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RESEARCH ARTICLE

Influence of patch, habitat, and landscape characteristics on patterns of Lower Keys marsh rabbit occurrence following Hurricane Wilma

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Abstract Degradation of coastal systems has led to increased impacts from hurricanes and storm surges and is of concern for coastal endemics species. Understanding the influence of disturbance on coastal populations like the endangered Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*) is important to understanding long-term dynamics and for recovery planning. We evaluated the effect of disturbance on the rabbits by determining which patch, habitat, and landscape characteristics influenced habitat use following Hurricane Wilma. We determined patch-level occurrence 6–9 months prior to Hurricane Wilma, within 6 months following the hurricane, and 2 years after the storm to quantify rates of patch abandonment and recurrence. We observed high patch abandonment (37.5% of used patches) 6 months after Hurricane Wilma and low rates of recurrence (38.1% of abandoned patches) 2 years after the storm, an indication that this storm further threatened marsh rabbit viability. We found the proportion of salt-tolerant (e.g., mangroves and scrub mangroves) and salt-intolerant (e.g., freshwater wetlands) vegetation within LKMR patches were negatively and positively correlated with probability of patch abandonment, respectively. We found patch size and the number of used patches surrounding abandoned patches were positively correlated with probability of recurrence. We suggest habitat use following this hurricane was driven by the differential response of non-primary habitats to saline overwash and habitat loss from past development that reduced the size and number of local populations. Our findings demonstrate habitat use studies should be conducted following disturbance and should incorporate on-going effects of development and climate change.

Keywords Hurricane Wilma · Lower Keys marsh rabbit · Patch abandonment · *Sylvilagus palustris hefneri*

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Introduction

Coastal ecosystems have been shaped by recurring disturbance events such as hurricanes (Boose et al. 1994; Whittaker 1995; Michener et al. 1997). Disturbances are any event that disrupts ecosystems, communities, or population structure, as well as changes the composition and availability of resources, substrates, or the physical environment (White and Pickett 1987). Species occurring in disturbance-prone coastal areas have evolved mechanisms, such as high dispersal ability, to cope with partial or total losses of local populations and habitats (Travis and Dytham 1999). Nonetheless, these adaptive mechanisms have been challenged in coastal systems where development has imperiled species, reduced biodiversity, and decreased resilience to disturbance (Bildstein et al. 1991; Michener et al. 1997; Vitousek et al. 1997; Lotze et al. 2006). In particular, the decreased resilience of degraded coastal systems has increased the negative effects of hurricanes and flooding created by storm surges (Bildstein et al. 1991; Swilling et al. 1998; Lotze et al. 2006).

The effects of hurricanes and coastal development are pronounced in the southeastern United States and the Lower Keys, Florida in particular. 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 (≤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*], silver rice rat [*Oryzomys palustris natator*]), and community associations (e.g., pine rocklands) that either do not occur on the mainland United States or have very limited distributions (U.S. Fish and Wildlife Service 2009). Small geographic distributions and high rates of endemism, in conjunction with extensive coastal development and hurricanes, threaten 22 species in the Lower Keys with extinction (Ibid.).

Hurricanes are a common disturbance event in the Keys but severe storm surges associated with hurricanes, such as those following Hurricanes Betsy in 1965, Georges in 1998, and most recently Wilma in 2005, are less common (Lopez et al. 2003; Pasch et al. 2006). The Lower Keys have a maximum elevation of 3 m making these islands and their associated flora and fauna highly susceptible to storm surges (Ross et al. 1992; McGarry MacAulay et al. 1994). Hurricane Wilma made landfall on 24 October 2005 and produced a storm surge that inundated the Lower Keys with seawater 1.5–2.4 m above mean sea level on 2 occasions, and caused substantial impacts to the endangered species and vegetative communities these islands support (Pasch et al. 2006; U.S. Fish and Wildlife Service 2009). The influence of disturbance events such as hurricanes is particularly relevant to endemic populations with limited distributions, such as the LKMR. LKMR are a 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). A population viability analysis that modeled hurricane effects demonstrated an increased extinction risk for the LKMR (Forys 1995; Forys and Humphrey 1999a). 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; Perry and Lopez 2005), evaluate the degree of subsequent recovery (USFWS 2007), or determine the effects on LKMR habitats.

LKMR and other lagomorphs that occur in successional habitats prone to 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 1999b; USFWS 1999). 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 with interaction between patches usually limited to one-way dispersal of individuals from their natal patch (Forys and Humphrey 1996; USFWS 1999; but see Perry and Lopez 2005). We defined a patch as an area of habitat suitable to LKMR separated by roads, bodies of water, or unsuitable habitat. Patches smaller than the minimum adult range (i.e., 0.5 ha; Forys and

Humphrey 1996) were included in our analysis to determine their potential use as dispersal corridors or temporary refugia.

