edge, increasing presence and diversity of herbaceous species, and reducing raccoon densities in LKMR patches.

INTRODUCTION

Lagomorph species throughout the world are threatened with extinction due to habitat loss and degradation, over-exploitation, competition (heterospecifics and introduced lagomorphs), and predation (Baillie et al. 2004, Smith 2008). Conservation and recovery efforts for lagomorphs and all species can be difficult when basic population ecology data are lacking (Hacklander et al. 2008). This is the case with the Lower Keys marsh rabbits (LKMR, *Sylvilagus palustris hefneri*), where gaps in knowledge of their population ecology are limiting conservation efforts.

The LKMR is a marsh rabbit subspecies (Lazell 1984) listed as endangered by the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission since 1990 (USFWS 1990). LKMRs are endemic to the Lower Keys, Florida, the end of a chain of limestone islands extending south and west from the southern tip of peninsular Florida (Fig. 2.1). Ecological information is lacking, particularly the parameters driving persistence of local populations and information specific to juvenile LKMRs necessary to develop, guide and evaluate recovery efforts (USFWS 2007).

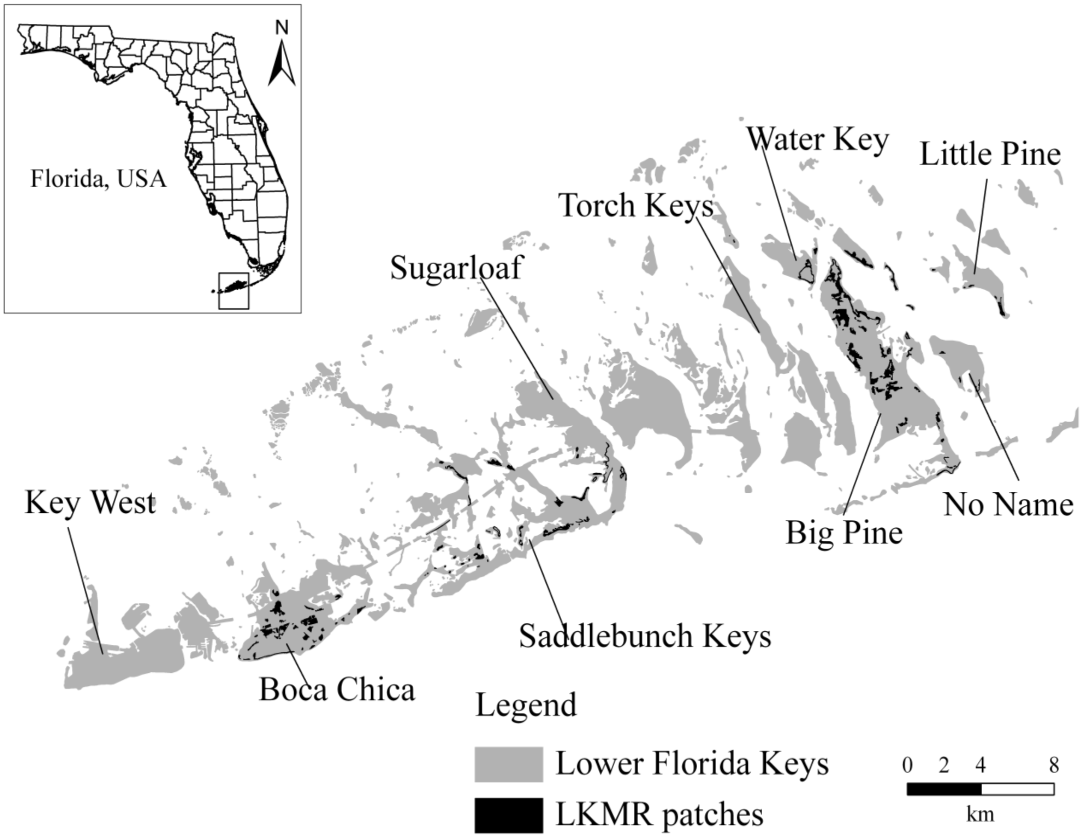

Figure 2.1. Distribution of Lower Keys marsh rabbit patches throughout the Lower, Florida, USA.

After the LKMR was listed under the Endangered Species Act, data on their ecology and metapopulation dynamics were collected and recovery strategies were implemented to reduce habitat loss, fragmentation, predation by free-roaming domestic cats (*Felis catus*), and mortalities caused by off-road vehicle use (USFWS 1999). Despite these efforts, LKMR populations continued to decline (USFWS 2007). Since the initial recovery plan for the LKMR was developed over a decade ago threats to LKMRs have changed. Some threats have become negligible, shifted or may have been previously unrecognized. For example, off-road vehicle mortality was abated due to restrictions of off-road vehicle use in certain areas critical to LKMR (USFWS 2007). Similarly, the threat of habitat loss from development has been reduced due to state and federal regulatory oversight (USFWS 2007). Nonetheless, during this same time, habitat may have been continually lost or degraded due to succession of vegetative communities, rendering LKMR patches unsuitable (Perry 2006, USFWS 2007). Finally, a new threat has been recognized but has yet to be evaluated. It is possible that native raccoons (*Procyon lotor*) may negatively influence LKMR populations particularly through nest predation (USFWS 2007).

LKMRs typically occupy wet areas with dense cover including salt marsh, buttonwood (*Conocarpus erectus*) transition zones, and freshwater marshes (Forys 1995, Faulhaber et al. 2007, 2008). LKMRs use habitats with dense, low (<1 m) forbs and grasses and little overstory vegetation and avoid areas in a later state of succession characterized by mature buttonwoods, high canopy cover and low ground cover (Perry 2006, Faulhaber et al. 2008). Hardwood or brush encroachment of coastal wetlands has been documented for the Lower Keys, Florida and has been attributed to LKMR population declines observed over the past 3 decades (Dickson 1955, Alexander and Dickson 1970, USFWS 1999, Perry 2006).

Free-roaming domestic cat predation was responsible for 50% of LKMR mortality and was cited as the largest factor limiting their population viability in the 1990s (Forys and Humphrey 1999*a*). Free-roaming domestic cat removal was initiated on Boca Chica Key subsequent to these findings; however, capture rates (235 raccoons vs. 20 cats) indicated raccoons were an order of magnitude more prevalent in treated areas (USFWS 2007). Raccoons, although omnivorous, have been shown to be efficient predators and to prey on rabbits (Dorney 1954, Urban 1970, Jennings et al. 2006). Raccoon populations can reach high densities in habitats that are indicative of the Lower Keys (McCleery et al. 2005). Raccoon populations also can become inflated in anthropogenically altered landscapes and in marsh habitats interspersed with hardwoods (Dorney 1954, Riley et al. 1998, Smith and Engeman 2002); these are 2 habitat types that are characteristic of many LKMR patches. Combined, these observations suggest that raccoons may pose risks to rabbits, particularly nestlings, because of their susceptibility to predation (USFWS 2007).

LKMR habitats are small, averaging ≈ 4 ha, and are distributed in discrete patches or sites, that function as a classic metapopulation (Forys 1995, Forys and Humphrey 1999*a*, USFWS 1999) or a “population” of spatially discrete local populations connected by dispersing individuals (Levins 1970). Subadult LKMRs are largely responsible for inter-patch dynamics through one-way dispersals from natal patches (Forys 1995, Forys and Humphrey 1996). Previous research has shown that only half of consistently occupied patches (Forys and Humphrey 1999*b*) were producing the juveniles that drive inter-patch dynamics and determine metapopulation persistence. The effects of patch and habitat attributes on juvenile LKMR populations have not previously been evaluated yet remain vital to successfully implementing recovery of this subspecies.

The purpose of my study is to quantify the relationship between LKMRs and a number of factors thought to be detrimental to their recovery. This information can be used to evaluate on-going recovery efforts and to develop new recovery strategies and actions as warranted by new findings that could then be incorporated into an adaptive resource management plan for the LKMR (Lancia et al. 1996, Perry 2006). My objectives were to evaluate the effect of patch demographics, raccoon abundance, and habitat attributes on adult and juvenile LKMRs. Specifically, I evaluated whether hardwood encroachment and raccoons are limiting LKMR populations.

STUDY AREA

The Lower Keys, Florida are located between 23.5 and 25.5 ° North latitude and exhibit a subtropical climate due to the Gulf Stream and other maritime influences (Fig. 2.1, Chen and Gerber, 1990; Forys and Humphrey, 1999*a*). The climate is characterized by distinct wet and dry seasons, with the dry season (November through April) contributing <33% of annual precipitation (Forys and Humphrey 1999*a*). Elevations rarely exceed 2 m, with slight variations in elevation producing distinct vegetation communities that transition from mangroves to coastal salt marsh/buttonwood transition zones inland to freshwater marshes, pine rocklands and tropical hardwood hammocks (McGarry MacAulay et al. 1994).

LKMRs are predominately found in coastal salt marsh prairies and freshwater marshes (Faulhaber et al. 2007). Coastal salt marsh prairies, also known as buttonwood transitions zones, are characterized by cord grasses (*Spartina spartinae, S. patens, S. bakeri*), sea daisies (*Borrichia frutescens, B. arborescens*), glassworts (*Salicornia spp*.), seashore dropseed (*Sporobolus virginicus*) and rushes (family *Cyperacea*) with various densities of salt tolerant hardwoods, predominantly buttonwood but also with white mangrove (*Laguncularia racemosa*), red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), joewood (*Jaquinia keyensis*), poisonwood (*Metopium toxiferum*) and wild dilly (*Manilkara bahamensis*) (Faulhaber 2003). Freshwater marshes are characterized by sawgrass (*Cladium jamaicensis*) and Gulf Coast spike rush (*Eleocharis cellulose*) interspersed with buttonwood (*C. erectus*) and other hardwoods depending on disturbance history (e.g., fire, cutting) and salinity. Invasive exotic plant species are distributed throughout the range of the LKMR and have been identified as a source of habitat loss and degradation. The most prevalent species form thick monocultures and include Australian pine (*Casuarina equisitifolia*), Brazilian pepper (*Schinus terebinthifolia*), lead tree (*Leucaena leucocephala*) and mahoe (*Hibiscus tiliaceus*).

METHODS

I sampled the entire known range of the LKMR by surveying patches identified from an updated distribution survey (Fig. 2.1; Faulhaber et al. 2007). I constructed a digital 30 x 30-m grid and placed it over a shapefile of the lower Florida Keys using a Geographic Information System (GIS; ArcGIS 9.3, ESRI 2008). Grid nodes falling within the boundaries of LKMR patches were selected and stored within the GIS. I navigated to grid nodes within each patch using a global positioning system (GPS), searched within a 1-m radius of each node (sample unit) for LKMR pellets, and quantified parameters hypothesized to influence their numbers (Schmidt 2009). I separated and tallied LKMR fecal pellets by age class (juvenile and adult pellets/node) to determine if ecological parameters affecting the rabbits differed for adults and juveniles. Incidence of fecal pellets has been shown to have a strong correlation with LKMR density and rabbit age is easily determined by pellet diameter (Forys 1995, Schmidt 2009).

As an indicator of habitat succession, I visually estimated foliar cover (%) of woody (*woody*) and herbaceous (*herb*) vegetation <0.5 m in height within each 1-m radius sampling unit. For each sample unit, I visually estimated the total cover for each category (woody, herb) to the nearest 5%. I summed woody and herbaceous ground cover estimates for all sample units within a patch to obtain patch totals. The structure of vegetation, including vegetation height and thickness of foliar cover has been shown to be important in the selection of diurnal forms or resting sites used in both saltwater and freshwater wetlands (Faulhaber et al. 2008). Perry (2006) characterized woody encroachment detrimental to LKMR habitat suitability as decreased ground cover vegetation and height.

I also measured habitat quality by quantifying the distribution within each patch of 4 genera of bunchgrasses and forbs important to LKMRs for food, cover and nesting (Forys and Humphrey 1999*b,* Faulhaber et al. 2008). I recorded the presence of cord grasses, sea daisies, bluestems (*Andropogon glomeratus, A. virginicus.*), and spike rush within each sample unit. I summed occurrences of these 4 herbaceous plant species for all sample units within a patch to obtain patch totals (*dist*). Bunch grass density and presence of forbs have been found to decline with increasing hardwood encroachment in LKMR habitat (Perry 2006). These species also have been found to be important indicators of consistency of patch occupancy (Forys and Humphrey 1999*b*).

To evaluate the influence of raccoons on LKMRs, I quantified a measure of raccoon activity (*proc*) by recording the presence or absence of raccoon scat or tracks at each sample unit. I then summed the total number of sample units where raccoon signs were present to create a categorical estimate of raccoon activity for each patch.

I measured patch area and perimeter using a GIS which I then used to calculate a patch shape index (*psi*) using the following equation for vector data:

$$\text{patch}\cdot\text{shape}\cdot\text{index}\,(\text{psi}) = ((\text{perimeter}(\text{m})) \div ((\sqrt{4\times\pi\times\text{area}}(\text{m}^\wedge 2)).$$

Patch shape indices estimate a perimeter to area ratio while standardizing for patch area (McGarigal and Marks 1995). Patch shape indices range from 1 to ∞ with an index of 1 indicating a perfectly circular shape whereas, higher values show that the amount of edge relative to patch interior is increasing in complexity. Edge effects may reduce a vertebrate species' distribution and dispersal ability and increase rates of predation and parasitism (as reviewed by Yahner 1988). Boundary shape also has been associated with rates of woody plant encroachment (Hardt and Forman 1989). Despite potential implications associated with edge habitats, quantification and measurement of edge effects remains difficult. I therefore assumed predation rates and hardwood encroachment would increase and habitat quality would decrease with increasing patch shape index.

Table 2.1. A priori and a posteriori models correlating total counts of adult LKMR pellets to patch characteristics in the Lower Keys, Florida, USA, 2008. This table contains number of parameters (K), -2*natural log of the maximum likelihood estimate (-2ln*L*), Akaike's Information Criterion adjusted for small sample size (AIC_c), change in AIC_c from the smallest AIC_c value (ΔAIC_c), and Akaike weights (w_i) for each model.

	Model [a]	K	-2ln*L*	AIC_c	ΔAIC_c	w_i
a priori						
1	Psi+woody+herb+dist+proc	6	1436.0	1448.6	0.0	0.45
2	Psi+woody+herb+dist	5	1438.3	1448.7	0.1	0.43
3	Woody+herb+dist	5	1447.5	1451.2	2.6	0.12
4	Proc+psi+woody+herb	4	1442.9	1457.9	9.3	0.00
5	Null	1	1463.6	1465.6	17.0	0.00
a posteriori						
6	Proc+psi+dist	4	1440.5	1448.8	0.0	0.86
7	Psi+dist	4	1448.6	1454.8	6.0	0.04
8	Proc+dist	3	1453.7	1455.9	7.0	0.03
9	Psi+proc	3	1450.3	1456.4	7.6	0.02
10	Proc+dist+proc*dist	4	1448.4	1456.7	7.8	0.02

[a] Variable notation for patch attributes: null = intercept only, psi = patch shape index, woody = total woody ground cover <0.5 m in height (%), herb = total herbaceous ground cover <0.5 m in height (%), dist = total occurrence of herbaceous plants (cord grass, sea daisy, bluestem, and spike rush), proc = total sample units where raccoon sign (scat or track) was observed.

Table 2.1. continued.

	Model [a]	K	-2ln$L$	AIC$_c$	ΔAIC$_c$	w_i
11	Psi+dist+psi*dist	4	1448.6	1456.9	8.1	0.02
12	Psi+proc+psi*proc	2	1448.7	1457.0	8.2	0.01
13	Psi	3	1453.9	1458.0	9.2	0.01
14	Species	2	1458.5	1462.6	13.8	0.00
15	Proc	2	1460.0	1464.1	15.3	0.00

Table 2.2. A priori and a posteriori models correlating total counts of juvenile LKMR pellets to patch characteristics in the Lower Keys, Florida, USA, 2008. This table contains number of parameters (K), -2*natural log of the maximum likelihood estimate (-2ln*L*), Akaike's Information Criterion adjusted for small sample size (AIC_c), change in AIC_c from the smallest AIC_c value (ΔAIC_c), and Akaike weights (w_i) for each model.

	Model [a]	K	-2ln*L*	AIC_c	ΔAIC_c	w_i
a priori						
16	Psi+woody+herb+dist	5	684.9	695.4	0.0	0.74
17	Psi+woody+herb+dist+proc	6	684.9	697.5	2.1	0.26
18	Proc+psi+woody+herb	5	703.6	714.0	18.6	0.00
19	Woody+herb+dist	4	717.2	725.5	30.1	0.00
20	null	1	750.5	752.5	57.1	0.00
a posteriori						
21	Psi+herb+dist	4	684.9	693.2	0.0	0.52
22	Psi+herb+dist+psi*herb+psi*dist	6	680.8	693.4	0.2	0.47
23	Psi+dist	3	700.9	707.1	13.9	0.00
24	Psi+dist+psi*dist	4	699.4	707.7	14.5	0.00
25	Psi	2	704.3	708.4	15.2	0.00

[a] Variable notation for patch attributes: null = intercept only, psi = patch shape index, woody = total woody ground cover <0.5 m in height (%), herb = total herbaceous ground cover <0.5 m in height (%), dist = total occurrence of herbaceous plants (cord grass, sea daisy, bluestem, and spike rush), proc = total sample units where raccoon sign (scat or track) was observed.

Table 2.2. continued.