The most straight-forward way to evaluate the effect of disturbance on the LKMR is to determine which patch, habitat, and landscape characteristics had the greatest influence on patch use following a hurricane, an opportunity provided by Hurricane Wilma. We knew that upland habitats, such as hammocks and pinelands, could potentially provide refugia for LKMR during severe storm events (Faulhaber et al. 2008) and we believed saltwater inundation from storm surges may disproportionately affect the suitability of salt-intolerant, low-lying freshwater habitats (e.g., freshwater marsh, freshwater pineland and freshwater hardwood; Ross et al. 1992) used by LKMR. LKMR primarily occupy low-lying wet areas with dense cover including salt marsh, buttonwood (*Conocarpus erectus*) transition zones, but also use freshwater marsh where available (Forys 1995; Faulhaber et al. 2007, 2008). Mosquito ditches dug throughout the Lower Keys, including within LKMR patches, effectively drained surface water from freshwater wetlands and increased flow of tidal waters inland, thus permanently altering hydrology, increasing salinity, and initiating long-term changes in vegetation composition (Hobbs et al. 2006; USFWS 2007). Roads and dredge spoils also impound saltwater from storm surges in low-lying areas (Ross et al. 2009), including freshwater wetlands used by LKMR. Further, LKMR were shown to have limited use of salt-tolerant mangrove communities but their importance is not well understood; however, marginal habitats were important for the post-hurricane recovery of other endemic subspecies living in fragmented coastal habitats threatened by development (e.g., beach mice [*Peromyscus polionotus* spp.], Swilling et al. 1998; Pries et al. 2009).

Our objective was to determine if patch, habitat, and landscape characteristics influenced rates of LKMR abandonment of and recurrence in patches after Hurricane Wilma. Specifically, we predicted that (1) large patches could have increased resource availability and heterogeneity, larger local populations, and would show reduced rates of abandonment and increased rates of LKMR recurrence (Forys and Humphrey 1999a, b; Hanski 1999); (2) patches farther from the coast, because of the lesser probability of extreme storm effects (e.g., wind, surge), would have lower abandonment rates by LKMR; (3) the number and proximity of patches used by LKMR would influence the number of dispersing rabbits and would influence rates of recurrence in abandoned patches (Forys and Humphrey 1999a, b; Hanski 1999); (4) patches with higher proportions of salt-intolerant vegetation (e.g., freshwater wetlands) would have higher abandonment rates and lower rates of LKMR recurrence; (5) patches with higher proportions of salt-tolerant vegetation (e.g., mangroves and scrub mangroves) would have lower abandonment rates and higher rates of LKMR recurrence; and (6) patches with higher proportions of upland habitats that could serve as refugia during a storm surge would have lower rates of abandonment by LKMR.

Methods

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. 1, Chen and Gerber 1990; Forys and Humphrey 1999a). 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 1999a). The maximum elevation is 3 m, with slight variations in elevation producing distinct vegetation communities that transition from salt tolerant and tidally influenced mangroves to coastal salt marsh/buttonwood transition zones inland to salt-intolerant freshwater marshes, pine rocklands and tropical hardwood hammocks (Fig. 2, Ross et al. 1992; Faulhaber 2003).

LKMR have been predominately found in coastal salt marsh prairies (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*) interspersed with salt tolerant hardwoods, predominantly buttonwood but also with white mangrove (*Laguncularia racemosa*), red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), joewood (*Jaquinia keyensis*), along with poisonwood (*Metopium toxiferum*) and wild dilly (*Manilkara bahamensis*), with the

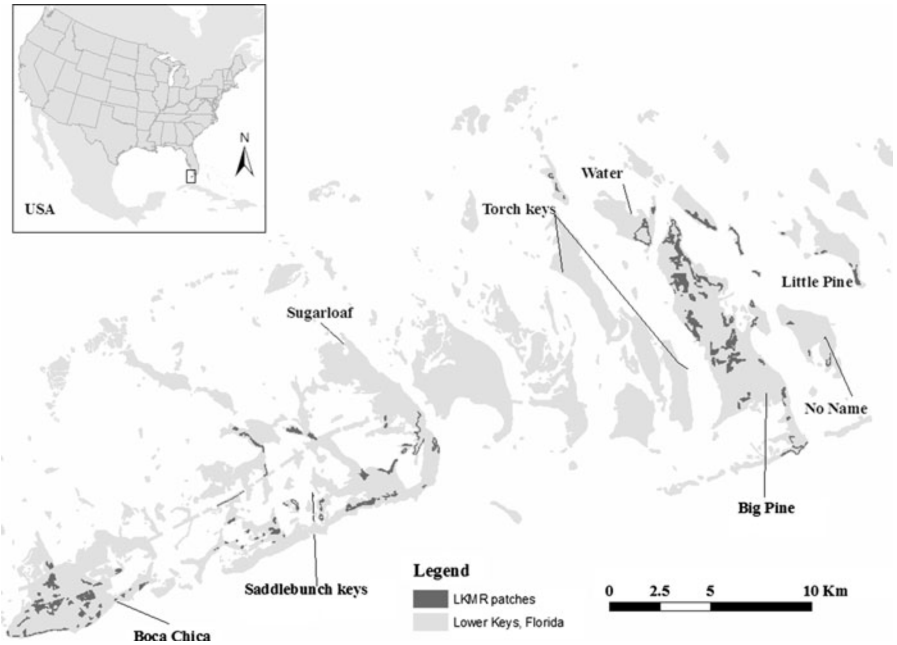

Fig. 1 Distribution of Lower Keys marsh rabbit patches throughout the Lower Keys, Florida, USA