	Model[a]	K	-2ln$L$	AIC$_c$	ΔAIC$_c$	w_i
26	Psi+herb+psi*herb	4	701.0	709.2	16.0	0.00
27	Psi+herb	3	704.3	710.5	17.3	0.00
28	Herb+dist+herb*dist	4	710.6	718.9	25.7	0.00
29	Herb+dist	3	729.5	735.6	42.4	0.00
30	Dist	2	748.1	752.2	59.0	0.00
31	Herb	2	750.2	754.3	61.1	0.00

Data Analysis

To determine patch and habitat characteristics with the greatest influence on the LKMR, I used generalized linear regressions and maximum likelihood estimation to relate patch and habitat variables to pellet counts. I evaluated model sets specific to adult and juvenile LKMRs fitted to a negative binomial distribution using SPSS software (Release 15.0.0, 2006). The negative binomial distribution contains an additional parameter that allows the variance to be greater than the mean and is appropriate for use when the count of failures, in this case the number of patches without rabbits, is greater than expected by the Poisson distribution (Agresti 2007). I included the log of the total number of sample units per patch as an adjustment term in all regression models to account for autocorrelation between sampling effort and patch area (Agresti 2007). Offset terms in regressions of count data maintain the proportionality of the response variable to the explanatory variable(s) so that a doubling of the number of sample units would correspond with a doubling of the expected outcome, in this case the number of pellets per patch. To minimize under-fitting or over-fitting my data, I ran a small number of a priori models specific to my objectives (Norman et al. 2004). To evaluate the effect of hardwood encroachment and raccoons on LKMRs, I evaluated 3 a priori models, a global model containing all 6 variables and an intercept-only (null) model using Akaike's Information Criterion corrected for small sample size (AIC_c) for adult (Table 2.1, models 1–5) and juvenile (Table 2.2, models 16–20) rabbits (Burnham and Anderson 2002). From the evaluation of the a priori models, I generated a posteriori model sets for adult (Table 2.1, models 6–15) and juvenile (Table 2.2, models 21–31) rabbits (Norman et al. 2004). I used the relative difference to the smallest AIC_c in each model set (ΔAIC_c) and Akaike weights (w_i) to select the best approximating models (Burnham and Anderson 2002). I considered models ≤ 2 AIC_c units to compete with the best models and discarded model >2 AIC_c units as unlikely representations of the data (Burnham and Anderson 2002). I then exponentiated the negative binomial regression analysis of the selected models (Agresti 2007) to derive a prediction equation that I used to evaluate the influence of each models' variables on the estimated number of adult and juvenile pellets (Guthery and Bingham 2007). To plot the effect of each covariate on total LKMR pellets, I held all other covariates in the exponentiated equation constant at their average and allowed the plotted covariate to vary throughout its range. To avoid over extrapolation of the data, I constrained plots to within the maximum range of the actual pellet counts for each age class (Guthery and Bingham 2007).

RESULTS

I conducted surveys of 150 patches throughout the range of LKMRs from 4 January through 20 March 2008. I detected adult and juvenile LKMR pellets in 73 and 21 patches, respectively. I sampled 6,922 1-m radius sample units for all patches combined. The average number of sample units per patch was 46 (*SE* = 6). Patch area ranged from 0.09 to 51.2 ha with an average of 4.2 (*SE* = 0.6) ha. Total pellet counts per patch for adult and juvenile rabbits ranged from 0.0–4,837.0 and 0.0–153.0 with an average of 97.1 (*SE* = 36.1) and 6.0 (*SE* = 1.8) per patch, respectively. Adult and juvenile pellets per ha combined ranged from 0.0–825.0 with an average of 25.6 (*SE* = 6.6). For all patches, I estimated a mean patch shape index of 2.16 (*SE* = 0.09).

Accounting for the correlation between patch area and sample effort, the mean woody cover (%) per sample unit was 7.48 (*SE* = 1.07) and the mean herbaceous cover (%) per sample unit was 14.2 (*SE* = 1.91). I did not observe any of the 4 targeted genera of bunchgrasses and forbs in 21 of the 150 patches surveyed. The mean occurrence of the 4 bunchgrass and forb species per sample unit was 0.42 (*SE* = 0.03). I observed raccoon activity in 25 of 150 patches surveyed. For patches with raccoons present the proportion of sample units with scat or tracks ranged from 1% to 13%, with a mean of 3.4% (SE = 0.01). Evaluating adult rabbit density, I found a priori models 1 and 2 best approximated the data (Table 2.1). From those models, I generated 10 new models and found a posteriori model 6 best approximated the data (Table 2.1). Model 6 had a $w_i \geq$ 0.86 indicating there is an 86% probability model 6 is the actual best model of the set and provides the best explanation of the data (Burnham and Anderson 2002). My examination of model 6's individual parameter estimates and 95% *CI* indicated none of the parameters contained 0 suggesting all were relevant predictors of total counts of adult pellets (Table 2.3). For model 6, I found a negative correlation between total counts of adult pellets and raccoons (Table 2.3, Fig. 2.2a) and between total counts of adult pellets and patch shape index (Table 2.3, Fig. 2.2b). For model 6, I also found a positive correlation between total counts of adult pellets and the total occurrence of bunchgrasses and forbs (Table 2.3, Fig. 2.2c).

Evaluating juvenile rabbit density, a priori model 16 provided the best approximation of the data (Table 2.2). From model 16, I generated 11 new models and found a posteriori models 21 and 22 provided the best approximation of the data (Table 2.2). Model 22 included the same main effects as model 21 and was within 0.2 AIC_c units of model 21; however, model 22 also included 2 interaction terms that did not improve the model likelihood, indicating these interactions were not relevant predictors of juvenile density (Table 2.2). When I examined the best model's (model 21) individual parameter estimates and 95% CIs, I found herbaceous cover (%) contained 0 indicating it was not a relevant predictor of the total count of juvenile pellets while patch shape index and the number of herbaceous species did not contain 0 and were relevant predictors (Table 2.4). For model 21, I also found a negative relationship between the total count of juvenile pellets and patch shape index (Fig. 2.3a) and a positive relationship between the total count of juvenile pellets and species (Fig. 2.3b).

Table 2.3. Model parameter estimates ($\hat{\beta}$) and 95% confidence intervals relating adult Lower Keys marsh rabbit densities to patch characteristics in the Lower Keys, Florida, USA, 2008.

Parameter [a]	$\hat{\beta}$	95% *CI*
Proc	-0.28	-0.45 to -0.11
Psi	-0.21	-0.34 to -0.08
Dist	0.01	0.003 to 0.02

[a] Variable notation for patch attributes: proc = total sample units where raccoon sign (scat or track) was observed, psi = patch shape index, dist = total occurrence of herbaceous plants (cord grass, sea daisy, bluestem, and spike rush).

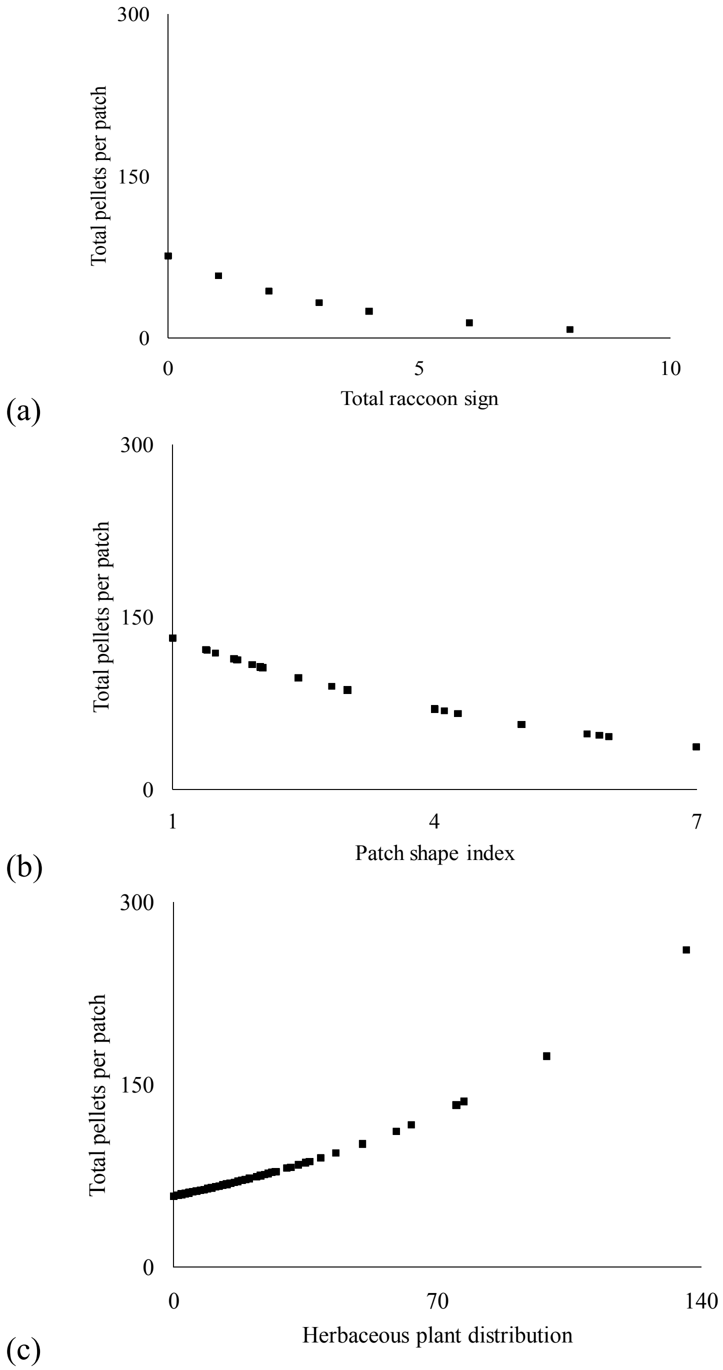

Figure 2.2. Number of adult Lower Keys marsh rabbit pellets per patch predicted as a function of (a) total sample units where raccoon sign (scat or track) was observed, (b) patch shape index, and (c) the total occurrence of herbaceous plants (cord grass, sea daisy, bluestem, and spike rush) for the Lower Keys, Florida, USA, 2008.

Table 2.4. Model parameter estimates and 95% confidence intervals correlating juvenile Lower Keys marsh rabbit densities to patch characteristics in the Lower Keys, Florida, USA, 2008.

Parameter [a]	$\hat{\beta}$	95% CI
Herb	0.00	-0.001 to 0.000
Psi	-0.668	-0.859 to -0.478
Dist	0.058	0.03 to 0.086

[a] Variable notation for patch attributes: herb = total herbaceous ground cover <0.5 m in height (%), psi = patch shape index, dist = total occurrence of herbaceous plants (cord grass, sea daisy, bluestem, and spike rush).

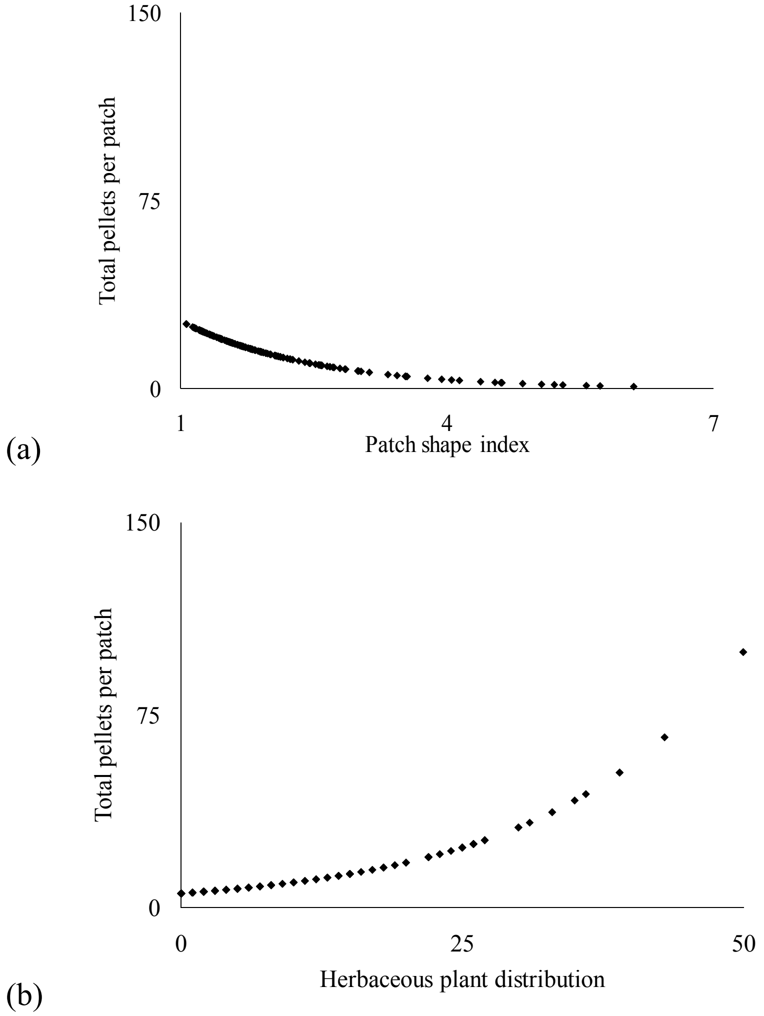

Figure 2.3. Number of juvenile Lower Keys marsh rabbit pellets per patch predicted as a function of (a) patch shape index and (b) total occurrence of herbaceous plants (cord grass, sea daisy, bluestem, and spike rush) for the Lower Keys, Florida, USA, 2008.

DISCUSSION

Based on my regression analysis, I found positive relationships between both adult and juvenile LKMRs and the distribution of 4 genera of herbaceous plants that previously were found to be important to LKMRs for food, cover, and nesting (Forys and Humphrey 1999*b,* Faulhaber et al. 2008). Numerous measures of herbaceous vegetation including availability of bunch grasses and forbs and ground vegetation height and thickness have all been associated with consistency of LKMR patch occupancy, habitat use and diurnal form use (Forys and Humphrey 1999*b*, Perry 2006, Faulhaber et al. 2008). It was suggested by Forys and Humphrey (1999*b*) that thick foliar cover was important to the LKMR for nesting and also provided protection from predators, including raccoons. My results are consistent with these studies and suggest a reduction in the number of bunchgrasses and forbs important to the LKMR may result in decreased densities, thus potentially reducing patch persistence and increasing extinction risk. This possibility provides support for habitat management strategies, such as removal of overstory hardwood vegetation and prescribed fire that would slow or reverse the rate of hardwood encroachment and improve the amount and diversity of herbaceous bunch grasses and forbs (USFWS 2007).

I found a negative relationship between raccoons and adult LKMRs, but I did not find a relationship between raccoons and juvenile LKMRs. Raccoons may affect LKMRs directly through mortality or indirectly when rabbits avoid areas with high levels of predators (Banks et al. 1999). Direct mortality of LKMRs has not been supported by data of adult LKMR mortality (Forys and Humphrey 1999*a*); however, total counts of adult LKMRs may be lower in areas with high raccoon activity because adult rabbits avoid areas with high densities of potential nest predators. Indirect effects of predation have been shown for European rabbits (*Oryctolagus cuniculus*) in Australia where rabbits were observed farther from refuge and maintained higher body condition in predator removal areas (Banks et al. 1999). An alternative explanation is that raccoons and adult LKMRs use different habitats. To test this hypothesis I conducted a post hoc analysis comparing the number of patches with raccoons and rabbits (N=19) to patches with raccoons and no rabbits (N=6) using a chi-square test of independence. I found rabbits and raccoons use the same patches more than expected (χ^2=6.8, P=0.01). I then compared patches without raccoons or rabbits (N=71) to patches with raccoons and no rabbits (N=6) and found raccoons use patches without rabbits less than expected (χ^2=54.9, P<0.001). These results suggest that the statistical relationship between raccoons and rabbits was not a product of different patch use by these 2 species.

The lack of support for a relationship between juvenile LKMRs and raccoons could be due to the paucity of data as only 21 of 150 patches contained juvenile rabbits. Therefore, even the simplest models would produce a parameter to data ratio far below what is statistically feasible and would cause a high probability of Type I or II error (Burnham and Anderson 2002). Indirect effects of juvenile LKMRs may be less prevalent as juvenile rabbits are not reproductive and would not need to selectively avoid areas with high levels of potential nest predators. While my data does not elucidate the mechanism by which raccoons affect LKMRs, my results support anecdotal observations that raccoons pose a threat to the LKMR (Dorney 1954, McCleery et al. 2005, USFWS 2007).

I found a negative relationship between increasing patch edge, indicated by an increase in patch shape index, and both adult and juvenile LKMRs. Edge effects have not previously been investigated for the LKMR. The effect of edges on other species, particularly songbirds, are numerous and may include reduced density, distribution, and dispersal ability and increased rates of predation and parasitism (Yahner 1988). Lower densities of adult and juvenile LKMR in patches with high amounts of edge would suggest these patches would have a higher probability of extinction. Post hoc analyses using Spearman's rank correlation coefficient revealed a significant ($\rho = 0.16$, $P = 0.03$), positive correlation between patch shape index and raccoon activity and a significant ($\rho = 0.25$, $P = 0.001$), positive correlation between patch shape index and the total percent foliar cover of woody vegetation, thus supporting the hypothesis that increased edge is associated with increased raccoon activity and woody vegetation.

Habitat succession and raccoons appear to pose a threat to the persistence and recovery of LKMR populations. Recovery efforts should focus on reducing patch edge by simplifying patch boundaries, habitat restoration, and reducing the prevalence of raccoons in LKMR patches. These efforts are not mutually exclusive as habitat restoration efforts would reduce patch edge, increase the prevalence and diversity of herbaceous plants important to the LKMR, and may also reduce predation risks from raccoons. In addition, the ability of patch shape indices, measures of raccoon activity and particular herbaceous plant species to predict LKMR densities indicates these parameters are important indicators of patch quality and should be included in long-term monitoring strategies. Likewise, these variables could provide useful information in selecting and prioritizing which LKMR patches receive recovery actions and for monitoring the effectiveness of such activities.

CHAPTER III

LOWER KEYS MARSH RABBIT PATCH EXTINCTION AND COLONIZATION FOLLOWING HURRICANE WILMA

SYNOPSIS

Lower Keys marsh rabbits (LKMR, *Sylvilagus palustris hefneri*) are an endangered subspecies of marsh rabbit. Their remaining habitats are small and distributed in discrete patches; interactions between local populations drive extinction and colonization rates and determine metapopulation persistence. Hurricane Wilma provided a rare opportunity to quantify extinction and colonization rates and to determine the factors that influence LKMR metapopulation persistence. I determined patch level occupancy 6 to 9 months prior to Hurricane Wilma, within 6 months following the hurricane, and 2 years after the storm event to quantify extinction and colonization rates for 2 LKMR metapopulations. I used generalized linear regressions and model likelihood estimates to evaluate whether patch, habitat, or landscape characteristics had the greatest influence on the probability of LKMR patch extinction and colonization. I observed high LKMR patch extinction rates (59%) following Hurricane Wilma. I found LKMR patches farther from the coast had a lower extinction probability. I found extirpated patches closer to occupied LKMR patches and larger patches had higher colonization probabilities. Full recovery had not occurred 2 years after the storm indicating direct intervention following catastrophic events might be required to prevent extinction of local LKMR populations. My results suggest managers

should prioritize protection and management of large, inland LKMR patches to mitigate increased extinction risk caused by hurricanes.

INTRODUCTION

Coastal ecosystems have evolved under a regime of rising sea-level and recurring disturbance events such as hurricanes (Boose et al. 1994, Whittaker 1995, Michener et al. 1997). Human alteration and degradation of coastal ecosystems can exacerbate impacts from sea-level rise and hurricanes, particularly with flooding created by storm surges (Lotze et al. 2006). In the southeastern U.S., coastal areas have been altered by high rates of development that have imperiled species, reduced biodiversity and decreased resilience to disturbance (Michener et al. 1997, Lotze et al. 2006).