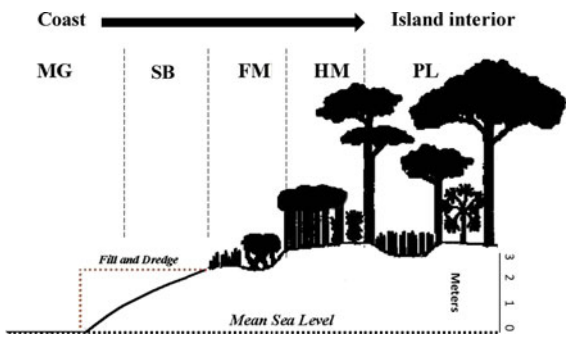

Fig. 2 Vegetation types of the Lower Keys, Florida, USA. MG = mangroves and scrub mangroves, SB = salt marsh and buttonwood transition zone, FM = freshwater marsh, HM = hardwood hammock and freshwater hardwoods, PL = pine rocklands and freshwater pinelands. Figure adapted from Lopez et al. (2004)

distribution of hardwoods dependent upon salinity and disturbance history (e.g., fire, cutting; Faulhaber 2003). LKMR use freshwater marshes characterized by sawgrass (*Cladium jamaicensis*) and Gulf Coast spike rush (*Eleocharis cellulose*) interspersed with hardwoods, whose distribution and abundance is also dependent upon disturbance history (Faulhaber et al. 2007). LKMR also use tidal swamps composed of mangroves and scrub mangroves, coastal beach berms, as well as upland areas including pine rocklands and tropical hardwood hammocks (Faulhaber et al. 2008).

The LKMR historically occupied most large islands from Big Pine to Boca Chica keys but currently occupy 4 main islands (Boca Chica, Saddlebunch, Sugarloaf, and Big Pine keys) and several smaller, outlying islands (Fig. 1, Faulhaber et al. 2007) that form 2 genetically distinct management units or clades (Crouse et al. 2009). We, therefore, examined the occurrence of LKMR in patches on Boca Chica and Big Pine keys, the 2 largest subpopulations representative of the geographic extent of this subspecies and each clade. Boca Chica is lower in elevation, generally has fewer upland habitats, and lacks pine rocklands and freshwater pinelands present on Big Pine (McGarry MacAulay et al. 1994). Further, the surge and impacts associated with Hurricane Wilma varied throughout the LKMR distribution, most likely due to differences in elevation. The maximum surveyed surge on Boca Chica, at the western edge of the LKMR geographic distribution, was 1.8 m and varied between 1.2 and 1.8 m on Big Pine, at the eastern extent of their distribution (Pasch et al. 2006).

Patch use

We used the occurrence of LKMR within a patch as a binomial measure of their habitat use after Hurricane Wilma. We used a Geographic Information System

(GIS; ArcGIS 9.3, ESRI 2008) to identify LKMR patches delineated during an updated distribution survey (Faulhaber et al. 2007) that occurred on Boca Chica and Big Pine keys. We determined LKMR occurrence within a patch for data collected 6–9 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). We employed 2 established monitoring protocols to determine LKMR occurrence (Faulhaber et al. 2007; Schmidt et al. 2011). Survey protocol 1 followed the USFWS annual monitoring protocol for LKMR and used 1 observer to search for rabbit sign (e.g. fecal pellets) within patches. The observer navigated to a randomly selected start point and searched in expanding concentric circles until LKMR pellets were detected or until 15 min had elapsed. We used a shapefile of patch boundaries uploaded to a handheld Global Positioning System (GPS) and visual identification of habitats associated with LKMR to ensure searches were constrained to the delineated patches. We used data collected with this method to determine LKMR occurrence in patches during survey periods 1 and 2. For survey protocol 2, we constructed a 30×30-m grid and placed it over a shapefile of the Lower Keys using a GIS. Grid nodes falling within the boundaries of LKMR patches on Boca Chica and Big Pine keys were selected. We searched within a 1-m radius of each node and recorded the presence or absence of LKMR pellets (Schmidt et al. 2011). We also identified patch boundaries using a GPS unit and visual identification of habitats for this method. We used data collected with survey protocol 2 to determine LKMR occurrence in patches during survey period 3. We classified patches as used if pellets were detected at $\geq$1 sample node.

Patch abandonment and rabbit recurrence

We classified patches as abandoned if LKMR occurred within the patch during survey period 1 but were absent during survey period 2. We assumed that all pellets were removed from patches as a result of the hurricane's storm surge and that any pellets in the patches during survey period 2 were deposited after Hurricane Wilma. We classified patches where LKMR did not occur during survey period 2 (within 6 months of Hurricane Wilma) but did occur 2 years after the storm (survey period 3) as a recurrence event. We included patches that were not used prior to Hurricane Wilma in our classification of recurrence events since our objective was to determine how Hurricane Wilma influenced LKMR habitat use after a severe storm event.

Patch, habitat, and landscape characteristics

We quantified patch, habitat, and landscape characteristics predicted to influence rates of abandonment and recurrence by LKMR after Hurricane Wilma. We used Hawth's Analysis Tools for ArcGIS (Beyer 2006) to calculate patch area (area [ha]) and to measure the minimum straight line distance from the centroid of patches where LKMR did not occur during survey period 2 to the centroid of patches where LKMR did occur during survey period 2 and were located within the average LKMR dispersal distance (e.g., 835 m, Forys 1995). We then averaged these distances for each patch to calculate a patch-level covariate (dpatch [km]). We used shapefiles depicting the boundaries of Boca Chica and Big Pine keys in GIS to measure the minimum straight line distance between the centroid of each patch and the coast (dcoast [km]). To calculate the proportion of each vegetation type in a patch, we used the Advanced Identification of Wetlands (ADID) GIS coverage vegetation classifications developed by the Florida Marine Research Institute (McGarry MacAulay et al. 1994). We grouped non-primary habitats according to various levels of salt tolerance and elevation (Ross et al. 1992; Faulhaber 2003) as follows: low-lying, salt-intolerant wetlands including freshwater marsh, freshwater pineland, and freshwater hardwood (fwlow); low-lying, highly salt-tolerant mangrove and scrub mangrove (hsalt); and upland pine rockland and hardwood hammock (upland).