The effects of coastal development, sea-level rise and hurricanes are particularly pronounced in the Lower Keys, Florida. The Lower Keys form the terminal end of a string of limestone islands extending south and west from the southern tip of Florida. The Lower Keys are small ($\leq$2,600 ha) and geographically isolated, supporting a number of endemic plants (e.g., Big Pine partridge pea [*Chamaecrista lineata* var. *keyensis*]), animals (e.g., Key deer [*Odocoileus virginianus clavium*], Lower Keys marsh rabbit [hereafter LKMR, *Sylvilagus palustris hefneri*]), and community associations (e.g., pine rocklands) that either do not occur on the mainland U.S. or have very limited distributions (U.S. Fish and Wildlife Service 2008). Small geographic distributions and high rates of endemism in conjunction with extensive coastal development and sea-level rise threaten 22 species in the Lower Keys with extinction.

The synergism between development, sea-level rise and hurricanes is particularly relevant to the endangered LKMR. LKMRs are an endemic subspecies of marsh rabbit listed as endangered by the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission in 1990 (Lazell 1984, USFWS 1990). LKMRs occupy wet areas with dense cover including salt marsh, buttonwood transition zones, and freshwater marsh (Forys 1995, Faulhaber et al. 2007, 2008). Prior to receiving federal protection, LKMR habitats were lost and fragmented because their proximity to the water made them highly desirable for coastal development (USFWS 1990). Remaining LKMR habitats are small, averaging ≈ 4 ha, and distributed in discrete patches or sites that function as a classic metapopulation with interaction between local populations limited to dispersal of individuals outside their natal patch (Levins 1970, Forys 1995, Forys and Humphreys 1996, USFWS 1999).

Hurricanes are a common disturbance event in the Keys but storm surges associated with hurricanes, such as those following Hurricanes Betsy in 1965, Georges in 1998, and Wilma in 2005 are less common (Lopez et al. 2003, Kasper 2005). The Lower Keys have a maximum elevation of 3 m making these islands highly susceptible to both sea-level rise and storm surges (McGarry MacAulay et al. 1994, Ross et al. 1994). Hurricane Wilma made landfall on 24 October 2005 and produced a storm surge that inundated the Lower Keys with seawaters 1.5–2.4 m above mean sea level on 2 occasions causing substantial impacts to the vegetative communities and endangered species these islands support (Kasper 2005). The maximum surveyed surge on Boca Chica at the western edge of the LKMR range was 1.8 m and varied between 1.2-1.8 m on Big Pine Key at the eastern extent of their range (Federal Emergency Management Agency 2006). A population viability analysis found hurricanes modeled in combination with inbreeding depression increased the extinction risk for all LKMR metapopulations (Forys 1995, Forys and Humphrey 1999*a*). A more recent study predicted 3 scenarios (0.3 m, 0.6 m, and 0.9 m) of sea-level rise would reduce the total habitat available to LKMRs (LaFever et al. 2007). In addition, a recent status review acknowledged LKMR populations declined precipitously after Hurricane Wilma, but it did not specify the mechanisms that caused the decline (e.g., drowning or starvation) nor did it evaluate subsequent recovery (USFWS 2007). Threats to LKMRs due to sea-level rise and hurricanes may be exacerbated if recent studies that link increasing sea surface temperatures caused by global climate change to the increase in hurricane frequency in the North Atlantic Ocean region and the Gulf of Mexico are correct (Holland and Webster 2007).

Colonization of habitat patches extirpated following a disturbance event varies by taxa, generation time and dispersal ability (Whittaker 1995, Spiller et al. 1998). LKMRs and other lagomorphs that occur in successional habitats maintained by disturbance are selected for high reproductive rates and are well suited for dispersal (Forys and Humphrey 1996, Chapman and Flux 2008). Nonetheless, fragmentation caused by coastal development has reduced the number, size and proximity of LKMR populations and the dispersal corridors between them (Forys and Humphrey 1999*b*, USFWS 1999). The theory of island biogeography predicts smaller patches farther apart have a higher probability of extinction and a lower probability of recolonization following disturbances (MacArthur and Wilson 1967). The interspersion of LKMR patches with development should further influence LKMR dispersal and colonization of patches extirpated by disturbance events (Forys and Humphrey 1996). In addition, the proximity of remaining patches to the coast, patch elevation and vegetative community are all likely to influence the impact of hurricanes and flooding from storm surges on LKMR populations.

Persistence of a metapopulation following a catastrophic loss of local populations will require colonization rates that are equal to or greater than extinction rates (Hanski 1999). LKMR population monitoring following a catastrophic event such as Hurricane Wilma provides a rare opportunity to determine their rate of recovery through the quantification of extinction and colonization rates and to elucidate factors that ultimately determine metapopulation persistence. The goal of my study was to evaluate the metapopulation dynamics of the endangered LKMRs following Hurricane Wilma. My specific objectives were to quantify extinction and colonization of local patches after Hurricane Wilma and determine if patch and landscape configuration and habitat composition affect local population dynamics.

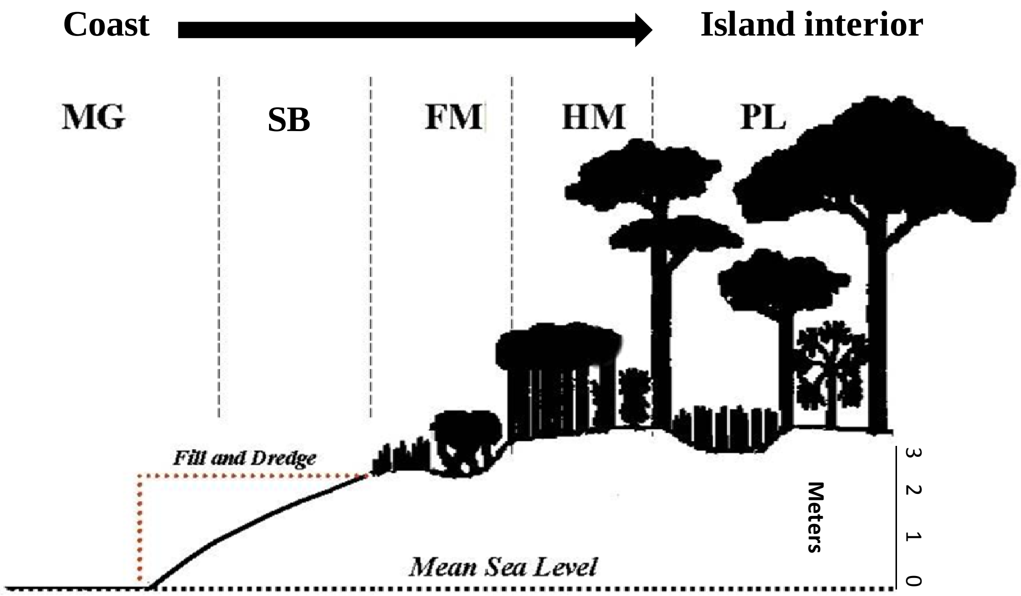

Figure 3.1. Vegetation types of the Lower Keys, Florida, USA. MG = mangroves and scrub mangroves, SB = salt marsh and buttonwood transition zone, FM = freshwater marsh, HM = hardwood hammock and freshwater hammocks, PL = pine rocklands and freshwater pinelands. Figure adapted from Lopez et al. (2004).

STUDY AREA

The Lower Keys, Florida, are located between 23.5 and 25.5° North latitude and exhibit a subtropical climate due to the Gulf Stream and other maritime influences (Fig. 2.1, Chen and Gerber 1990; Forys and Humphrey 1999*a*). The climate is characterized by distinct wet and dry seasons, with the dry season (November through April) contributing <33% of annual precipitation (Forys and Humphrey 1999*a*). Elevations rarely exceed 2 m, with slight variations in elevation producing distinct vegetation communities that transition from mangroves to coastal salt marsh/buttonwood transition zones inland to freshwater marshes, pine rocklands and tropical hardwood hammocks (Fig. 3.1, McGarry MacAulay et al. 1994).

LKMRs have been predominately found in coastal salt marsh prairies and freshwater marshes (Faulhaber et al. 2007). Coastal salt marsh prairies, also known as buttonwood transitions zones are characterized by cord grasses (*Spartina spp*.), sea daisies (*Borrichia spp*.), glassworts (*Salicornia spp*.), seashore dropseed (*Sporobolus virginicus*) and rushes (family *Cyperacea*) with salt tolerant hardwoods, predominantly buttonwood but also with white mangrove (*Laguncularia racemosa*), red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), joewood (*Jaquinia keyensis*), poisonwood (*Metopium toxiferum*) and wild dilly (*Manilkara bahamensis*) (Faulhaber 2003). Freshwater marshes are characterized by sawgrass (*Cladium jamaicensis*) and Gulf Coast spike rush (*Eleocharis cellulose*) interspersed with buttonwood (*C. erectus*) and other hardwoods depending on disturbance history (e.g., fire, cutting) and salinity.

LKMRs currently occupy 4 main islands (Boca Chica, Saddlebunch, Sugarloaf, and Big Pine keys) and several smaller, outlying islands (Fig. 2.1, Faulhaber et al. 2007). Because LKMRs occur in 2 genetically distinct management units or clades, I examined metapopulation dynamics on Boca Chica Key and Big Pine Key, the 2 largest subpopulations representative of the geographic extent of this subspecies (Faulhaber et al. 2007). Boca Chica Key is lower in elevation, generally has fewer upland habitats and lacks pine rocklands and freshwater pinelands present on Big Pine Key (McGarry MacAulay et al. 1994).

METHODS

To evaluate the effects of Hurricane Wilma on the metapopulation dynamics of LKMRs, I quantified extinction and colonization rates for 2 metapopulations within the LKMR distribution, Boca Chica and Big Pine keys. I determined patch level occupancy using data collected 6 to 9 months prior to Hurricane Wilma (survey period 1), within 6 months following the hurricane (survey period 2) and 2 years after the storm event (survey period 3). I determined patch level occupancy using 1 of 2 established monitoring protocols (Faulhaber et al. 2007, Schmidt 2009). One protocol used 1 observer to search within LKMR patches that were delineated during an updated distribution survey by the USFWS (Faulhaber et al. 2007). The observer navigated to a randomly selected start point and then walked in expanding concentric circles. The observer searched until LKMR pellets were found or until 15 minutes had elapsed. I used data collected with this method to determine patch occupancy for both Boca Chica and Big Pine keys during survey period 1 and for Big Pine Key during survey period 2.

For the second protocol, I constructed a 30 x 30-m grid and placed it over a shapefile of the Lower Keys using a Geographic Information System (GIS; ArcGIS 9.3, ESRI 2008). Grid nodes falling within the boundaries of LKMR patches on Boca Chica and Big Pine keys were selected and stored within the GIS. I sampled grid nodes within each patch by searching within a 1-m radius of each node (the sample unit) and recording the presence or absence of LKMRs pellets.

I classified patches as occupied if any sample unit within the patch contained at least 1 pellet. To estimate the probability of failure to detect LKMRs when present, I randomly selected 40 patches to be re-surveyed in 2008. Using a removal design, I resurveyed patches where rabbits were not detected in the first survey until rabbit presence was detected or for a maximum of 3 surveys (assuming a detection probability >0.6 and an occupancy estimate <0.5; MacKenzie and Royle 2005). I then used Program MARK to estimate detection probability for LKMR surveys (White and Burnham 1999). I used data collected with the second method to determine patch occupancy for survey periods 2 and 3 on Boca Chica Key and survey period 3 on Big Pine Key.

To calculate the number of extinction events following Hurricane Wilma, I counted the number of unoccupied patches during survey period 2 that were occupied in survey period 1 (prior to the hurricane). To calculate the number of colonization events after Hurricane Wilma, I counted patches occupied 2 years after the storm that were not occupied 6 months after the storm. I calculated recovery rates as the percent of patches extirpated within 6 months of Hurricane Wilma that were recolonized within 2 years.

Patch and Landscape Characteristics

The theory of island biogeography predicts larger islands, in this case LKMR patches that are larger will have a lower extinction probability and islands that are closer to source populations will have higher colonization probabilities. I predicted rabbit patches farther from the coast (storm surge) would have a lower extinction probability. Due to the level of empirical support for the relationship between extinction and colonization rates as functions of area and distance, I analyzed these 2 predictors together as a null hypothesis model. I also examined several additional factors thought to influence extinction and colonization rates. It has been proposed that upland habitats such as hammocks and pinelands provide refugia for LKMRs during flooding associated with severe storm events (Faulhaber et al. 2008). In addition, saltwater inundation from storm surges may disproportionately affect the suitability of salt-intolerant upland (pine rockland and hammock) and low-lying freshwater habitats (freshwater marsh, freshwater pineland and freshwater hammock) used by LKMRs. I expected LKMR patches with higher proportions of salt-intolerant vegetation would have higher extinction rates. Dispersing rabbits used densely vegetated native habitats including mangroves, hammocks, and transition zones more than expected and used disturbed habitats less than expected (Forys and Humphrey 1996). I would therefore, expect buffers of extirpated patches with high proportions of LKMR habitat or suitable vegetation types to have higher colonization rates following Hurricane Wilma than patches that have buffers with high proportions of unsuitable land types.

I quantified patch and landscape characteristics predicted to influence extinction and colonization rates. I used Hawth's Analysis Tools for ArcGIS (Beyer 2004) to calculate patch area (area [ha]), to measure the minimum straight line distance between the centroid of each patch and the coast (dcoast [km]), and to measure the minimum straight line distance from the centroid of extirpated patches to the centroid of the nearest patch occupied during survey period 2 (dpatch [km]). To calculate the proportion of each vegetation type in a patch, I used the Advanced Identification of Wetlands (ADID) GIS coverage vegetation classifications developed by the Florida Marine Research Institute (McGarry MacAulay et al. 1994). I grouped vegetation types according to various levels of salt tolerance as follows: salt-intolerant low-lying wetlands including freshwater marsh, freshwater pineland, and freshwater hammock (fm); highly salt-tolerant mangrove and scrub mangrove (mg); salt-intolerant upland pine rockland and low-lying freshwater pineland (pl); variably salt-tolerant mangrove, scrub mangrove, buttonwood transition, and salt marsh (salt); and moderately salt-tolerant buttonwood transition and salt marsh (sb). Overlap in vegetation classifications (e.g., salt marsh being in 2 categories) allowed me to test multiple competing hypotheses to evaluate whether varying degrees of salt-tolerance affected LKMR extinction and colonization rates. For example, if I found support for a model with all 4 salt tolerant vegetation classifications (mangrove, scrub mangrove, buttonwood transition, and salt marsh), I could evaluate whether the degree of salt-tolerance affected extinction rates by simultaneously evaluating support for models with highly salt-tolerant vegetation (mangrove, scrub mangrove) and moderately salt-tolerant vegetation (buttonwood transition and salt marsh).

I created a 300-m buffer around each patch's perimeter using Hawth's Analysis Tools for ArcGIS (Beyer 2004) to classify land surrounding extirpated patches. The average distance traveled by dispersing LKMRs was previously estimated at 300 m (Forys 1995, LaFever et al. 2008). I then used ADID maps to calculate the proportion of patch buffers in each of the following land classifications: developed land (devel); freshwater marsh, freshwater pineland, and freshwater hammock (fm); mangrove and scrub mangrove (mg); other delineated rabbit patches (patch); roads (road); all natural land potentially suitable for LKMRs including (mangrove, scrub mangrove, buttonwood transition, salt marsh, pine rockland, hammock, freshwater marsh, freshwater pine rockland and freshwater hammock [suit]): buttonwood transition and salt marsh (sb); upland hammock and pine rockland (up); developed land, open water and roads unsuitable for LKMRs (unsuit); and open water beyond coastline (water).

Data Analysis

To determine which patch, habitat, and landscape characteristics had the greatest influence on the probability of LKMR patch extinction and colonization following Hurricane Wilma, I used generalized linear regressions and model likelihood estimates to relate explanatory variables to patch extinction and colonization events. For the first analysis patches were classified as 1 if an extinction event occurred and 0 otherwise. For the second analysis patches were classified as 1 if a colonization event occurred and 0 otherwise. I used an information theoretic approach to evaluate the relative fit of a suit of potential models (Burnham and Anderson 2002). I used SPSS software (Release 15.0.0, 2006) to run a small number of a priori model sets specific to extinction and colonization events fitted to a binomial distribution (Burnham and Anderson 2002). To evaluate the effect of patch and habitat variables on the probability of LKMR patch extinction, I evaluated11 a priori models, a null hypothesis model evaluating the effect of patch area and distance from coastline, and an intercept-only (null) model using Akaike's Information Criterion corrected for small sample size (AIC_c, Burnham and Anderson 2002, Table 3.1, models 1–13). To evaluate the effect of patch and buffer characteristics on LKMR colonization, I evaluated 12 a priori models, a null hypothesis model evaluating the effect of patch area and distance to the nearest occupied patch, and an intercept-only (null) model using AIC_c (Table 3.2, models 14–27). I used the relative difference to the smallest AIC_c in each model set (ΔAIC_c) and Akaike weights (w_i) to select the best approximating models (Burnham and Anderson 2002). I considered models ≤ 2 AIC_c units to compete with the best models and discarded model >2 AIC_c units as unlikely representations of the data (Burnham and Anderson 2002). I then exponentiated the binomial regression analysis of the selected models to derive a prediction equation that I used to evaluate the influence of the best models' variables on the probability of patch extinction and colonization (Agresti 2007, Guthrey and Bingham 2007). To plot the effect of each covariate on patch colonization rates, I held the other covariate in the exponentiated equation constant at its average and allowed the plotted covariate to vary throughout its range.

Table 3.1. A priori models evaluating patch and landscape characteristics hypothesized to influence patch extinction following Hurricane Wilma for 51 Lower Keys marsh rabbit patches in the Lower Keys, Florida, USA, between 2004 and 2005. This table displays the number parameters (K), -2* natural log of the maximum likelihood estimate ($-2\ln L$), Akaike's Information Criterion adjusted for small sample size (AIC_c), change in AIC_c from the smallest AIC_c value (ΔAIC_c), and Akaike weights (w_i) for each model.

	Model [a]	K	$-2\ln L$	AIC_c	ΔAIC_c	w_i
1	DCoast	2	64.4	68.6	0.0	0.20
2	DCoast+area	3	62.6	69.1	0.5	0.16
3	DCoast+salt	3	63.1	69.6	1.0	0.12
4	DCoast+sb	3	63.6	70.1	1.5	0.09
5	DCoast+mg	3	63.9	70.4	1.8	0.08
6	DCoast+fm	3	64.2	70.7	2.1	0.07
7	Salt	2	66.6	70.8	2.2	0.07
8	SB	2	66.6	70.9	2.3	0.06
9	Null	3	69.1	71.2	2.6	0.05
10	Area	2	68.3	72.6	4.0	0.03
11	Mg	2	68.8	73.0	4.4	0.02
12	Fm	2	69.0	73.3	4.7	0.02
13	Pl	2	69.0	73.3	4.7	0.02

[a] Variable notation for patch attributes: null = intercept only, dCoast = distance from each patch centroid to the nearest coastline (km), area = rabbit patch area (ha), all remaining variables are the % each patch in that land classification: fm = freshwater marsh, freshwater pine rockland and hammock; mg = mangrove and scrub mangrove; pl = pine rockland and freshwater pinelands; salt = buttonwood transition, mangrove, salt marsh, and scrub mangrove; sb = buttonwood transition and salt marsh.

Table 3.2. A priori models evaluating patch and landscape characteristics hypothesize to influence patch colonization following Hurricane Wilma for 47 Lower Keys marsh rabbit patches in the Lower Keys, Florida, USA, between 2005 and 2008. This table displays the number parameters (K), -2* natural log of the maximum likelihood estimate (-2ln*L*), Akaike's Information Criterion adjusted for small sample size (AIC_c), change in AIC_c from the smallest AIC_c value (ΔAIC_c), and Akaike weights (w_i) for each model.

Model [a]		K	-2ln*L*	AIC_c	ΔAIC_c	w_i
14	DPatch+area	3	41.42	48.0	0.0	0.97
15	Area	2	51.99	56.3	8.3	0.02
16	DPatch	2	53.02	57.3	9.3	0.01
17	Water	2	56.04	60.3	12.3	0.00
18	Devel	2	56.61	60.9	12.9	0.00
19	Null	1	61.51	63.6	15.6	0.00
20	Road	2	60.52	64.8	16.8	0.00
21	Mg	2	61.16	65.4	17.4	0.00
22	Up	2	61.30	65.6	17.6	0.00
23	Sb	2	61.31	65.6	17.6	0.00
24	Patch	2	61.39	65.6	17.6	0.00
25	Suit	2	61.42	65.7	17.7	0.00
26	Fm	2	61.40	65.7	17.7	0.00
27	Unsuit	2	61.50	65.8	17.8	0.00

[a] Variable notation for patch attributes: null = intercept only, dPatch = distance from each patch centroid to the nearest coastline (km), area = rabbit patch area (ha). The following attributes are the land classification of each patch's buffer zone (%): devel = developed land; fm = freshwater marsh, pineland and hammock; mg = mangrove and scrub mangrove; patch = other delineated rabbit patches; road = roads; suit = suitable (all natural land classifications); sb = buttonwood transition and saltwater marsh; up = uplands (hammock and pineland); unsuit = unsuitable (development, open water and roads); water = open water beyond coastline.

Table 3.3. Number of Lower Keys marsh rabbit patches occupied by island and vegetation classification (salt-intolerant lowland and uplands = freshwater marsh, freshwater pineland, freshwater hammock and pine rockland; moderately salt-tolerant inland marsh = buttonwood transition and salt marsh; and highly salt-tolerant mangrove and scrub mangrove) for patches surveyed 6–9 months prior to Hurricane Wilma (October 2005), 6 months and 2 years after the hurricane.

Island Vegetation classification	Pre-Hurricane (6–9 months)	Post-Hurricane (6 months)	Post-Hurricane (24 months)
		Patches occupied	
Big Pine Key	26	10	14
Freshwater lowlands and uplands	17	8	10
Inland salt marsh	8	2	3
Mangrove	1	0	1
Boca Chica Key	25[a]	11[a]	20[a]
Freshwater lowlands and uplands	1	1	2
Inland salt marsh	12	5	8
Mangrove	10	3	8

[a] Two patches on Boca Chica Key did contain any of these vegetation classifications.

RESULTS

With assistance from the USFWS, I surveyed Boca Chica and Big Pine keys prior to Hurricane Wilma from 1 January–30 March 2004 (survey period 1), following the hurricane from 13 November 2005–7 March 2006 (survey period 2) and 2 years after the hurricane from 10 December 2007–26 February 2008 (survey period 3). Seventy patches were monitored in both survey period 1 and 2. For both Boca Chica and Big Pine Key, I found 51 patches were occupied during survey period 1; however, 21 of the 51 (41%) occupied patches during period 1 were still occupied during period 2, whereas 30 (59%) were extirpated. Between survey periods 1 and 2, I observed extinctions in 14 of 25 (56%) occupied patches on Boca Chica Key and in 16 of 26 (62%) occupied patches on Big Pine Key. Of the 21 patches that were occupied 6 months after the hurricane, 11 were on Boca Chica Key and 10 were on Big Pine Key. Vegetation classifications for patches occupied during all survey periods are summarized in Table 3.3. Of the 69 patches I monitored in both survey period 2 and 3, 47 were not occupied during survey period 2. Seventeen of the 47 (36%) unoccupied patches were colonized by survey period 3 and 30 remained unoccupied. I observed colonizations in 10 of 17 unoccupied patches (59%) on Boca Chica Key and in 7 of 30 unoccupied patches (23%)

on Big Pine Key during period 3. Recovery rates following Hurricane Wilma were 71% on Boca Chica Key and 44% on Big Pine Key. Detection probabilities for the second survey methodology used during survey period 3 were $\geq$0.85. Detection probability did not improve by increasing the number of surveys.

Evaluating extinction probability, I found models 1–5 best approximated the data (Table 3.1). Models that included the distance to coastline (km) had a combined w_i = 0.72 indicating a 72% probability one of these 5 models best explained the data. Models 2–5 all contained distance to coastline (km) plus 1 additional parameter and were within 2 ΔAIC_c units of the best model. This scenario results because models 2–5 each added 1 additional parameter that was not a relevant predictor of extinction probability (Burnham and Anderson 2002). I found patches farther inland had a lower probability of extinction ($\hat{\beta} = -1.82$, 95% $CI = -3.54$ to -0.10) than patches closer to the coast (Fig. 3.2). Patches that went extinct after Hurricane Wilma were on average 0.57 km from the coast while patches that remained occupied were on average 0.79 km from the coast (Table 3.4).

Evaluating colonization probability, I found model 14 best approximated the data and had a $w_i = 0.97$ indicating there was a 97% probability the null hypothesis model best explained the data (Table 3.2). When I examined the individual parameters of this model, the parameter estimates and 95% *CI* did not contain 0 indicating both the distance (km) to the nearest patch occupied in survey 2 and patch area (ha) were relevant predictors of patch colonization. I found LKMR patches farther from patches occupied immediately following Hurricane Wilma had a lower probability of colonization ($\hat{\beta}$ = −1.83, 95% *CI* = −3.61 to −0.06) than patches that were closer to patches occupied after the hurricane [Fig. 3.3(a)]. I found large patches had a higher probability of colonization ($\hat{\beta}$ = 0.36, 95% *CI* = 0.01 to 0.71) following Hurricane Wilma than small patches [Fig. 3.3(b)]. Patches that were recolonized following Hurricane Wilma were on average 0.59 km from an occupied patch and 8.03 ha in size (Table 3.5). Patches that remained unoccupied 2 years following Hurricane Wilma were on average 1.56 km from an occupied patch and were 2.03 ha in size.

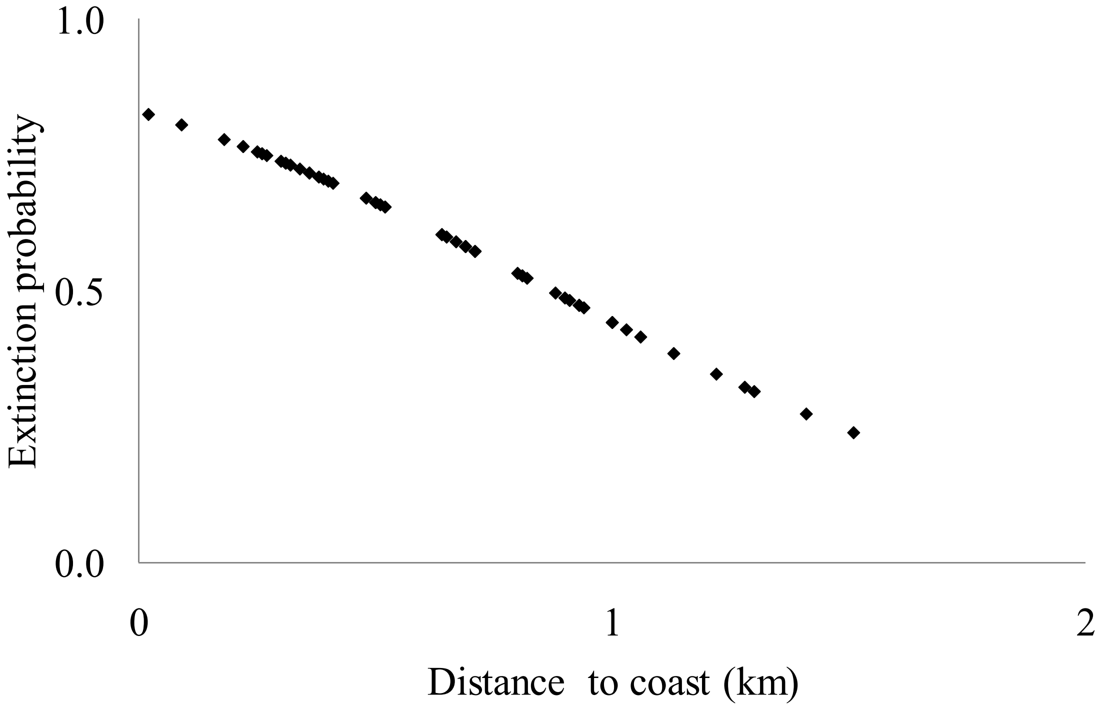

Fig. 3.2. Estimated probability of extinction following Hurricane Wilma (24 October 2005) as a function of the distance from an occupied to the coast for Lower Keys marsh rabbit patches in the Lower Keys, Florida, USA.

Table 3.4. Range, mean and standard errors for variables hypothesized to influence extinction of Lower Keys marsh rabbit patches 6 months following Hurricane Wilma's landfall (24 October 2005) in the Lower Keys, Florida, USA.

Predictor [a]	Extinction	Min.–Max.	$\bar{x}$ (*SE*)
Area (ha)	Y	0.10–51.20	5.21 (1.81)
Area (ha)	N	0.20–44.00	7.94 (2.47)
Dcoast (km)	Y	0.02–1.28	0.57 (0.06)
Dcoast (km)	N	0.18–1.51	0.79 (0.08)
Fm (%)	Y	0.00–100.00	35.99 (8.16)
Fm (%)	N	0.00–100.00	39.38 (9.75)
Mg (%)	Y	0.00–88.17	10.08 (4.61)
Mg (%)	N	0.00–88.84	14.24 (5.24)
Pl (%)	Y	0.00–57.47	8.89 (3.14)
Pl (%)	N	0.00–66.80	10.44 (4.29)
Salt (%)	Y	0.00–100.00	51.51 (7.42)
Salt (%)	N	0.00–97.38	33.37 (8.68)
Sb (%)	Y	0.00–99.67	33.43 (6.52)
Sb (%)	N	0.00–74.78	19.13 (5.80)

[a] Variable notation for patch attributes: area = rabbit patch area (ha), dCoast = distance from each patch centroid to the nearest coastline (km), all remaining variables are the % each patch in that land classification: fm = freshwater marsh, pineland and hammock, mg = mangrove and scrub mangrove, pl = pine rockland, salt = buttonwood transition, mangrove, saltwater marsh, and scrub mangrove, sb = buttonwood transition and saltwater marsh.

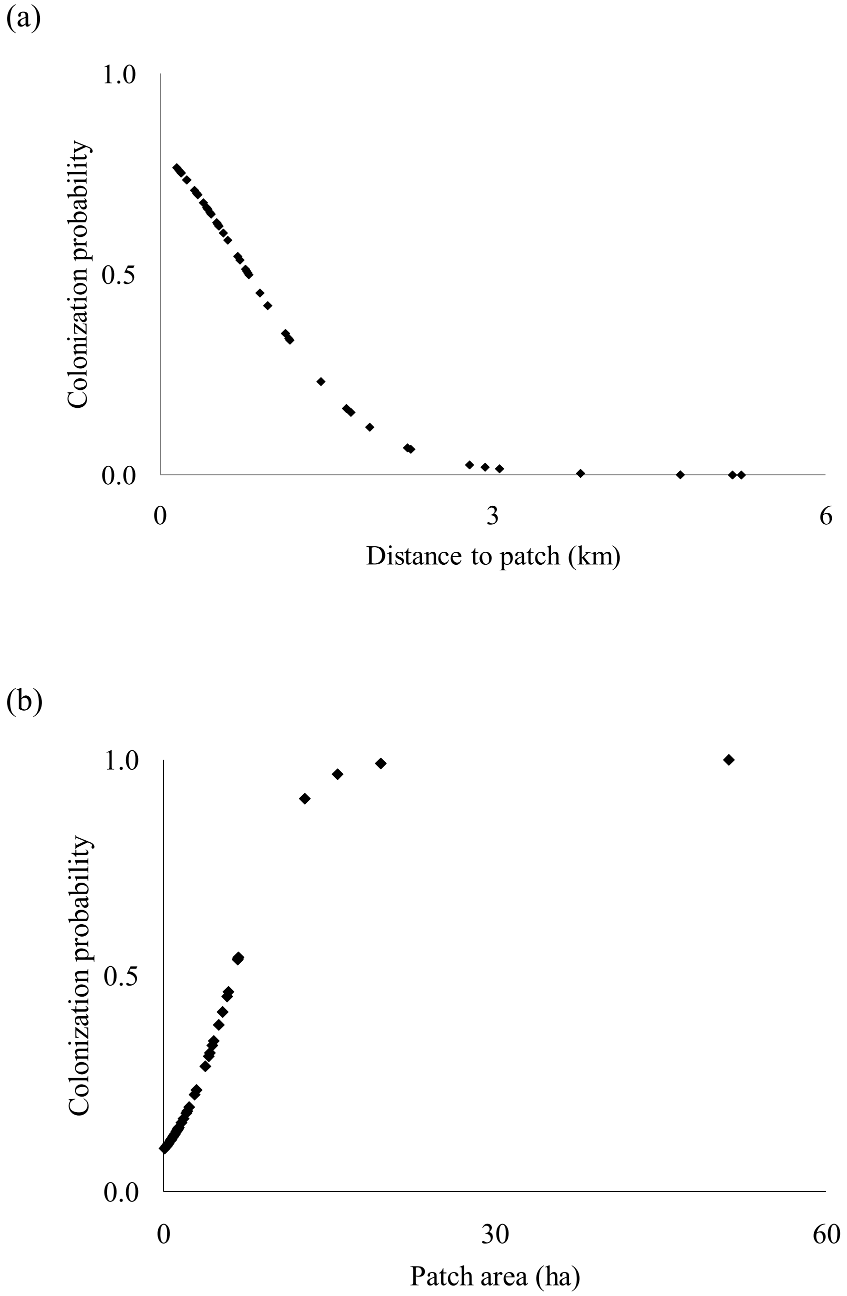

Figure 3.3. Estimated probability of colonization 2 years following Hurricane Wilma (24 October 2005) as a function of (a) the minimum distance from an extirpated patch to an occupied patch (km) holding area constant at its mean and (b) patch area (ha) holding the minimum distance from an extirpated patch to an occupied patch constant at its mean for Lower Keys marsh rabbit patches in the Lower Keys, Florida, USA.

Table 3.5. Range, mean and standard errors for variables hypothesized to influence colonization for Lower Keys marsh rabbit patches 2 years following Hurricane Wilma's landfall (24 October 2005) in the Lower Keys, Florida, USA.

Predictor [a]	Colonization	Min.–Max.	$\bar{x}$ (*SE*)
Area (ha)	Y	0.31–51.15	8.03 (3.02)
Area (ha)	N	0.12–6.79	2.03 (0.37)
Dpatch (km)	Y	0.15–1.72	0.59 (0.10)
Dpatch (km)	N	0.18–5.24	1.56 (0.28)
Devel (%)	Y	4.00–67.00	28.41 (5.04)
Devel (%)	N	0.00–49.00	16.37 (2.75)
Fm (%)	Y	0.00–46.00	6.76 (3.31)
Fm (%)	N	0.00–38.00	5.60 (1.92)
Mg (%)	Y	0.00–36.00	15.29 (2.92)
Mg (%)	N	0.00–49.00	17.70 (2.66)
Patch (%)	Y	0.59–27.91	10.22 (2.26)
Patch (%)	N	0.00–31.22	9.30 (1.50)

[a] Variable notation for patch attributes: area = rabbit patch area (ha) and dpatch = distance from each patch centroid to the nearest coastline (km). The following attributes are the land classification of each patch's buffer zone (%): devel = developed land; fm = freshwater marsh, pineland and hammock; mg = mangrove and scrub mangrove; patch = other delineated rabbit patches; road = roads; sb = buttonwood transition and saltwater marsh; suit = suitable (all natural land classifications); unsuit = unsuitable (development, open water and roads); up = uplands (hammock and pineland); and water = open water beyond coastline.

Table 3.5. continued.

Predictor	Colonization	Min. – Max.	$\bar{x}$ (*SE*)
Sb (%)	Y	0.00–21.00	5.94 (1.46)
Sb (%)	N	0.00–23.00	6.77 (1.16)
Suit (%)	Y	17.00–92.00	53.24 (6.04)
Suit (%)	N	18.00–91.00	55.30 (4.11)
Unsuit (%)	Y	4.00–67.00	35.94 (4.93)
Unsuit (%)	N	0.00–82.00	35.27 (4.44)
Up (%)	Y	0.00–90.00	18.71 (6.00)
Up (%)	N	0.00–92.00	22.10 (4.66)
Water (%)	Y	0.00–38.00	6.18 (2.34)
Water (%)	N	0.00–69.00	16.93 (3.45)

DISCUSSION

I observed high LKMR patch extinction (59%) within 6 months following Hurricane Wilma. Two years after the storm, 47 of 69 monitored patches remained unoccupied and the number of patches colonized (17) was only 57% of the number of patches that went extinct (30), indicating this storm event further threatened the viability of LKMRs. LKMR populations on Boca Chica Key had recovered more (71%) 2 years after the storm than had populations on Big Pine Key (44%). High rates of detection indicate misclassifying an occupied LKMR patch as unoccupied was not likely (<15%) and that subsequent estimates of extinction and colonization rates should not have been biased by false absences or detections (MacKenzie et al. 2006).