We used Hawth's Analysis Tools for ArcGIS (Beyer 2006) to create a 0.06-km buffer around each patch's perimeter that we based on the average radius of adult ranges previously used to determine if neighboring patches form interacting local populations (Faulhaber 2003). We then used ADID maps to calculate the proportion of each patch's buffer in the following land classifications: developed land (devel); open water beyond coastline (water); and all natural land potentially suitable for LKMR including mangrove, scrub mangrove, buttonwood transition, salt marsh, pine rockland, hammock, freshwater marsh, freshwater pineland and freshwater hardwood (suit). We calculated the total area of each patch's buffer that was delineated rabbit habitat (patch [ha]). Finally, for each patch where LKMR did not occur following Hurricane Wilma (survey period 2) we counted the number of patches used by LKMR during the same survey period with centroids within the average dispersal distance (tot_occ).

Data analysis

To determine which patch, habitat, and landscape characteristics had the greatest influence on the probability of LKMR occurrence after Hurricane Wilma, we used generalized linear regressions and model likelihood estimates to relate explanatory variables to rates of LKMR patch abandonment and recurrence. For the first analysis, patches were classified as 1 if they had been abandoned by LKMR and 0 otherwise. For the second analysis, patches were classified as 1 if LKMR recurred in an abandoned patch and 0 otherwise. We used an information theoretic approach to evaluate the relative fit of a suite of potential models (Burnham and Anderson 2002). We used SPSS software (Release 15.0.0, 2006) to run a priori model sets specific to rates of LKMR abandonment of and recurrence in patches that was fitted to a binomial distribution (Burnham and Anderson 2002). We evaluated 24 a priori models, including an intercept-only model, to evaluate the effect of patch, habitat, and landscape variables on the probability LKMR abandoned patches after Hurricane Wilma (Table 1, models 1–24) and 29 a priori models, including an intercept-only model, to evaluate the effect of patch, buffer habitat, and landscape characteristics on the probability LKMR recurred in abandoned patches 2 years after the storm (Table 2, models 25–53). We used Akaike's Information Criterion, corrected for small sample size (AIC_c), to evaluate model fit to our data (Burnham and Anderson 2002). Because our data were non-normally distributed and wide-ranging, we used the Z transformation to standardize all continuous covariates to prevent the numerical optimization algorithm from converging on local minima or failing to converge, thus producing erroneous parameter estimates. This approach also produces coefficients that are relative to one another and allows comparison of the magnitude of effect of each independent variable upon the dependent variable. We used the relative difference to the smallest AIC_c in each model set (ΔAIC_c) to select the best approximating models (Burnham and Anderson 2002). We considered models ≤ 2 AIC_c units to compete with the best models and discarded models >2 AIC_c units as unlikely representations of the data (Burnham and Anderson 2002). We then exponentiated the binomial regression analysis of the selected models to derive a prediction equation that we used to evaluate the influence of the best models' variables on the probability LKMR abandoned and recurred in patches (Agresti 2007; Guthery and Bingham 2007). To plot the effect of each covariate on rates of abandonment and recurrence, we held the other covariate(s) in the equation constant and allowed the plotted covariate to vary throughout the range of the data collected.

Estimation of detection

Using a removal design, we randomly selected 21 patches monitored in survey period 3; if rabbits were not detected in the first survey, we resurveyed patches until rabbit presence was detected or for a maximum of 3 surveys (assuming a detection probability >0.6 and an occurrence rate <0.5; MacKenzie and Royle 2005). Failure to account for false absences may negatively bias estimates of LKMR occurrence within a patch and subsequently bias estimates of abandonment and recurrent (MacKenzie et al. 2006). A removal design was appropriate as we assumed false positives were not an issue because LKMR pellets are easily distinguishable from the other mammalian species in the area (e.g., Key deer, silver rice rat, raccoon [*Procyon lotor*]). We then used Program MARK to estimate detection and probability of occurrence for LKMR patches for survey period 3 data collected using survey protocol 2 (White and Burnham 1999). We compared naïve rates of occurrence to estimates corrected for detection to assess potential for negative bias. We used Eq. 1 to evaluate the influence of survey effort on detection:

$$p* = 1 - (1 - p)^{K} \quad (1)$$

$p*$ is the probability of detecting LKMR at least once during K surveys of used patches. We could not assess detection probability for survey protocol 1 nor estimate abandonment and recurrence rates corrected for false absences as the USFWS annual monitoring

Table 1 A priori models correlating the probability habitat patches were abandoned by Lower Keys marsh rabbits following Hurricane Wilma to patch characteristics for 56 patches in the Lower Keys, Florida, USA, between 2005 and 2006