A population viability analysis of LKMRs conducted in the 1990s estimated a 100% probability of extinction within 50 years and that the Boca Chica Key metapopulation was likely to go extinct faster than the Big Pine Key metapopulation. (Forys and Humphrey 1999*a*). Forys and Humphrey (1999*a*) suggested larger patches, like those found in the Big Pine Key metapopulation had a greater affect on the viability of LKMRs than hurricanes or inbreeding depression from decreased rates of dispersal. My results indicate hurricanes and storm surges increase the probability of metapopulation extinction and that extinction and colonization patterns following severe storm events were not consistent throughout the range of LKMRs.

Patterns of local extinction following Hurricane Wilma were a function of the distance of a LKMR patch from the coastline. Patches within 0.10 km of the coastline were 2 times more likely to go extinct than patches 1 km farther inland (Fig 3.2). The most inland patch was 1.5 km from the coastline and had an extinction probability of 0.25 indicating LKMRs will remain susceptible to hurricane effects due to the small size of the islands that support them. Patch elevation is a function of distance from the coastline with salt-intolerant uplands located farther inland (Folk 1991, McGarry MacAulay et al. 1994, Lopez et al. 2004). Lower extinction rates of inland patches following Hurricane Wilma appear to support the hypothesis that upland habitats provide refugia for LKMRs during storm surges (Faulhaber et al. 2008). I did not find that proportion of salt-tolerant habitats within LKMR patches affected extinction probability; however, I may not have been able to detect an effect of habitat composition due to the small proportion of freshwater and upland habitats delineated within LKMR patches.

Patterns of colonization 2 years after Hurricane Wilma were a function of the distance between an extirpated LKMR patch and the nearest occupied patch and patch size. A patch of average size (~4 ha) had an estimated colonization probability of 0.3 while the largest patch (~51 ha) had an estimated colonization probability of 1. Extirpated patches >3 km from an occupied patch had a colonization probability of 0, consistent with the maximum distance recorded for a dispersing LKMR (Forys and Humphrey 1996). Development of coastal areas within the LKMRs' range has been attributed to their decline but development and roads within 300 m of unoccupied patches had no effect on colonization patterns following Hurricane Wilma. Dispersing LKMRs were previously found to use densely vegetated natural communities more than expected and used disturbed areas less than expected (Forys and Humphrey 1996). I did not find that the extent and type of natural community or disturbed land including roads and development within 300 m of unoccupied patches effected colonization patterns.

Recolonization of habitat islands or patches extirpated following a disturbance event varies by taxa and is determined by generation time and dispersal ability (Whittaker 1995, Spiller et al. 1998). The role of island area and distance in determining extinction and colonization rates following disturbance events also has been supported empirically for arthropods of the Florida Keys (Simberloff and Wilson 1969, Simberloff 1976) and for a lizard of the Bahamas (Schoener et al. 2001). Systems and species occurring in disturbance-prone coastal areas have evolved mechanisms to cope with partial or total losses of local populations including losses associated with fluctuating habitat availability following a catastrophic event (Travis and Dytham 1999).

LKMRs are selected for high reproductive rates and are well suited for dispersal indicating they should recover from disturbance events such as hurricanes that occur throughout their geographic range (Forys and Humphrey 1996, Chapman and Flux 2008). My results indicate LKMRs have only partially recovered from the effects of Hurricane Wilma and the associated flooding. The effect of individual storm events in conjunction with sea-level rise may result in changes to ecosystems that reduce the amount and quality of habitat available below the amount required for species recovery (Keymer et al. 2000). Impacts associated with Hurricane Wilma and prior storms (e.g., Hurricanes Betsy and Georges) may have impaired the ability of the Big Pine Key metapopulation to recover.

Extinction and colonization thresholds must be understood to effectively protect and recover endangered species, such as LKMRs, that have been heavily impacted by coastal development and are predicted to be further impacted by habitat loss associated with sea-level rise. My findings suggest managers should prioritize protection and management of large, inland LKMR patches to mitigate increased risks associated with hurricanes and rising sea-levels. These efforts will ensure protection of local LKMR populations most likely to recover following disturbance events. High colonization rates following large numbers of extinctions indicates LKMRs are adept at finding empty habitat patches and that translocation to empty patches within the maximum dispersal distance is not likely to improve their viability. Rather, recovery efforts should focus on improving the habitat quality and carrying capacity of large, inland patches that will serve as source populations thus improving LKMR metapopulation recovery following disturbance events including hurricanes.

CHAPTER IV

EFFECTS OF PRESCRIBED FIRE ON THE LOWER KEYS MARSH RABBIT

SYNOPSIS

Prescribed fire in coastal salt marsh prairies of the Lower Keys and its effects on the Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*) have not been evaluated. I evaluated the effects of prescribed fire on LKMR densities and coastal salt marsh habitat. I burned 2 occupied LKMR patches and sampled LKMR pellets, woody and herbaceous foliar cover, and distribution of herbaceous bunchgrasses and forbs availability using a standardized grid. I used 10-m transects to estimate maximum vegetation height, canopy cover, vegetation density, and diversity. Surveys were conducted prior to the burn (February 2007) and 3 times post-burn (3 months, 9 months, and 18 months). I compared changes in response variables between pre-fire surveys and each post-fire survey. Differences between control and burn units for each site were compared using a Kruskal-Wallis test. Following the burns, adult pellets increased (P = 0.011) in one burn unit by the third post-fire survey. Juvenile pellets decreased in one burn unit by the second (P = 0.002) and third (P = 0.029) post-fire surveys. Woody vegetation for one burn unit had decreased by the first (P = 0.012) and third (P < 0.001) post-fire survey. The distribution of herbaceous bunchgrasses and forbs increased (P = 0.032) in one burn unit by the second post-fire survey. Vegetation height (m), canopy cover (%) or diversity remained the same for all surveys. Vegetation density was lower (P = 0.039) in one burn unit by the first post-fire survey. My results provide initial support for use of prescribed fire to restore coastal salt marshes for the benefit of

LKMRs. I recommend various prescribed fire applications and resulting fire behavior be evaluated for use in managing LKMR habitats.

INTRODUCTION

The Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*) is a subspecies of marsh rabbit found in the southeastern United States (Lazell 1984) and listed as endangered by the U.S. Fish and Wildlife Service (USFWS) and the Florida Fish and Wildlife Conservation Commission (USFWS 1990). LKMRs are endemic to the Lower Keys that form the terminal end of a string of limestone islands extending south and west from the southern tip of Florida. LKMRs recovery is limited by habitat loss, fragmentation, predation by cats, and road mortalities caused by automobiles (USFWS 1999).

LKMRs are most often found in coastal salt marsh prairies and buttonwood (*Conocarpus erectus*) transition zones but also in freshwater marshes (Forys 1995, Faulhaber et al. 2007). LKMRs use habitats with dense, low (<1 m) forbs and grasses with little overstory vegetation. They avoid areas with mature buttonwoods, high canopy cover and low ground cover (Perry 2006, Faulhaber et al. 2008). Coastal salt marsh prairie in the late successional stage can be characterized by a dense canopy of hardwoods, particularly buttonwoods, and reduced grasses and forbs. Hardwood encroachment of coastal wetlands has been documented for the Lower Florida Keys including areas used by LKMRs (Dickson 1955, Alexander and Dickson 1970). This hardwood encroachment along with fragmentation has been attributed to LKMR population declines observed over the past 3 decades (USFWS 1999) and is likely detrimental to LKMR viability (Perry 2006). Protection and management of remaining coastal prairie fragments is imperative to meet the recovery goals of this subspecies and to protect this unique ecosystem (Perry 2006).

Mechanical removal of hardwood vegetation or inception of a prescribed fire regime in the buttonwood transition zone and high salt marsh could enhance LKMR habitat by promoting understory vegetation (Recovery action H2.4, USFWS 1999; Perry 2006). An appropriate fire regime could prevent late succession woody encroachment in important habitats and promote regeneration of forbs and grasses that are important resources for LKMR (Perry 2006).

Although fire from early Native Americans, lightning strikes, or spread from adjacent fire-dependent habitats (e.g., pine rocklands) has been integral to the ecology of southern Florida and the Lower Florida Keys, fires have been suppressed in the Lower Keys since the 1960's and 1970's (USFWS 2000). Prior to this period, accounts noted the open nature of coastal salt marsh prairies in areas historically occupied by LKMRs (N. Silvy, Texas A&M University, personal communication), conditions that favor herbaceous species important to LKMR for food, cover and nesting (e.g., Gulf cordgrass (*Spartina spartinae*), seashore dropseed (*Sporobolus virginicus*), and sea oxeye daisy (*Borrichia frutescens*). Additionally, early settlers of the Lower Keys harvested buttonwood from coastal salt marsh prairies to produce charcoal; this process would have created a more open coastal salt marsh prairie (Viele 1996). Prescribed fire has been used throughout south Florida ecosystems to restore and maintain fire adapted habitats (Wade et al. 1980); however, the use of prescribed fire in coastal salt marsh prairies of the Lower Keys or its effects on LKMRs has yet to be evaluated.

The Naval Air Station Key West (NASKW) on Boca Chica Key currently has the highest density of occupied LKMR patches within the subspecies' range (USFWS 2007). Increased canopy cover and woody vegetation are an airfield management and safety concern because this vegetation reduces visibility in airfield clearance zones. Prescribed fire may be an effective management tool to maintain vegetation within the NASKW airfield while simultaneously restoring the coastal prairie ecosystem for LKMR. My objective was to evaluate the use of prescribed fire in maintaining coastal salt marsh prairies important to LKMRs. I compared LKMR densities, foliar cover, and distribution of herbaceous bunchgrasses and forbs in burned and unburned patches of coastal salt marsh prairie and determined if prescribed fire changed the overall vegetative composition of coastal salt marsh prairies.

STUDY AREA

The Lower Keys, Florida, are located between approximately 23.5 and 25.5 degrees North latitude and exhibit a subtropical climate due to the Gulf Stream and other maritime influences (Fig. 2.1, Chen and Gerber 1990; Forys and Humphrey 1999*a*). The climate is characterized by distinct wet and dry seasons, with the dry season (November through April) contributing less than one third of annual precipitation (Forys and Humphrey 1999*a*). Elevations rarely exceed 2 m, with distinct variations in elevation producing distinct vegetation communities that transition from mangroves to coastal salt marsh/buttonwood transition zones inland to freshwater marshes, pine rocklands and tropical hardwood hammocks (McGarry MacAulay et al. 1994).

Coastal salt marsh prairies, also known as buttonwood transitions zones are characterized by cord grasses (*Spartina spp*.), sea daisies (*Borrichia spp*.), glassworts (*Salicornia spp*.), seashore dropseed and rushes (Family *Cyperacea*) with various densities of salt tolerant hardwoods, predominantly buttonwood (*C. erectus*) but also with white mangrove (*Laguncularia racemosa*), red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), joewood (*Jaquinia keyensis*), poisonwood (*Metopium toxiferum*) and wild dilly (*Manilkara bahamensis*) (Faulhaber 2003). This vegetation type is distributed throughout the range of LKMRs. Freshwater marshes are characterized by sawgrass *(Cladium jamaicensis)*, Gulf Coast spike rush (*Eleocharis cellulose)* and with buttonwood *(C. erectus)* and other hardwoods depending on disturbance history (e.g., fire, cutting) and salinity.

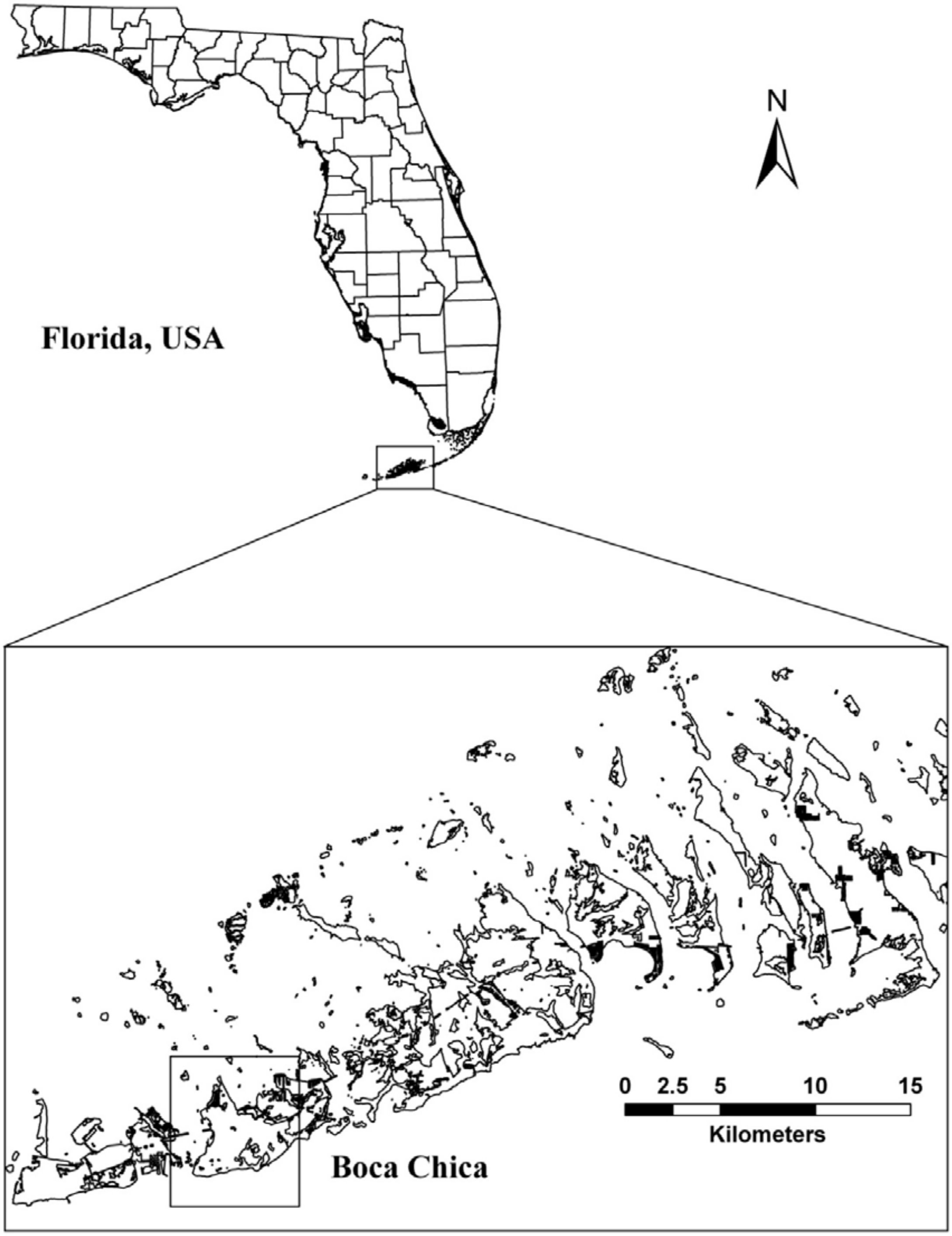

Figure 4.1. The island of Boca Chica Key located in the Lower Keys, Florida, USA.

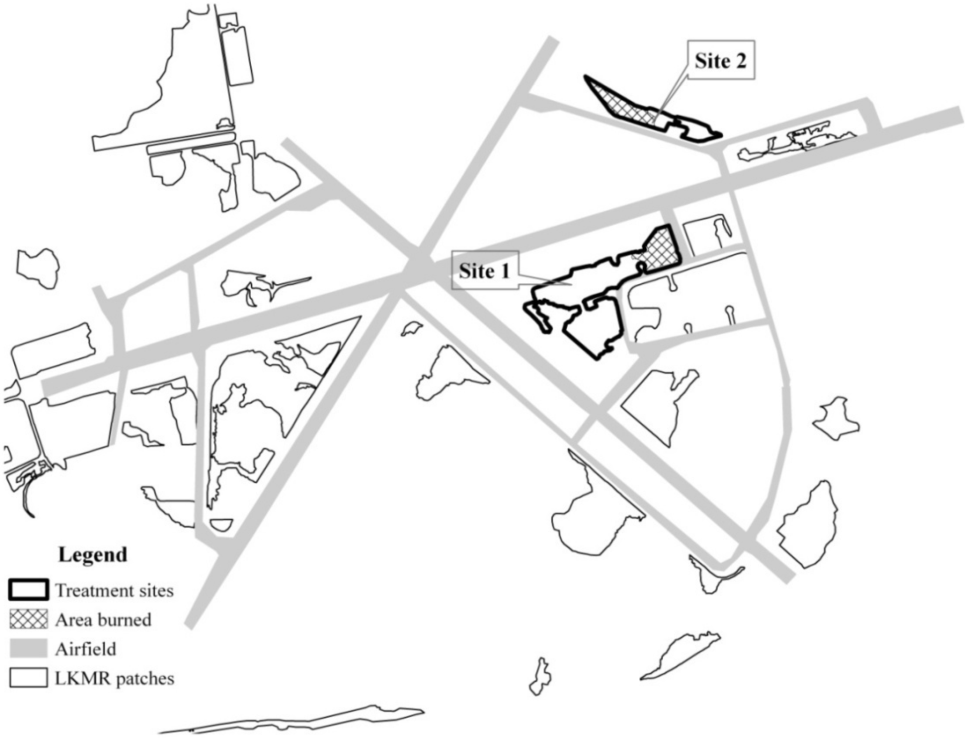

Figure 4.2. Prescribed fire study sites on Naval Air Station Key West (NASKW), Boca Chica Key, Lower Keys, Florida, USA.

METHODS

Prescribed Fire Treatment

In April 2007, private contractors in cooperation with NASKW personnel conducted experimental prescribed fires on Boca Chica Key in portions of 2 LKMR patches (Fig. 4.1). Site 1 was approximately 9.6 ha and was divided into a 1.9 ha burn unit and a 7.8 ha control unit (Fig. 4.2). Site 2 was approximately 2.8 ha and was divided into a 1.4 ha burn unit and a 1.5 ha control unit (Fig. 4.2). I selected these sites because they were consistently occupied by LKMRs and had reliable fire lines. NASKW kept the treatment areas relatively small so I could evaluate prescribed fire effects without threatening LKMR viability. I characterized the fires' behavior as backing fires with flame lengths up to 1 m and a 1 chain (20.1 m)/ hour rate of spread. I conducted systematic transect surveys immediately following the fire to visually characterize first order fire effects (e.g., tree mortality and fuel consumption) and to search for LKMRs and other wildlife that were injured or killed by the fires.