Model[a]		K	$-2\ln L$	AIC_c	ΔAIC_c
1	hsalt	2	68.7	73.0	0.0
2	fwlow	2	68.9	73.1	0.2
3	fwlow + hsalt	3	67.2	73.6	0.7
4	fwlow + dCoast	3	67.2	73.7	0.7
5	area + fwlow +area * fwlow	4	64.9	73.7	0.7
6	hsalt + dCoast	3	67.3	73.7	0.8
7	fwlow + hsalt + fwlow * hsalt	4	65.5	74.3	1.3
8	area + hsalt + area * hsalt	4	66.4	75.2	2.2
9	area + hsalt	3	68.7	75.2	2.2
10	hsalt + dCoast + hsalt * dCoast	4	66.4	75.2	2.2
11	area + fwlow	3	68.8	75.3	2.3
12	fwlow + hsalt + uplands	4	67.2	76.0	3.0
13	fwlow + dCoast + fwlow * dCoast	4	67.2	76.0	3.0
14	intercept	1	74.1	76.2	3.2
15	dCoast	2	72.0	76.2	3.3
16	upland	2	73.0	77.3	4.3
17	upland + dCoast	3	71.3	77.8	4.8
18	area	2	74.1	78.3	5.4
19	area + dCoast	3	71.9	78.4	5.4
20	area + dCoast + area * dCoast	4	69.8	78.6	5.6
21	area + dCoast + upland + fwlow + hsalt	6	65.4	79.1	6.1
22	area + upland	3	73.0	79.5	6.5
23	upland + dCoast + upland * dCoast	4	71.1	79.9	7.0
24	area + upland + area * upland	4	72.7	81.5	8.5

We display the number of parameters (K), −2* natural log of the maximum likelihood estimate ($-2\ln L$), Akaike's Information Criterion adjusted for small sample size (AIC_c), and change in AIC_c from the smallest AIC_c value (ΔAIC_c) for each model

[a] Variable notation for patch attributes: distance from each patch centroid to the nearest coastline (dCoast[km]) and patch area (area[ha]). All remaining variables are the % of each patch in the following habitat classifications: freshwater marsh, freshwater pineland, and freshwater hardwood (fwlow); upland pine rockland and hardwood hammock (upland); and highly salt-tolerant mangrove and scrub mangrove (hsalt). We also modeled probability of patch abandonment as a constant function (intercept)

protocol did not incorporate repeat surveys within a given season.

Results

Patch use

We surveyed Boca Chica and Big Pine keys prior to Hurricane Wilma (24 October 2005) from 1 January–30 March 2005 (survey period 1), following the hurricane from 19 January 2006–11 May 2006 (survey period 2), and 2 years after the hurricane from 10 December 2007–26 February 2008 (survey period 3). We monitored 78 patches in all 3 survey periods. We found LKMR occurred in 56 patches during survey period 1 (naïve rate of occurrence = 71%), 32 on Boca Chica and 24 on Big Pine; 36 patches during survey period 2 (naïve rate of occurrence = 46%), 26 on Boca Chica and 10 on Big Pine; and 46 patches during survey period 3 (naïve rate of occurrence = 59%), 31 on Boca Chica and 15 on Big Pine.

Patch abandonment and rabbit recurrence

We observed 21 abandonment events (37.5% of used patches; Table S1 in Electronic Supplementary

Table 2 A priori models correlating probability of Lower Keys marsh rabbit recurrence in patches abandoned after Hurricane Wilma to characteristics for 42 patches in the Lower Keys, Florida, USA, between 2006 and 2008

Model[a]		K	$-2\ln L$	AIC_c	ΔAIC_c
25	area + tot_occ	3	33.2	39.9	0.0
26	fwlow + tot_occ + area	4	32.6	41.6	1.7
27	hsalt + tot_occ + area	4	33.2	42.3	2.4
28	area + tot_occ + area * tot_occ	4	33.2	42.3	2.4
29	patch + suit + patch * suit	4	38	47.2	7.3
30	area + mDist	3	41.2	47.8	7.9
31	patch + tot_occ	3	42.4	49.1	9.2
32	patch + suit	3	44.0	50.5	10.6
33	tot_occ	2	46.2	50.5	10.6
34	suit	2	47.0	51.3	11.4
35	patch + tot_occ + patch * tot_occ	4	42.4	51.5	11.6
36	devel + water	3	45.4	52.1	12.2
37	devel + water + devel * water	4	45.4	52.1	12.2
38	tot_occ + mDist	3	46.0	52.6	12.7
39	area	2	48.8	53.2	13.3
40	patch + mDist	3	46.6	53.3	13.4
41	tot_occ + patch + mDist + tot_occ * patch * mDist	5	41.8	53.4	13.5
42	devel + patch + water + suit	5	42	53.6	13.7
43	develop	2	49.4	54.1	14.2
44	fwlow + area	3	-48.0	54.7	14.8
45	hsalt + area	3	48.4	55	15.1
46	mDist	2	51.2	55.4	15.5
47	patch	2	51.6	55.9	16.0
48	water	2	52.4	56.7	16.8
49	area + fwlow + area * fwlow	4	48.0	57.1	17.2
50	area + hsalt + area * hsalt	4	48	57.2	17.3
51	intercept	2	55.8	57.9	18.0
52	fwlow	2	55.2	59.4	19.5
53	hsalt	2	55.4	59.8	19.9

We display the number of parameters (K), −2* natural log of the maximum likelihood estimate ($-2\ln L$), Akaike's Information Criterion adjusted for small sample size (AIC_c), and change in AIC_c from the smallest AIC_c value (ΔAIC_c) for each model