Pellet and Vegetation Sampling

I conducted surveys at each unit (control and treatment) of the 2 study sites prior to the burn (dry season February 2007) and again 3 months (wet season, August 2007), 9 months (dry season, January 2008) and 18 months (dry season, November 2009) post-fire. I placed a grid over a shapefile of the lower Florida Keys using a Geographic Information System (GIS); 30 x 30-m grid nodes falling within the boundaries of the study were selected and stored within the GIS (ESRI 2008). I sampled grid nodes within each of the study sites by searching within a 1-m radius of each point (the sample unit), tallying the number of adult and juvenile pellets and the number of preferred food species (Forys 1995) present (cordgrass, sea daisy, bluestem [*Andropogon spp.*], spike rush, and dropseed) as well as percent ground cover estimates of woody and herbaceous vegetation. I separated fecal pellets by age class (juvenile and adult); the diameter of adult pellets are approximately 6.7 mm or larger and pellets with a diameter of 6.6 mm or smaller are considered juvenile (Forys 1995). Increased incidence of fecal pellets correlates with an increase in rabbit numbers (Forys 1995). I averaged total pellet counts at each sample unit to obtain the mean number of adult and juvenile rabbit pellets per treatment unit. I averaged vegetation characteristics (woody, herb, and food) at each sample unit to obtain mean estimates per site by treatment.

I used transects to characterize vegetation composition on each site pre- and post-fire in conjunction with pellet surveys. I randomly selected 9 grid sample points from each study site. Transect starting points were permanently marked with rebar and flagged to facilitate resampling. I extended each transect 10 m in a random cardinal direction. I determined mean maximum vegetation height (dm), mean obstruction of vision (OV; Robel et al. 1970), and mean percent canopy cover (using a spherical convex densitometer, Lemmon 1957) by sampling at 5 points (0 m, 2.5 m, 5 m, 7.5 m, and 10 m) along the transect. I used the line intercept method to determine the length of the line occluded by each plant species <1.5 m in height (Canfield 1941). The proportion of transect occluded by each species was used to estimate Simpson's Index of Diversity for each transect (Krebs 1999).

Data Analysis

I subtracted each post-fire observation (3 months, 9 months, and 18 months) from the pre-fire observation to calculate the mean change over time for each response variable. I used normality plots and the Shapiro-Wilk test for normality of response variables (Zar 1999). All response variables were non-normally distributed; therefore, I used the Kruskal-Wallis test (Zar 1999) to compare the mean change in each response variable by treatment independently for each site (1 and 2) and time period (3 months, 9 months, and 18 months post-fire). I performed all analytical tests using SPSS software (Release 15.0.0, 2006). I evaluated results for statistical significance at an alpha level $\leq$ 0.05.

RESULTS

I visually characterized first order fire effects as complete consumption of herbaceous and woody fuels, live and dead, in small areas distributed throughout the treatment areas. Consumption of live woody fuels that resulted in mortality of trees and shrubs was limited to small localized areas. Herbaceous and woody fuel consumption was patchily distributed and intermixed with numerous areas that contained herbaceous and woody fuels, both live and dead that were not consumed. I did not observe any injured or dead LKMRs.

Table 4.1. Mean number of adult and juvenile Lower Keys marsh rabbit pellets by site from pre-burn (February 2007) to 3 months, 9 months, and 18 months post-burn on Naval Air Station Key West, Boca Chica Key, Florida, USA.

Response variable	Site–treatment[a] (*n*)	Pre-fire		Post-fire 3 month		Post-fire 9 month		Post-fire 18 month	
		$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*
Adult pellets	1-C (89)	5.0	2.7	1.0	0.6	1.9	0.5	3.7	1.3
	1-B (20)	35.4	17.8	47.8	17.3	37.6	13.9	18.7	6.1
	2-C (17)	21.1	10.7	32.1	20.2	19.8	11.0	17.3	6.2
	2-B (16)	0.0	0.0	3.6	3.0	9.1	8.0	32.4	8.5
Juvenile pellets	1-C (89)	0.03	0.03	0.0	0.0	0.1	0.1	0.02	0.02
	1-B (20)	9.5	5.6	6.9	3.9	0.5	0.4	1.5	0.7
	2-C (17)	1.8	1.2	0.9	0.6	4.6	4.3	7.8	4.3
	2-B (16)	0.1	0.1	0.0	0.0	4.7	3.2	8.9	3.5
Total pellets	1-C (89)	5.8	2.6	2	1.2	2.3	0.7	3.4	1.2
	1-B (20)	44.8	19.5	54.7	18.4	38	14	20.1	6.1
	2-C (17)	22.9	11.5	33.0	20.2	24.4	12.2	26.6	10.5
	2-B (16)	0.1	0.1	3.6	3	13.8	11	41.2	11.2

[a] C = control, B = burn.

I surveyed 109 samples in Site 1, 89 in the control and 20 in the burn. I surveyed 33 samples in Site 2, 17 in the control and 16 in the burn. In Site 1, the change in mean adult LKMR pellets per sample unit decreased in the control unit following the prescribed fire for all 3 post-fire surveys (66%, 62%, and 42%, respectively) and increased in the burn unit for the first 2 post-fire surveys (35% and 6%, respectively) before decreasing 47% (Table 4.1). Differences I observed between control and treatment units were not significant for all surveys ($P = 0.265, 0.288, 0.424$, respectively). In Site 2, the change in mean adult LKMR pellets per sample unit in the control unit initially increased 52% following prescribed fire then decreased for the last 2 post-fire surveys (6% and 18%, respectively) to pre-fire densities (Table 4.1). In the burn unit, I observed an increase from a mean of 0 pellets/ sample unit pre-fire to 4, 9, and 32 pellets per sample unit for the first, second, and third post-fire surveys, respectively, with the latter being statistically significant ($P = 0.011$, Table 4.1).

Mean juvenile LKMR pellets per sample unit in Site 1's control unit were generally low and fluctuated between a 100% decrease immediately post-fire to a 200% increase by the second post-fire survey. For the first pre-fire survey, I observed decreases in both the burn and control units with the decrease in the burn unit being 33% smaller; however, this result was not significant ($P = 0.511$, Table 4.1). In the burn unit, decreases for the second and third surveys were an order of magnitude larger ($P = 0.002$ and $P = 0.029$, respectively; Table 4.1) than decreases observed in the control unit. Juvenile pellets in Site 2 decreased in both the control and burn unit. I observed a decrease in Site 2's control unit 16 times larger than the decrease observed in the burn unit but this observation was non-significant (*P* = 0.915, Table 4.1). I observed increases in both the control and burn units for the second and third post-fire surveys; increases in juvenile pellets in the burn unit were 1.6 and 1.5 times larger than the control unit but these observations were not supported statistically (*P* = 0.443 and 0.295, respectively; Table 4.1).

The mean change in woody cover increased in control units (59%, 66% and 75%, respectively) and decreased in burn units (46%, 17%, and 86%, respectively) for all 3 post-fire surveys in Site 1 (Table 4.2); changes in woody cover in burn units were larger in the first and third post-fire surveys (*P* = 0.012 and *P* < 0.001, respectively; Table 4.2) but I did not find a difference for the second survey (*P* = 0.146, Table 4.2). I found no difference in woody cover between control and burn units on Site 2 (*P* = 0.520, 0.445, and 0.587, respectively; Table 4.2). Herbaceous cover increased in both control and burn units on both sites (Table 4.2). Increases were generally larger (up to 8 times) in the burn units but this was not supported statistically (Site 1: *P* = 0.596, 0.157, and 0.071; Site 2: *P* = 0.900, 0.270, and 0.637). The distribution of herbaceous bunchgrasses and forb plants also increased in all units in both patches for all post-fire surveys (Table 4.2). I found no difference between increases in control and burn units in Site 1 for all surveys (*P* = 0.210, 0.955, and 0.542, respectively). The increase in the distribution of herbaceous bunchgrasses and forb plants in Site 2 was the same for the control and burn unit for the first and third survey (*P* = 0.319 and 0.951, respectively) but was larger (*P* = 0.032) in the burn unit for the second survey.

Table 4.2. Mean woody and herbaceous vegetation (%) and herbaceous plant distribution by site from pre-burn (February 2007) to 3 months, 9 months, and 18 months post-burn on Naval Air Station Key West, Boca Chica Key, Florida, USA.

Response variable	Site–treatment[a]	Pre-fire		Post-fire 3 month		Post-fire 9 month		Post-fire 18 month	
	(*n*)	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*
Woody vegetation (%)	1-C (89)	12.3	1.5	19.5	2.5	20.4	2.3	21.4	2.6
	1-B (20)	19.5	5.8	10.5	3.9	16.3	4.5	2.8	1.4
	2-C (17)	19.0	4.7	12.4	4.2	7.3	2.7	24.1	7.0
	2-B (16)	5.8	2.9	6.9	4.6	4.4	3.7	4.4	3.8
Herbaceous vegetation (%)	1-C (89)	17.7	2.3	24.8	2.9	19.2	2.3	30.7	3.1
	1-B (20)	25.1	5.4	41.8	6.1	41.0	6.3	51.6	7.1
	2-C (17)	39.9	8.7	51.4	8.8	46.3	10.1	51.6	10.7
	2-B (16)	58.1	7.5	62.6	7.9	69.4	7.9	80.7	8.8
Herbaceous plant distribution	1-C (89)	0.2	0.05	0.6	0.1	0.4	0.1	0.7	0.1
	1-B (20)	0.2	0.1	0.4	0.2	0.4	0.1	0.5	0.1
	2-C (17)	0.7	0.1	1.1	0.2	0.9	0.1	1.1	0.2
	2-B (16)	0.3	0.1	0.8	0.2	0.9	0.2	0.7	0.2

[a] C = control, B = burn.

I surveyed 9 transects in each patch; Site 1 had 6 transects in the control unit and 3 transects in the burn unit, Site 2 had 7 transects in the control unit and 2 transects in the burn unit. I found no significant changes in mean maximum vegetation height (Site 1: $P = 0.606$, 0.606, and 0.071; Site 2: $P = 0.242$, 0.143, 0.143), canopy cover (Site 1: $P = 0.606$, 0.439, and 0.606; Site 2: $P = 0.186$, 0.143, 0.143) or plant species diversity (Site 1: $P = 0.302$, 0.197, and 0.606; Site 2: $P = 0.770$, 0.770, and 0.380) between control and burn units for either patch (Table 4.3). Vegetation OV in the control unit of Site 1 increased 43% ($P = 0.039$) during the first post-fire survey and remained virtually unchanged in the burn unit. I found no difference in vegetation OV between the control and burn unit ($P = 0.121$ and 0.604, respectively; Table 4.3) of Site 1 for the second and third post-fire survey nor between the control and burn unit for Site 2 ($P = 0.143$, 0.143 and 0.558; Table 4.3).

Table 4.3. Mean maximum vegetation height (m), canopy cover (%), vegetation OV (dm) and plant species diversity (0 = no diversity to 1 = maximum diversity) by site from pre-burn (February 2007) to 3 months, 9 months, and 18 months post-burn on Naval Air Station Key West, Boca Chica Key, Florida, USA.

Response variable	Site–treatment[a] (*n*)	Pre-fire		Post-fire 3 month		Post-fire 9 month		Post-fire 18 month	
		$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*
Vegetation height	1 C (6)	7.5	2.2	7.3	3.1	7.9	2.5	7.1	2.7
	1 B (3)	7.0	3.1	6.3	2.7	8.7	2.2	11.2	3.4
	2 C (7)	11.8	2.4	11.4	1.9	12.8	2.2	11.4	2.3
	2 B (2)	11.8	6.7	6.4	2.6	5.6	1.4	6.9	3.9
Canopy cover	1 C (6)	19.3	12.1	29.7	14.5	29.7	14.8	24.3	15.5
	1 B (3)	9.4	6.1	17.0	14.6	37.4	20.8	19.7	9.9
	2 C (7)	27.2	8.7	51.3	13.1	59.9	14.7	53.1	12.7
	2 B (2)	8.8	8.6	18.9	18.9	16.9	16.9	18.3	18.3
Vegetation OV	1 C (6)	3.2	0.5	7.0	1.2	6.7	1.3	2.5	0.5
	1 B (3)	8.0	3.0	7.8	2.6	8.4	2.8	8.0	3.1
	2 C (7)	8.7	1.6	12.7	1.6	11.7	2.4	4.7	2.4
	2 B (2)	5.0	1.0	6.4	0.7	4.6	0.7	2.6	0.3

[a] C = control, B = burn.

Table 4.3. continued

Response variable	Site–treatment[a] (*n*)	Pre-fire		Post-fire 3 month		Post-fire 9 month		Post-fire 18 month	
		$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*	$\bar{x}$	*SE*
Plant species diversity	1 C (6)	0.5	0.1	0.6	0.1	0.4	0.1	0.4	0.1
	1 B (3)	0.7	0.04	0.7	0.1	0.8	0.1	0.6	0.1
	2 C (7)	0.7	0.02	0.7	0.02	0.7	0.05	0.7	0.1
	2 B (2)	0.7	0.1	0.6	0.03	0.6	0.1	0.7	0.02

DISCUSSION

I observed no direct mortality of LKMRs in either burn unit. My observations of first order fire effects indicate fire behavior provided ample refugia within treatment units for LKMRs. My results were consistent with other studies on mortality-related effects of other cottontail species (*Sylvilagus* sp.; see Taylor 1981 for review). Adult rabbit pellets decreased in 2 of 3 post-fire surveys in the control unit and increased in 3 of 3 post-fire surveys in the burn unit of Site 1. Adult rabbit pellets decreased in 3 of 3 post-fire surveys in the control unit and increased in 2 of 3 post-fire surveys in the burn unit of Site 2. Total pellet numbers for the control and burn unit decreased (6%, 19%, and 40%) for all 3 post-fire surveys in Site 1 and increased (68%, 35%, 126%) for all 3 post-fire surveys in Site 2. Decreased total pellets for Site 1 and the control unit with corresponding increases in the burn unit indicates rabbits moved from unburned to burned areas with re-growth. Increased total pellets for Site 2 and the burn unit with corresponding decreases in the control unit indicates rabbit movement from unburned to burned areas and also may indicate rabbits moved from nearby patches. The increases in adult pellets I observed in burn units were sustained up to 9 months post-fire in Site 1 and up to 18 months post-fire in Site 2. Overall, adult rabbit pellets increased, woody vegetation decreased, herbaceous vegetation and food plant availability increased following prescribed fire in both burn units.

My findings were consistent with studies in Oklahoma that found increased densities and improved condition of cottontail rabbits (*S. floridanus*) following herbicide application and prescribed fire (Lochmiller et al. 1991, 1995) and with studies in a southeastern Illinois tall grass prairie, where eastern cottontails preferred 3-year post-fire communities that had not been mowed over unburned plots and 3-year post-fire plots that had been mowed (Westemeier 1983).

Juvenile rabbit pellets increased in half of the surveys in control units and decreased in 4 of 6 surveys in burn units. Juvenile rabbits decreased in control and burn units at both sites 3 months post-fire. This was the only survey conducted during the dry season and could correspond with general decreases in reproduction associated with season. I timed prescribed fires to correspond with the lowest levels of observed nesting to avoid mortality of nestling rabbits (Forys 1995). We observed decreases in juvenile pellets in the burn unit of Site 1 that were sustained up to 18 months post-fire.

Increased use of burned areas by adult rabbits following prescribed fire may have occurred to the detriment of juvenile rabbits at Site 1. Adult snowshoe hare (*Lepus americanus*) densities increased in burned areas following a wildfire (Keith and Surrendi 1971). The authors reported a similar reduction in juvenile snowshoe hares that corresponds with increased adult densities and postulated that juvenile densities were reduced due to on-going emigrations of juveniles out of burned areas that resulted from increased social interactions as adult densities increased. It is plausible that juvenile LKMRs were competitively excluded from burned areas by con-specific adults. It is unclear whether decreases in juvenile LKMRs observed were related to a decline in habitat suitability as overall we saw no relationship between changes in juvenile pellet densities following prescribed fire and changes in woody and herbaceous vegetation or food plant availability. Elsewhere, declines in eastern cottontail habitat quality were observed for several months following prescribed fires before later improving to meet or exceed pre-fire levels (George et al. 1978). On-going monitoring of juvenile LKMRs and their habitat will be required to determine long-term impacts resulting from prescribed fire treatments.

I observed no change in the general vegetative characteristics of coastal salt marsh (e.g., vegetation height, canopy cover, plant diversity), but did observe small decreases in OV. I recommend the use of prescribed fire in additional coastal salt marsh areas and increasing burn unit size to improve sample size and the ability to detect effects of future prescribed fires on LKMRs and coastal salt marsh vegetation. Pre-treatment of woody vegetation through mechanical removal and/ or herbicide application prior to future prescribed fire activities could improve benefits to LKMRs and their habitats as has been observed in other lagomorphs (Lochmiller et al. 1995). Fire's effect on LKMRs and their habitat also depend on fire behavior. I recommend various prescribed fire applications and resulting fire behavior be evaluated for use in managing LKMR habitats.

Declines in other lagomorph species dependent upon disturbance maintained habitats, such as the pygmy rabbit (*Brachylagus idahoensis*) in the western United States and European hare (*Oryctolagus cuniculus*), have been associated with altered fire regimes (Larrucea and Brussard 2008 and Moreno and Villafuerte 1995, respectively). My results indicate fire suppression and resulting degradation of transitional habitats used by LKMRs could exacerbate on-going population declines. Information on the historic role of fire related disturbance in coastal salt marsh habitats of the Lower Florida

Keys is lacking. As such, on-going monitoring of LKMRs and coastal salt marsh characteristics in prescribed fire treatment areas will be required to determine when prescribed fire benefits wane and at what point prescribed fire should again be introduced.

CHAPTER V

EVALUATION OF MANAGEMENT STRATEGIES FOR THE RECOVERY OF LOWER KEYS MARSH RABBITS

SYNOPSIS

The Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*), is a subspecies of marsh rabbit endemic to the Lower Keys, Florida threatened with extinction due to habitat loss and development. Habitat degradation through brush encroachment and predation by free-roaming cats (*Felis catus*) and native raccoons (*Procyon lotor*) continue to threaten LKMR viability and recovery. Conservation benefits can be improved if recovery actions and locations are simultaneously evaluated to determine which scenarios will maximize benefits. My objective was to evaluate the efficacy of translocations, habitat management, and raccoon control for the recovery of LKMRs. I used estimates of population change based on annual monitoring data to validate adult survival rates and constructed a spatially realistic demographic model to evaluate various levels of recovery scenarios. Model results indicated intensive habitat management actions that improve local carrying capacity and juvenile survival and control of raccoon populations to increase reproductive rates are effective population recovery strategies. Translocation failed to prevent decreases in LKMR populations. Model validation indicated changes in carrying capacity, juvenile survival, and reproduction expected from these recovery scenarios were robust.

INTRODUCTION

The Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*), is a subspecies of marsh rabbit endemic to the Lower Keys, Florida that was listed as endangered by the U.S. Fish and Wildlife Service and the Florida Fish and Wildlife Conservation Commission in 1990 (Lazell 1984, USFWS 1990). Historically LKMRs were abundant and found throughout the Lower Keys but development has limited their distribution to 4 main islands (Boca Chica, Saddlebunch, Sugarloaf, and Big Pine keys) and several smaller, outlying islands (de Pourtales 1877, Faulhaber et al. 2007). Remaining LKMR habitats are small, averaging ≈ 4 ha, and distributed in discrete patches or sites that function as a classic metapopulation with interaction between local populations limited to dispersal of individuals outside their natal patch (Levins 1970, Forys 1995, Forys and Humphrey 1996, USFWS 1999). Habitat loss has not only reduced the number of LKMR populations but also has reduced the numbers of rabbits within these populations and increased the distance between suitable habitats (USFWS 1999). LKMR recovery also is limited by habitat loss and degradation from brush encroachment, predation by free-roaming cats and raccoons (Forys and Humphrey 1999*a*, USFWS 1999).

Recent findings have shown measures of habitat degradation and brush encroachment including the complexity of a patch’s perimeter or edge and the quantity of herbaceous bunchgrasses and forbs important for food, nesting and cover influence densities of both adult and juvenile LKMRs (Chapter II). In addition, measures of raccoon activity were shown to influence densities of adult LKMRs (Chapter II).

Further, the effect of high levels of raccoon activity on adult LKMRs was reduced when large numbers of bunchgrasses and forbs were available (Chapter II). The relationship between measures of habitat quality, raccoon activity and LKMR densities are clear, however, mechanisms that produce these patterns have not been elucidated. For example, habitat quality may affect carrying capacity of local habitat patches. Likewise, both habitat quality and raccoon activity may influence survival and maternity rates.

There is a consensus that active management of populations and habitats will be required to increase the number and density of LKMR patches (USFWS 1999). Previous management actions taken to aid in the recovery of this endangered subspecies have included the translocation of rabbits to unoccupied patches of suitable habitat on 2 outlying islands (Faulhaber et al. 2006, USFWS 2007). These efforts successfully established populations at 1 of 2 reintroduction sites (Faulhaber et al. 2006, USFWS 2007). Additionally, removal of free-roaming cats and raccoons was conducted on Boca Chica Key. Predator control programs have not been evaluated but annual monitoring has indicated recovery of LKMR patches extirpated following Hurricane Wilma (24 October 2005) was higher for Boca Chica Key than other areas where predator control was not conducted (USFWS 2007). Finally, small prescribed fires also have been implemented to reduce brush encroachment and restore coastal salt marsh in 2 occupied LKMR patches on Boca Chica Key (USFWS 2007, Chapter IV). Initial results indicated prescribed fire may increase densities of adult LKMRs, increase the number of bunchgrasses and forbs that previously were found to be important to LKMRs for food, cover, and nesting (Forys and Humphrey 1999*b,* Faulhaber et al. 2008), and decrease woody vegetation (Chapter IV). These results indicate prescribed fire may be an appropriate habitat management strategy for LKMR habitats (Chapter IV).

Implementation and evaluation of recovery actions on a small scale has been important for assessing the validity of translocation, trapping and fire as recovery tools. However, prior to implementation at larger spatio-temporal scales the examination of individual recovery strategies at the local population scale does not provide information on their potential for the recovery of the metapopulation. In addition, managers responsible for implementation of recovery actions have limited resources and must select among several potential recovery strategies and localities. Conservation benefits can be improved if recovery actions and locations are simultaneously evaluated to determine which scenarios will maximize benefits to the species at spatio-temporal scales that will influence metapopulation dynamics and extinction risk (Hanski 2002).

Demographic models are a useful tool to explore population ecology and dynamics of highly complex natural systems (Grant et al. 1997, Beissinger and Westphal 1998). Population models can incorporate available demographic and habitat data, as well as the effects of demographic and environmental stochasticity and uncertainty in parameter estimation on model projections (Beissinger and Westphal 1998¸ Akçakaya and Sjogren-Gulve 2000). Population viability analyses (PVAs) are a class of demographic models commonly used to predict changes in endangered species or populations and to evaluate relative effects of proposed conservation strategies (Beissinger and Westphal 1998, Akçakaya and Sjogren-Gulve 2000). PVAs also may be applied to endangered species that occur in metapopulations to assess the relative influence of management actions on population projections and extinction risk (Hanski 2002).

PVAs for the LKMR have previously been used to predict their extinction risk under current conditions, to evaluate the effect of habitat loss, as well as to assess various mitigation and conservation strategies including the establishment of salt marsh habitat and reducing mortality from free-roaming cats (Forys 1995, Forys and Humphrey 1999, LaFever et al. 2008). This study sought to expand the use of PVAs for the LKMR by including the most recent data on the response of the rabbits to both habitat changes and raccoons, and to use the modeling framework to evaluate the potential of the most promising management scenarios for this subspecies. My objective was to evaluate relative success of translocations, habitat management and raccoon control using a PVA of the Lower Keys marsh rabbit. Specifically, I used estimates of population change based on annual monitoring data to validate vital rates, and constructed a spatially explicit demographic model to evaluate various levels of recovery scenarios implemented throughout the LKMRs range.

STUDY AREA

The Lower Keys, Florida, are located between 23.5 and 25.5 ° North latitude and exhibit a subtropical climate due to the Gulf Stream and other maritime influences (Fig. 2.1, Chen and Gerber 1990, Forys and Humphrey 1999*a*). The climate is characterized by distinct wet and dry seasons, with the dry season (November through April) contributing <33% of annual precipitation (Forys and Humphrey 1999*a*). Elevations rarely exceed 2 m, with slight variations in elevation producing distinct vegetation communities that transition from mangroves to coastal salt marsh/buttonwood transition zones inland to freshwater marshes, pine rocklands and tropical hardwood hammocks (McGarry MacAulay et al. 1994).

Coastal salt marsh prairies, also known as buttonwood transitions zones are characterized by cord grasses (*Spartina spp*.), sea daisies (*Borrichia spp*.), glassworts (*Salicornia spp*.), seashore dropseed (*Sporobolus virginicus*) and rushes (family *Cyperacea*) with various densities of salt tolerant hardwoods, predominantly buttonwood but also with white mangrove (*Laguncularia racemosa*), red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), joewood (*Jaquinia keyensis*), poisonwood (*Metopium toxiferum*) and wild dilly (*Manilkara bahamensis*) (Faulhaber 2003). Freshwater marshes are characterized by sawgrass (*Cladium jamaicensis*) and Gulf Coast spike rush (*Eleocharis cellulose*) interspersed with buttonwood (*C. erectus*) and other hardwoods depending on disturbance history (e.g., fire, cutting) and salinity.

Table 5.1. Model parameter estimates and data sources used to select adult survival rates consistent with observed population trajectories and to evaluate recovery strategies for the Lower Keys marsh rabbit, Lower Keys, Florida, USA. Fecundity is the average number of female offspring produced per female per year multiplied by stage specific survival.

Parameter	Estimate (*SE*)	Source
Fecundity:		
Adult 1	2.19 (0.07)	Forys 1995
Adult 2+	1.70 (0.10)	
Survival:		
Juvenile (<1 year)	0.50 (0.12) [a]	Forys 1995
Adult 1		
Low	0.52 (0.09)	Forys 1995
Medium	0.66 [b]	
High	0.79 (*SE* not provided)	Faulhaber et al. 2006
Adult 2+		
Low	0.10 (0.12)	Forys 1995
Medium	0.45 [b]	
High	0.79 (*SE* not provided)	Faulhaber et al. 2006
Juvenile Dispersal:		
Average	300 m	Forys 1995
Maximum	3,000 m	
Carrying Capacity	Patch specific	Forys and Humphrey 1996

[a] Juvenile survival is the juvenile survival estimate multiplied by the subadult survival estimate to calculate the probability individuals will survive their first year. [b] Medium adult survival is the average of the low and high estimates.

METHODS

Model Overview

I used RAMAS-Metapop (Applied Biomathematics, Version 4.0, Akçakaya and Root 2002) to construct a spatially explicit demographic model for the LKMR. My model included female rabbits in 3 demographic stages: juveniles, first year adults, and 2 year and older adults. I incorporated demographic stochasticity into the model by selecting survival rates from a binomial distribution and reproductive rates from a Poisson distribution (Akçakaya 1991). I modeled environmental stochasticity by randomly sampling survival and fecundity using a “standard deviation matrix” (Akçakaya 1991).

I estimated the carrying capacity for each patch by dividing patch area determined using a Geographic Information System (GIS) by the mean estimate of adult core area (ESRI 2008, Forys and Humphrey 1996, Table 5.1). I modeled ceiling type density-dependence so that patches were allowed to increase exponentially until carrying capacity (K) was reached and were then held constant at K. As a patch reached carrying capacity dispersing individuals moved into a neighboring patch that was within the maximum dispersal distance and below carrying capacity or died if no patch was available (LaFever et al. 2008). I used ceiling type density-dependence because it allowed dispersal rates to increase linearly as a patch approached carrying capacity without reducing mortality and natality (MacArthur and Wilson 1967, Lande 1993, Griffin and Mills 2004). I assumed this form of density-dependence was most appropriate for a metapopulation study of an endangered lagomorph subspecies considered well below its population carrying capacity (Forys and Humphrey 1999*a*).

I modeled juvenile dispersal using a distance-function matrix with dispersal between patches decreasing as distance increased. I assumed a negative, exponential dispersal function using mean and maximum dispersal distances of 300 m and 3,000 m, respectively (Forys and Humphrey 1996, LaFever et al. 2008, Table 5.1). Dispersal data has shown that only juvenile rabbits disperse and the greatest distance a radio-collared rabbit was tracked was 2,500 m (Forys 1995).

Demographic Parameterization

I used model parameters from both published and unpublished sources that were estimated using pellet counts, live-trapping, and telemetry data (Forys 1995, Forys and Humphrey 1996, Faulhaber et al. 2006, Schmidt 2009, Table 5.1). I used initial abundance estimates obtained from pellet counts and live-trapping (Forys 1995, Schmidt 2009). Reproduction (R) was estimated as the product of the mean number of female offspring and the mean number of litters per female per annum (Forys 1995). Adult fecundity was determined from the product of the female sex ratio (Sr), reproduction (R), and subadult/adult/ survival (S_s, S_a) (F = Sr*R*S; Forys 1995, Akçakaya and Root 2002).

Survival estimates for adult age classes of LKMRs have varied throughout the literature (Forys1995, Forys and Humphrey 1999*a*, Faulhaber et al. 2006). As a result, I evaluated 3 estimates of adult survival: low, medium, and high to determine which estimate projected an annual change most similar to observed population trends (Table

5.1). I initialized this subset of models using estimates of female abundance for 29 patches surveyed in both July of 1992 and 2008 (Forys 1995, Schmidt 2009). Two major hurricanes with associated storm surges occurred during this 17-year period, Hurricane Georges in 1998 and Hurricane Wilma in 2005 (Lopez et al. 2003, Kasper 2005). Fifty-nine percent of patches monitored before and after Hurricane Wilma went extinct; patches closer to the coast had a higher extinction probability than patches farther inland (Chapter III). To incorporate the effect of these 2 hurricanes I simulated extinctions as removal of 100% of a local population for 17 of 29 (59%) patches in year 7 and 14 (corresponding to 1998 and 2005). I selected patches with the highest estimated probability of extinction based on their distance from the coast (Chapter III).

I ran 1,000 replicate stochastic iterations for 17 years of simulated time with a time step of 1 year. I subtracted the projected mean final abundance from the initial abundance/17 to calculate annual change in abundance (%). I selected the adult survival rate that projected the annual population change closest to the actual estimate of change for use in all subsequent models.

Habitat Parameterization

Mean male core area for high quality patches was 50% smaller than low quality patches indicating carrying capacity is affected by habitat quality (Forys and Humphrey 1999*a*). In addition, measures of brush encroachment and habitat quality including estimates of patch shape index or edge (psi) and the distribution of herbaceous bunchgrasses and forbs important to LKMRs (species) have been shown to influence adult and juvenile LKMR densities. I therefore assumed habitat management through brush control and prescribed fire would increase patch carrying capacity and juvenile survival (Chapter II). Because the best quality habitat was shown to potentially increase density by up to 50%, I expected intensive (high) habitat management would increase carrying capacity up to 50% while less intensive (low and medium) habitat management would increase carrying capacity by 10% and 25%, respectively. The effect of habitat quality on juvenile survival has not been estimated for this subspecies; however, doubling the distribution of 4 genera of herbaceous grasses and forbs that previously were found to be important to LKMRs for food, cover, and nesting (Forys and Humphrey 1999*b,* Faulhaber et al. 2008) predicted juvenile densities that were 2.3 times higher than the average (Chapter II). I, therefore, expected low, medium, and high levels of habitat management would increase juvenile survival by 15%, 30%, and 60%.

Raccoons are efficient predators known to prey on rabbits (Dorney 1954, Urban 1970, Jennings et al. 2006). I assumed nestling LKMRs would be most susceptible to raccoon depredation and that reductions in raccoon activity would increase reproduction estimates, defined as the number of female offspring produced per adult female rabbit per annum that survive the nestling stage (0-3 months). The proportion of LKMR or other lagomorph nestling mortality attributable to raccoons is not known, however, muskrat (*Ondatra zibethicus*) kits <30 days old represented 9–40% of raccoon diets in Wisconsin (Dorney 1954). Muskrat kits, like nestling LKMRs, are altricial at birth and dependent upon the mother for the first several weeks of life making them susceptible to predation while within the nest (Dorney 1954). In addition, muskrat reproduction was 63% higher in areas with raccoon densities that were 70% lower than densities reported for other areas in the study (Dorney 1954). I therefore conservatively expected low, medium, and high levels of raccoon control would increase LKMR reproduction 7.5%, 15%, and 25%. The effects of habitat management and raccoon control scenarios were assumed constant for each time step and treatments were only applied to occupied patches.

Previously, I determined patch size and distance from the coast influenced extinction and colonization rates of LKMR patches following Hurricane Wilma (Chapter III). I incorporated this information into the model by modeling 2 spatial configurations of habitat management and raccoon control: I treated the 15 largest patches >0.80 km from the coast or I treated 15 randomly selected patches regardless of size or distance to the coast.

Model Use

I applied parameter estimates as described above to evaluate the influence of no recovery action, 3 levels of habitat management and raccoon control (low, medium, and high) and 2 translocations scenarios on the LKMR population. Model scenarios were as follows:

1. Baseline scenario = no change.
2. Low, medium, and high levels of habitat management applied to large, inland patches.
3. Low, medium, and high levels of habitat management applied to randomly selected patches.

4. Low, medium, and high levels of raccoon control applied to large, inland patches.
5. Low, medium, and high levels of raccoon control applied to randomly selected patches.
6. Low, medium, and high levels of habitat management and raccoon control applied to large, inland patches.
7. Low, medium, and high levels of habitat management and raccoon control applied to randomly selected patches.
8. Translocation to 2 suitable patches on Big Torch Key.
9. Translocation to 2 suitable patches on south Big Pine Key.

For both translocation scenarios, 4 adult rabbits were introduced to each translocation site one time before the first time step. LKMRs have been extirpated from the Torch Keys (Little, Middle, and Big Torch keys) and patches south of US Highway 1 on Big Pine Key. These patches are located beyond the maximum dispersal distance from currently occupied populations making natural colonization unlikely. I selected the 2 largest patches with >50% public ownership as translocation sites from each potential reintroduction area. I modeled the patch on Little Pine Key with the highest abundance estimate from 2008 as the donor population. Patches on Little Pine Key were recently used as a source population for translocations to Water Key (P. Hughes, U.S. Fish and Wildlife Service, personal communication). Only 4 rabbits were introduced at each site to prevent negative effects to the source population (Todd 2002). Translocation of >4 individual per patch or to >2 patches per site would have been preferable; however, I did not consider translocating rabbits from potential source populations on Boca Chica Key as mixing individuals from the 2 genetically distinct management units was not advised (Crouse et al. 2009).

For recovery scenarios 1 through 7 and 9, I ran 1,000 replicate stochastic iterations for 10 years of simulated time with a time step of 1 year for 150 patches initialized with estimates of abundance from 2008 (Schmidt 2009). To provide dispersal opportunities during scenario 8, I also included all suitable habitat patches (13) on Big Torch Key. I used 2 criteria to evaluate the efficacy of each scenario: final population size averaged over all simulations and risk of terminal quasi-extinction. I defined terminal quasi-extinction risk as the probability the LKMR population range wide would fall below 50 individuals within 10 years to account for potential Allee effects (Allee 1931).

Model validation—The effects of recovery actions on carrying capacity, juvenile survival, and reproduction are not known and would be difficult to assess using a statistically valid field experiment due to the endangered status of this rabbit and their limited distribution. I therefore validated my assumptions from low, medium, and high levels of habitat management and raccoon control by comparing model projections to estimates predicted using measures of habitat quality and raccoon activity from a known population.

I evaluated model scenarios with predicted changes in carrying capacity, juvenile survival and reproduction for low, medium, and high rates of habitat management, raccoon control and both habitat management and raccoon control. I created a subset of models for 10 patches. I randomly selected patch sizes representative of the 150 possible patches to account for demographic stochasticity associated with small populations. I estimated the initial number of female rabbits using prediction equations described in Chapter II. As previously determined, only adult densities were affected by raccoon activity. I held each patch attribute (e.g., patch shape index, herbaceous species distribution, and raccoon activity) constant at its average and allowed patch size to vary to estimate the number of rabbit pellets per hectare. Rabbit densities were converted to abundances using methods described by Schmidt (2009) and divided by 2 to determine the number of female rabbits per patch. Patch carrying capacity was again determined by dividing patch area by the mean core area (Forys and Humphrey 1996).

I simulated low, medium and high levels of habitat management, raccoon control, and a combination of the 2 strategies by increasing patch carrying capacity, juvenile survival and reproduction as previously described. I ran 1,000 replicate stochastic iterations for 3 years of simulated time using a 1 year time step. Changes in LKMRs and their habitat were observed within 3 months following a prescribed fire (Chapter IV). Removal of raccoons was assumed to immediately reduce predation of nestling rabbits, thus increasing reproduction. I assumed the effect of recovery actions implemented would immediately affect carrying capacity, juvenile survival, and reproduction but ran simulations for 3 years to allow models to stabilize.