[a] Variable notation for patch attributes: patch area (area [ha]), the number of used LKMR patches whose centroids were within the average dispersal distance (tot_occ), the mean minimum straight line distance from each patch's centroid to the centroids of patches that were used during survey period 2 and located within the average LKMR dispersal distance (mDist [km]), and the % of each patch classified as freshwater marsh, freshwater pineland, and freshwater hardwood (fwlow) or highly salt-tolerant mangrove and scrub mangrove (hsalt). The following attributes are land classifications for each patch's buffer zone: % developed land (devel); % open water beyond coastline (water); % natural land potentially suitable for LKMR including mangrove, scrub mangrove, buttonwood transition, salt marsh, pine rockland, hammock, freshwater marsh, freshwater pineland and freshwater hardwood (suit), and total area delineated rabbit habitat (patch[ha]). We also modeled probability of rabbit recurrence in abandoned patches as a constant function (intercept)

Material) between survey period 1 and survey period 2; 7 on Boca Chica and 14 on Big Pine. When we evaluated probability of patch abandonment, we found models 1–7 best approximated the data (Table 1). Models that evaluated the proportion of each patch's habitat that was salt-intolerant low-lying wetlands including freshwater marsh, freshwater pineland, and freshwater hardwood (fwlow [%]) and highly salt-tolerant mangrove and scrub mangrove (hsalt [%]) provided the most likely explanation of the data. We did not consider models that differed from the top models by one parameter and were within 2 ΔAIC_c units of the best model to be supported (i.e., Models 4–7; Table 1) and therefore, we did not consider patch area (area [ha]) or the distance from each patch centroid to the nearest coastline to be a relevant predictor of patch abandonment because the addition of these parameters failed to improve model fit (Burnham and Anderson 2002). In addition, the proportion of upland habitats was unimportant to model fit in any context (Table 1).

We found patches with a higher proportion of highly salt-tolerant mangrove and scrub mangrove wetlands had a lower probability of being abandoned by LKMR after Hurricane Wilma ($\hat{\beta} = -0.79$, 95% CI = −1.57 to −0.01; Fig. 3a) whereas patches with a higher proportion of salt-intolerant low-lying wetlands had a higher abandonment probability ($\hat{\beta} = 0.64$, 95% CI = 0.08–1.20; Fig. 3b) following the hurricane. The influence of these two predictors on probability of abandonment while opposite in direction, was comparable in magnitude. When we examined the percent of each patch composed of highly salt-tolerant mangroves and scrub mangrove vegetation the mean was 65% higher in patches that were not abandoned ($\bar{x} = 23.5\%$, 95% CI = 13.5–33.4; Table S1 in Electronic Supplementary Material) than in patches that were abandoned after the hurricane ($\bar{x} = 8.3\%$, 95% CI = 1.1–15.5; Table S1 in Electronic Supplementary Material). In contrast, the mean for the percent of each patch composed of low-lying, salt-intolerant wetland vegetation for patches that LKMR did not abandon was 46% lower ($\bar{x} = 23.6\%$, 95% CI = 10.1–37.2; Table S1 in Electronic Supplementary Material) than patches that were abandoned ($\bar{x} = 50.9\%$, 95% CI = 30.0–1.9; Table S1 in Electronic Supplementary Material).

We observed LKMR recurrence in 16 abandoned patches (38.1% of unused patches; Table S2 in Electronic Supplementary Material) between survey periods 2 and 3; 9 on Boca Chica and 7 on Big Pine. When we evaluated probability of LKMR recurrence following patch abandonment, we found model 25 best approximated the data (Table 2). We again did not consider models that differed from the top models by one parameter and were within 2 ΔAIC_c units of the best model to be supported (i.e., Model 26; Table 2)

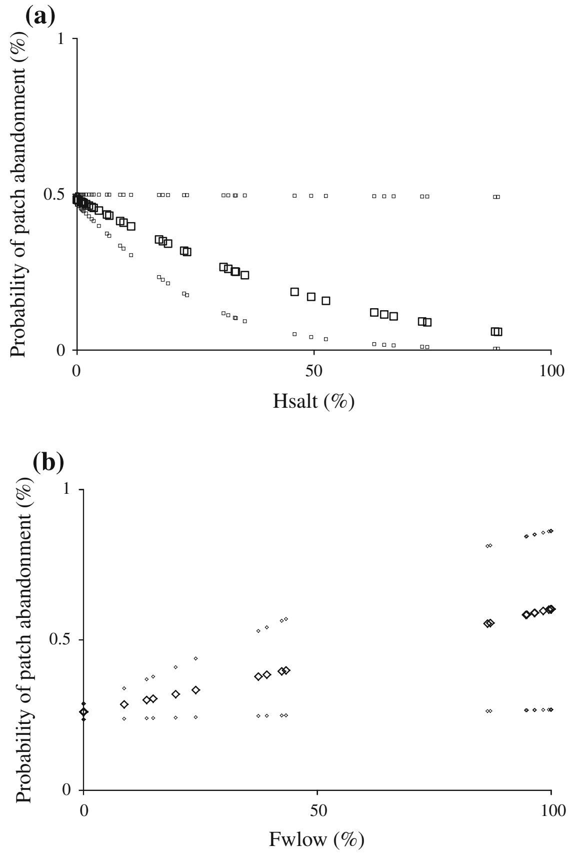

Fig. 3 Estimated probability of patch abandonment (smaller symbols represent 95% CI) 6 months following Hurricane Wilma (24 October 2005) as a function of the proportion (%) of (**a**) highly salt-tolerant wetland (e.g., mangrove and scrub mangrove; hsalt) habitats and (**b**) salt-intolerant freshwater wetland (e.g., freshwater pineland, freshwater marsh and freshwater hardwood; fwlow) for Lower Keys marsh rabbit patches in the Lower Keys, Florida, USA

and therefore, we did not consider the percent of patches composed of low-lying, salt-intolerant wetland vegetation to be a relevant predictor of LKMR recurrence in abandoned patches. In addition, the percent of each patch composed of highly salt-tolerant mangroves and scrub mangrove vegetation, buffer habitats (i.e., suitable habitat, developed land, open water beyond the coastline, and total area of delineated rabbit habitat), or the mean minimum straight line distance from each patch's centroid to the centroids of patches with rabbits during survey period 2 and located within the average LKMR dispersal distance were unimportant to model fit in any context (Table 2).

For model 25, we found support for a positive effect of patch area ($\hat{\beta} = 4.48$, 95% CI = 0.67–8.29; Fig. 4a) and the number of patches with LKMR that were within the average dispersal distance ($\hat{\beta} = 0.75$, 95% CI = 0.28–1.22; Fig. 4b) on LKMR recurrence in abandoned patches. The influence of patch area on the probability LKMR recurred in abandoned patches was six times greater than the influence of the number of patches with LKMR that were within the average LKMR dispersal distance. LKMR recurred in patches abandoned after Hurricane Wilma that were almost 4 times larger ($\bar{x} = 7.8$, 95% CI = 1.0–14.6; Table S2 in Electronic Supplementary Material) compared to patches where LKMR did not recur ($\bar{x} = 2.1$, 95% CI = 1.3–3.0; Table S2 in Electronic Supplementary Material). LKMR recurred in patches abandoned after Hurricane Wilma that had almost 3 times more patches with LKMR that also were within the average dispersal distance ($\bar{x} = 3.4$, 95% CI = 2.0–4.9; Table S2 in Electronic Supplementary Material) compared to patches where LKMR did not recur ($\bar{x} = 1.2$, 95% CI = 0.5–1.9; Table S2 in Electronic Supplementary Material).

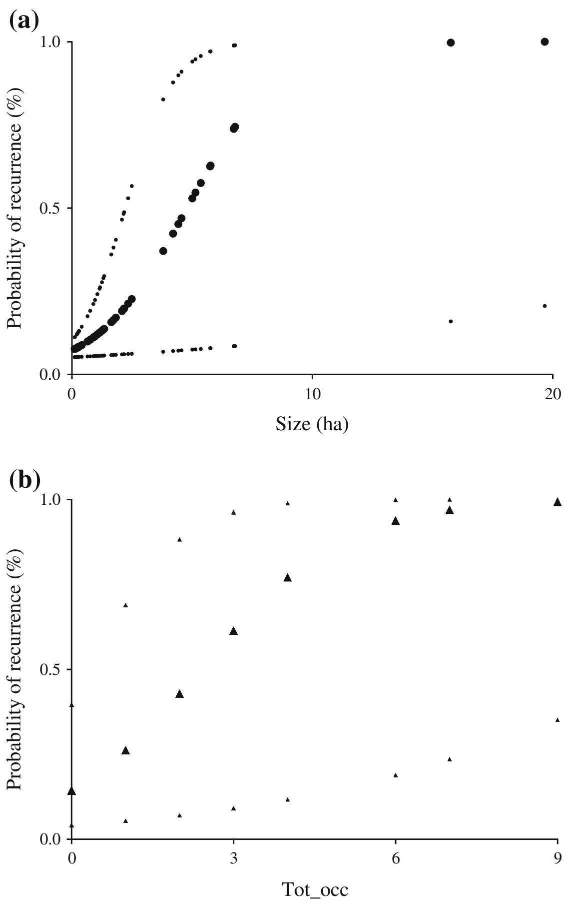

Fig. 4 Estimated probability of rabbit recurrence (smaller symbols represent 95% CI) in patches abandoned after Hurricane Wilma (24 October 2005) as a function of (**a**) patch area (area [ha]) and (**b**) the number of patches with rabbits whose centroids also were within the average dispersal distance (tot_occ) for Lower Keys marsh rabbit patches 2 years following Hurricane Wilma in the Lower Keys, Florida, USA

Detection probability

Of the 21 patches we randomly selected to estimate detection probability for survey protocol 2 used during survey period 3, we resurveyed a total of 8 patches 1 additional time and detected pellets in 1 of those patches. We resurveyed 7 patches 2 additional times and detected pellets in 0 of those patches. We estimated there was an 88.1% probability that LKMR would be detected if present using survey protocol 2. We determined detection probability increased to 98.5% when 2 surveys were conducted using protocol 2. The naïve estimate of LKMR occurrence within a patch for survey period 3 (61.5%) was lower but comparable to the estimate corrected for detection probability (67.4%, 95% CI = 0.52–0.79).