For the 10 patches also used in model simulations, I also used equations described in Chapter II to predict the change in pellet density that would result from habitat management, raccoon control and a combination of both strategies. I assumed low, medium and high levels of habitat management through brush control and prescribed fire could be expected to produce 25%, 50%, and 75% reductions in patch shape index (psi) and 25%, 50%, and 75% increases in the distribution of herbaceous bunchgrasses and forbs (dist) and low, medium and high levels of raccoon removal were expected to produce 25%, 50%, and 75% reductions in measures of raccoon activity (proc). I again converted estimated pellets densities to abundances using methods described by Schmidt (2009).

Finally, I compared model projections based on expected changes in carrying capacity, juvenile survival and reproduction to estimates predicted by expected changes in patch shape index, distribution of herbaceous bunchgrasses and forbs, and raccoon activity. I considered model results valid if the population size predicted using changes in patch shape index, distribution of bunchgrasses and forbs and raccoon activity were within the 95% confidence interval of model projections.

Table 5.2. Initial and final abundance, and total and annual population change for 29 Lower Keys marsh rabbit patches projected by models using low, medium and high estimates of adult survival compared to actual estimates of population change for these patches between 1992 [a] and 2008 [b]. Comparisons were used to validate estimates of adult survival for parameterization of population models that evaluated the efficacy of LKMR recovery strategies. Model projections were for 17 years of simulated time with a 1 year time step and initialized using abundance estimates from 1992 (Forys 1995).

	Initial abundance	Final abundance [c]	Total change (%)	Annual change (%)
Models:				
Low	56	29 (*SD*=14.2)	−48	−2.8
Medium	56	38 (*SD*=8.6)	−32	−1.9
High	56	43 (*SD*=4.4)	−23	−1.4
Estimates	56 [a]	30 [b]	−46	−2.7

[c] One *SD* is based on 1,000 replicate stochastic model iterations.

Table 5.3. Mean final abundance (1 *SD)* and abundance corrected for area (ha) managed projected by models used to evaluate recovery scenarios for the Lower Keys marsh rabbit: habitat management (2 and 3), raccoon control (4 and 5) and a combination of the 2 strategies (6 and 7) applied to the largest 15 occupied patches >0.80 km from the coast (even scenarios) and 15 randomly selected occupied patches (odd scenarios). Models simulated 150 patches initialized with 2008 abundance estimates (160 individuals) and used 1,000 stochastic iterations, 10 years of simulated time and a 1 year time step.

	Implementation level					
	Low		Medium		High	
Scenario [a]	$\bar{x}$ (*SD*)	*N* per ha	$\bar{x}$ (*SD*)	*N* per ha	$\bar{x}$ (*SD*)	*N* per ha
2	112.4 (30.9)	13.5	121.8 (32.7)	14.7	157.2 (35.3)	18.9
3	129.4 (34.9)	12.3	135.1 (36.3)	12.9	188.3 (40.0)	17.9
4	134.3 (31.7)	16.2	101.3 (30.5)	12.2	104.9 (31.6)	12.6
5	139.8 (33.5)	13.6	105.9 (33.5)	10.3	113.8 (31.6)	11.0
6	107.4 (30.0)	12.9	120.7 (31.5)	14.5	140.9 (31.9)	17.0
7	119.6 (34.7)	11.6	146.0 (35.2)	14.2	176.8 (30.8)	17.2

[a] Mean final abundance for Scenario 1, the baseline scenario, $\bar{x}$ = 94.3 (*SD* = 29.1).

Table 5.4. Mean final abundance with 1 *SD* and terminal quasi-extinction risk with 95% *CI*s for a population viability analysis simulating the baseline scenario (1) and 2 recovery strategies: translocation to Big Torch Key (8) and translocation to south Big Pine Key (9), for the Lower Keys marsh rabbit. Quasi-extinction risk is defined as the probability the LKMR population will fall below 50 individuals within 10 years. Model simulations were initialized with 2008 abundance estimates (160 individuals) and used 1,000 stochastic iterations, 10 years of simulated time and a 1 year time step.

Scenario	Final population $\bar{x}$ (*SD*)	Terminal quasi-extinction risk (95% *CI*)
1	94.3 (29.1)	0.05 (0.02–0.08)
8	102.4 (30.9)	0.02 (0.00–0.05)
9	107.2 (32.2)	0.03 (0.00–0.06)

RESULTS

Demographic Parameters

I estimated a 2.7% annual decrease in abundance estimates for 29 LKMR patches (1992 to 2008, Table 5.2). When I evaluated 3 estimates of adult survival for these 29 patches the model that used the lowest estimate of adult survival projected annual population changes closest to the estimated annual change in population (Table 5.2). Both the medium and high estimates of adult survival projected annual population changes that were lower than the observed rate of change (Table 5.2). All subsequent model simulations were evaluated using the low estimate of adult survival.

Model Use

Populations were initialized with 160 individuals. Population decreased from the initial population size for the baseline and all recovery scenarios excluding high levels of scenarios 2, 3, and 5 (Table 5.3). Only the latter scenarios prevented decreases of the LKMR population and produced small population increases (Table 5.3). Scenarios 2 through 7 implemented at low, medium and high levels all projected mean final populations that were larger than the mean final population projected by the baseline scenario (Table 5.3). The smallest mean final population was projected for medium levels of raccoon control applied only to large, inland patches (scenario 4, Table 5.3). The largest population increase (18%) was projected for high levels of habitat management applied to randomly selected patches (scenario 3, Table 5.3). Higher levels of habitat management and a combination of habitat management and raccoon control projected larger population changes than lower levels of these strategies (Table 5.3). In contrast, raccoon control applied without habitat management projected the largest population change when implemented at the lowest level (Table 5.3).

Mean final population sizes were larger for all levels of all scenarios when applied to randomly selected patches compared to population projections for strategies when applied only to the largest patches >0.80 km the coast (Table 5.3). The total area treated for scenarios applied to the large, inland patches and randomly selected patches was 8.3 ha and 10.5 ha, respectively. When I corrected the mean final population projected by each scenario to account for the total area treated, I found population changes per hectare treated were similar when applied to randomly selected patches and to the largest patches >0.80 km for the coast (Table 5.3). Translocation scenarios 8 and 9 projected mean final populations that were 36% and 33%, respectively, smaller than the initial population size (Table 5.4). In contrast, the population reductions projected by the translocation scenarios were smaller than the 41% reduction projected by the baseline scenario (Table 5.4).

Terminal quasi-extinction risk for the baseline scenario (1) was 5% (95% *CI* = 0.02–0.08). Based on the 95% *CI*s the terminal quasi-extinction risk was lower for all levels of scenarios that included habitat management (scenarios 2,3, 6, and 7) and the lowest level of scenarios 4 and 5 (raccoon control) when compared to the baseline scenario (Table 5.5). Terminal quasi-extinction risk for medium and high levels of scenarios 4 and 5 were not different from the baseline scenario (Table 5.5). Terminal quasi-extinction risk also did not differ between scenarios applied to large, inland patches (2, 4, and 6) and scenarios applied to randomly selected patches (3, 5, and 7). Based on 95% *CI*s neither translocation scenario significantly reduced the terminal quasi-extinction risk from the baseline scenario (Table 5.4).

Model validation— Model simulations for all levels of habitat management, raccoon control and a combination of the 2 strategies did not differ from population estimates obtained from prediction equations (Table 5.6). The largest difference between predicted and projected populations was 6.9 rabbits for the highest level of habitat management and raccoon control (Table 5.6).

Table 5.5. Terminal quasi-extinction risk and 95% *CI* projected by low, medium, and high levels of habitat management (scenarios 2 and 3), raccoon control (scenarios 4 and 5) and a combination of habitat management and raccoon control (scenarios 6 and 7) applied to the largest 15 occupied patches >0.80 km from the coast (even numbered scenarios) and 15 randomly selected occupied patches (odd numbered scenarios) for a population viability analysis of Lower Keys marsh rabbit. Quasi-extinction risk is defined as the probability the LKMR population range wide will fall below 50 rabbits within10 years. Model simulations were for 1,000 stochastic iterations for 10 years using a 1 year time step initialized with 160 individuals.

Scenario [a]	Implementation level		
	Low	Medium	High
2	0.01 (0.00–0.03)	0.01 (0.00–0.04)	0.00 (0.00–0.03)
3	0.01 (0.00–0.03)	0.00 (0.00–0.03)	0.00 (0.00–0.03)
4	0.00 (0.00–0.03)	0.03 (0.00–0.06)	0.02 (0.00–0.05)
5	0.00 (0.00–0.03)	0.03 (0.00–0.06)	0.02 (0.00–0.05)
6	0.01 (0.00–0.04)	0.01 (0.00–0.04)	0.00 (0.00–0.03)
7	0.01 (0.00–0.04)	0.00 (0.00–0.03)	0.00 (0.00–0.03)

[a] Scenario 1 is the baseline scenario, terminal quasi-extinction risk = 0.05 (95% *CI* = 0.02–0.08).

Table 5.6. Mean final abundance and 95% *CI* projected for low, medium and high levels of recovery scenarios for the Lower Keys marsh rabbit. Model projections were for 10 patches of randomly selected sizes and 1,000 stochastic iterations for 3 years simulated time using a 1 year time step. Predicted abundances are based on 25%, 50%, and 75% decreases in patch edge (psi) and raccoon activity (proc) and 25%, 50%, and 75% increases in the distribution of herbaceous plants species (dist). Comparisons were used to validate assumed changes in carrying capacity, juvenile, and maternity expected from proposed recovery strategies.

	Low	Medium	High
Scenario [a]	Model $\bar{x}$ (95% *CI*)	Model $\bar{x}$ (95% *CI*)	Model $\bar{x}$ (95% *CI*)
Prediction variable	*Predicted N*	*Predicted N*	*Predicted N*
Habitat management	17.1 (14.0–20.2)	18.3 (15.0–21.7)	24.8 (20.9–28.7)
(*psi, dist*)	*15*	*18*	*23*
Raccoon control	12.9 (9.8–16.0)	13.3 (9.8–16.8)	16.3 (12.4–20.2)
(*proc*)	*12*	*13*	*14*
Habitat management & raccoon control	15.5 (12.1–28.4)	20.4 (17.4–23.4)	29.3 (25.4–33.2)
(*psi, dist and proc*)	*15*	*18*	*23*

[a] Mean final abundance and 95% *CI* for the baseline model scenario: $\bar{x}$ =12.3 (*9.4*–15.2) and the predicted abundance estimate for all patches:*10*.

DISCUSSION

Model Use

Not surprisingly, simulated recovery strategies including habitat management, raccoon control and a combination of the 2 when applied to 32% (15 of 47) of occupied patches reduced LKMR population declines over the 10 years of simulated time that were observed in the baseline scenario . Habitat management, habitat management in combination with raccoon control, and finally raccoon control projected the greatest benefit to LKMR population. Benefits projected by habitat management and a combination of raccoon control and habitat management increased with increased effort; however, only high levels of habitat management when applied to randomly selected patches projected an increase in the rabbit population above the initial abundance.

Raccoon control modeled without concurrent habitat management showed the smallest population increases when compared to habitat management or a combination of the 2 strategies. Counter to expectations, simulations suggested higher levels of raccoon control failed to prevent further decline in the rabbit population when compared to the lowest level of habitat management. This resulted because higher levels of raccoon control, simulated as higher reproductive rates, drove treated patches to carrying capacity without allowing additional population growth because carrying capacities remained unchanged. In contrast, habitat management and habitat management strategies in combination with raccoon control were simulated as increased carrying capacity, juvenile survival, and reproductive rates. Because these strategies increased either juvenile survival or reproduction concurrently with carrying capacity, local populations were able to grow.

Mean final abundance for recovery scenarios applied to randomly selected patches were larger than scenarios applied to the largest patches >0.80 km from the coast. I did not find a difference in spatial configuration of recovery scenarios when I accounted for total area managed. Although the model did not show spatial configuration of recovery efforts affected LKMR populations, recovery efforts should still be focused on populations most likely to persist and recover after a hurricane as these models did not include potential effects of future hurricanes on LKMR populations (Forys and Humphrey 1999*a*).

Both translocations to Big Torch and Big Pine keys projected population declines that were smaller than the decline projected under the baseline scenario but failed to reduce projections of terminal quasi-extinction risk. Most patches on Big Torch Key were located farther than the maximum dispersal distance from occupied patches in other areas of the range potentially explaining the poorer performance of this recovery strategy when compared to translocation to south Big Pine Key. The ability of LKMRs to disperse from translocation sites on Big Torch Key to potentially suitable patches on nearby Little and Middle Torch keys that were not included in the model may improve the performance of this scenario (Forys and Humphrey 1996). Reintroduction patches on south Big Pine Key were farther apart (≈3,200 m) but all patches in the reintroduction area were within the maximum dispersal distance potentially explaining this scenario's slight performance improvement. In addition, population increases for translocation scenarios may be improved if >4 individuals per population were translocated or if translocations occurred more than once assuming impacts to source populations could be limited (Todd et al. 2002).

LKMR translocations have been successfully used to establish local populations on Water and Little Pine keys (Faulhaber et al. 2006). Both translocation sites were relatively isolated from other rabbit populations and it is unclear whether rabbits can naturally disperse to these outer islands to augment translocated populations or to recolonize extirpated patches. Twelve adult rabbits, 5 male and 7 female were originally translocated to Little Pine Key in 2002 and the population was estimated at 35 individuals in 2008, an increase of 66%. The Little Pine Key population appears stable despite serving as the donor population to subsequent translocations. Seven adult rabbits were originally translocated to Water Key, however, the population did not persist following Hurricane Wilma and a subsequent translocation of 2 males and 2 females was not successful (USFWS 2007). Disparities between the Little Pine and Water keys translocations may result from differences in habitat quality. For example, there appears to be more, higher quality habitat on Little Pine Key than Water Key. My model was unable to consider the effect of variations in habitat quality or availability on translocation scenarios. Despite this limitation my results indicate translocation strategies only provide limited reductions in population declines when compared to other recovery scenarios.

PVA results predicted low terminal quasi-extinction risk (probability population would fall below 50 individuals in10 years) for the entire LKMR population if no recovery actions were taken. Recovery scenarios 2, 3, 6, and 7 and low levels of raccoon control predicted quasi-extinction risks that were lower than the baseline scenario. Population projections were a more suitable measure of relative differences between recovery scenarios for this PVA due to low predictions of quasi-extinction risk for all scenarios in combination with high variability for these estimates.

Model validation–Model results indicate habitat management actions simulated by improved local carrying capacity and juvenile survival and control of raccoon populations simulated by increased reproduction are effective population recovery strategies. While carrying capacity, juvenile survival and reproduction are difficult to measure for the LKMR, changes in patch characteristics (e.g., patch shape index, distribution of herbaceous species, and raccoon activity) expected to influence these demographic parameters corresponded well with model projections. In addition, model simulations were consistent with prior results that showed measures of habitat quality including the extent of patch edge (psi) and the number of herbaceous bunchgrasses and forbs (species) and raccoon activity (proc) influence local densities of LKMRs (Chapter II). Brush control and prescribed fire are potential habitat management actions that could be used to restore and maintain LKMR habitats (USFWS 2000). Numerous strategies exist to reduce raccoon activity in LKMR patches and include trap and removal, shooting, and reducing anthropogenic food sources near LKMR habitats (Judson et al. 1995).

Two PVAs previously conducted for the LKMR produced large variations in terminal extinction and quasi-extinction risk and high sensitivity to changes in estimates of demographic parameters (Forys 1999*a*, LaFever et al. 2008). The current models' simulations provided robust estimates of population projections, evaluated 4 recovery strategies for the entire LKMR population, and thus could be used as an effective conservation planning tool. Recovery scenarios were evaluated using a population model parameterized with adult survival rate estimates that I verified using annual population changes based on abundance estimates from 1992 and 2008 (Forys 1995, Schmidt 2009). Changes in carrying capacity, juvenile survival and reproduction expected to result from low, medium and high levels of habitat management and raccoon control were validated using population predictions from observed differences in habitat quality and raccoon activity for a subset of LKMR patches. Model validation was done using data that was independent of data used to build the model (Grant and Swannack 2008). Nonetheless, model assumptions could be further verified with additional research to determine the effect of prescribed fire and brush control on measures of carrying capacity and juvenile survival, as well as the proportion of nest depredation attributable to free-roaming cats and raccoons.

CHAPTER VI

SUMMARY AND CONCLUSIONS

My study sought to determine local and landscape factors that influence Lower Keys marsh rabbit (LKMR, *Sylvilagus palustris hefneri*) metapopulation ecology and dynamics, to apply findings by building and validating a metapopulation model, and to evaluate strategies for their recovery. My objectives were 1) to evaluate the effect of patch demographics, raccoon abundance, and habitat attributes on adult and juvenile LKMRs, 2) to quantify extinction and colonization of local patches after Hurricane Wilma and determine if patch and landscape configuration affect local population dynamics, 3) to evaluate the use of prescribed fire in maintaining and restoring coastal salt marsh prairies important to LKMRs, and finally 4) to evaluate translocations, habitat management and raccoon control using a population viability analysis of the Lower Keys marsh rabbit.

I found LKMR densities were higher in patches with greater numbers of bunchgrasses and forbs and less edge, and lower in patches with higher measures of raccoon activity. Following Hurricane Wilma (24 October 2005), I found the distance between LKMR patches and the coast had a negative influence on extinction probability; the distance between an extirpated and occupied LKMR patch had a negative influence on colonization probability, and patch size had a positive influence on colonization probability. Adult use of burned areas increased, woody vegetation decreased and the distribution of herbaceous bunchgrasses and forbs used by LKMRs for food, cover, and nesting increased following prescribed fire. Model results indicated habitat management actions that improve local carrying capacity and juvenile survival and control raccoon populations to increase maternity rates are effective population recovery strategies.

These results provide a conservation planning tool that can be used to select recovery strategies and locations that will maximize benefits to LKMRs, thus improving their viability and recovery. Recovery efforts should be focused on reducing patch edge, increasing presence and diversity of herbaceous bunchgrasses and forbs important to LKMRs for food, cover, and nesting, and reducing raccoon densities in LKMR patches. Managers should prioritize protection and management of large, inland LKMR patches to mitigate increased extinction risk caused by hurricanes. Prescribed fire should be applied to larger LKMR patches to further evaluate its use for managing LKMR habitats. Habitat management strategies that reduce or reverse brush encroachment and predator management strategies to decrease raccoon activity in LKMR habitats should be implemented. Lastly, measures of habitat quality such as the distribution of herbaceous bunchgrass and forb plants and measures of raccoon activity should be incorporated into long-term monitoring strategies and evaluation of recovery actions.

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