Discussion

Our results indicated salt-tolerant habitats (i.e., mangroves and scrub mangroves) used by LKMR are more resistant to hurricanes and storm surges, presumably because these plant communities are adapted to the high and variable salinities that occur after saline overwash (Ross et al. 1992; Danielsen et al. 2005). The use of salt-tolerant mangrove communities by LKMR was only recognized recently (Faulhaber et al. 2007, 2008); their role in the overall life history of LKMR is not well-understood and requires further study. These habitats have increased in distribution in the last 50 years (Ross et al. 1994) and are expected to increase further given future sea-level rise and recurring pulse disturbances (i.e., hurricanes; Ross et al. 2009).

Salt-tolerant habitats used by LKMR may be lower quality under normal conditions (i.e., closely spaced mangroves seasonally dry due to impoundments; Faulhaber et al. 2007) but may provide a more stable habitat after disturbance; thus, patches with high proportions of salt-tolerant vegetation may serve as refugia important to the recovery of LKMR following hurricanes. The importance of 'marginal' habitats for population recovery after hurricanes also has been demonstrated for 2 subspecies of beach mice (*Peromyscus polionotus* spp.) in Alabama, endemics also threatened by coastal development (Swilling et al. 1998; Pries et al. 2009). Florida box turtles (*Terrapene carolina bauri*) also relied upon minimally affected habitats following disturbances, including saline over wash (Dodd et al. 2006). Often, habitat use studies do not occur following disturbance or consider long-term changes due to climate change and other stressors (e.g., development); therefore, habitats that may not be used or preferred under normal conditions may not be recognized or their utility to the long-term persistence of a population may be understated. Recognizing non-primary habitats that serve as refugia following disturbance events is important for the protection of endangered species with limited distributions, particularly endemic species in highly fragmented, coastal environments.

Our findings support the hypothesis that freshwater wetlands were negatively impacted by Hurricane Wilma and contributed to the loss of LKMR populations (USFWS 2007). Patch abandonment rates on Boca Chica, mostly lacking in freshwater habitats, were 50% lower than Big Pine which had the largest number of LKMR patches in freshwater wetlands. Salt-intolerant wetlands experienced drastic increases in salinity due to salt water inundation from Hurricane Wilma's storm surges (USFWS 2007), an effect that is exacerbated when storm waters are impounded by roads and dredge spoils (Ross et al. 2009). Freshwater habitats used by LKMR have suffered from human activities that have altered hydrology, increased salinity levels, and caused long-term changes in vegetative composition (Hobbs et al. 2006; USFWS 2007) and these effects appear to have lowered the resilience of these communities to disturbances such as hurricanes and storm surges. A similar pattern of habitat loss was demonstrated within salt-intolerant pine rockland habitats of the Lower Keys due to sea-level rise (Ross et al. 1994, 2009), an on-going stressor that is expected to exacerbate degradation of freshwater habitats. The use of salt-intolerant freshwater wetland habitats by LKMR requires further study, including a determination of the extent of change in distribution in these habitats attributed to human activities and sea-level rise. Further, restoration efforts should focus on hydrology of these habitats and the response of LKMR.

Our results indicated patterns of LKMR recurrence in habitat patches abandoned after Hurricane Wilma were driven by patch (i.e., area) and landscape characteristics (i.e., number of nearby patches with LKMR). Both findings are consistent with previous work that found patch size explained a significant but small amount of variability in patch occupancy (Forys and Humphrey 1999b). Following a disturbance, large patches have a higher probability of supporting an animal's minimum habitat requirements (Ehrlich and Murphy 1987) and have a higher probability of intercepting a dispersing individual (Gutzwiller and Anderson 1992). Further, large patches have fewer edge effects, previously shown to have a negative effect on densities of adult and juvenile LKMR (Schmidt et al. 2010). Island area was an important predictor of colonization of islands by a common lizard in the Bahamas following a hurricane (Schoener et al. 2001). In addition, our results indicated that LKMR are more likely to recur in patches abandoned by LKMR if those patches were surrounded by higher numbers of patches with rabbits that also were within the dispersal range because they would have a larger pool of potential dispersers.

Habitat loss and fragmentation due to coastal development reduced the size and number of LKMR habitat patches and was a major factor contributing to their decline (USFWS 1990; Forys and Humphrey 1999b) and continues to negatively influence recovery following Hurricane Wilma, a catastrophic disturbance event. Highly diverse and heterogeneous landscapes are presumed to largely be created and maintained by disturbance; however, anthropogenic threats such as development can decrease the size and connectivity of patchily distributed habitats and cause habitat degradation. Stochastic disturbance events, such as hurricanes, can exacerbate the effects of habitat loss and fragmentation (Pries et al. 2009) and can 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). Understanding the influence of disturbance on these communities is important to understand long-term dynamics and for planning and implementation of recovery efforts (Johnson and Winker 2010). This information will be critical given the increase in hurricane frequency in the North Atlantic Ocean region and the Gulf of Mexico (Goldenberg et al. 2001; Holland and Webster 2007; Saunders and Lea 2008), a scenario that could further harm coastal systems degraded by development and the threatened and endangered species they support.

In this study we evaluated the influence of disturbance on LKMR patch use in response to one hurricane event; therefore, our findings should be viewed in light of the spatial and temporal variability associated with disturbance effects (White and Pickett 1987). Additional studies with greater taxonomic, spatial, and temporal range could further our understanding of disturbance, particularly hurricanes, in degraded coastal systems (Danielsen et al. 2005; Stokstad 2005; Lotze et al. 2006).

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