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Use of a population viability analysis to evaluate human-induced impacts and mitigation for the endangered Lower Keys marsh rabbit

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Abstract: Rapid development and urbanization of the lower Florida Keys in the last 30 years has fragmented the habitat of the Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), hereafter called marsh rabbit, and threatened it with extinction. On the Naval Air Station–Key West (NAS), Boca Chica Key, marsh rabbits exist as a meta-population of discrete habitat patches in a matrix of wetlands and airfield facilities. Airfield safety regulations require NAS to maintain vegetation below a minimum height on runway peripheries (clear zones). We developed a spatially-explicit, stage-structured, stochastic matrix model using the programs RAMAS-Metapop and ArcGIS. Model parameters were estimated using pellet counting (2001–2002), radio tracking (1991–1992 and 2001–2005, *n = 75*), and published literature. We compared a baseline no-action model to Alternative 1 that simulated impacts from the NAS airfield clearance project with no conservation measures for marsh rabbits and Alternative 2 that also simulated airfield clearance impacts. Alternative 2 included mitigation actions to offset impacts to marsh rabbits in the form of reduced mortality via free-roaming cat (*Felis catus*) control and creation of marsh rabbit habitat (e.g., salt marsh). Both alternatives increased the extinction risk (probability of extinction) from a baseline of 0.499 to 0.90 and 0.713 for Alternatives 1 and 2, respectively. Although airfield clearance with creation of marsh rabbit habitat (Alternative 2) increased extinction risk from the baseline scenario, reducing marsh rabbit mortality associated with control of free-roaming cats was an effective strategy to decrease this risk. Our research demonstrates the use of population viability analysis as a conservation planning tool for reducing human–wildlife conflicts.

Key words: cat control, human–wildlife conflicts, Lower Keys marsh rabbit; population viability analysis, sensitivity analysis, *Sylvilagus palustris hefneri*

The Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*), hereafter referred to as the marsh rabbit, was listed as a federally endangered species in 1990 (U.S. Fish and Wildlife Service 1990). Historically, the marsh rabbit inhabited most of the Lower Florida Keys, but rapid development since the 1970s has resulted in a decline of the marsh rabbit population and its long-term viability (Forys and Humphrey 1999*a*). Over the last 20 years >50% of the suitable marsh rabbit habitat in the Lower Florida Keys has been lost due to human development. Further, indirect impacts (e.g., free-roaming cats [*Felis catus*]) created by human proximity to remaining habitat continue to reduce marsh rabbit numbers (Howe 1988, Forys 1995, U.S. Fish and Wildlife Service 1999).

The Naval Air Station–Key West (NAS), located on Boca Chica Key, Florida, USA, manages the largest meta-population of marsh rabbits (Forys 1995; Figure 1) and currently

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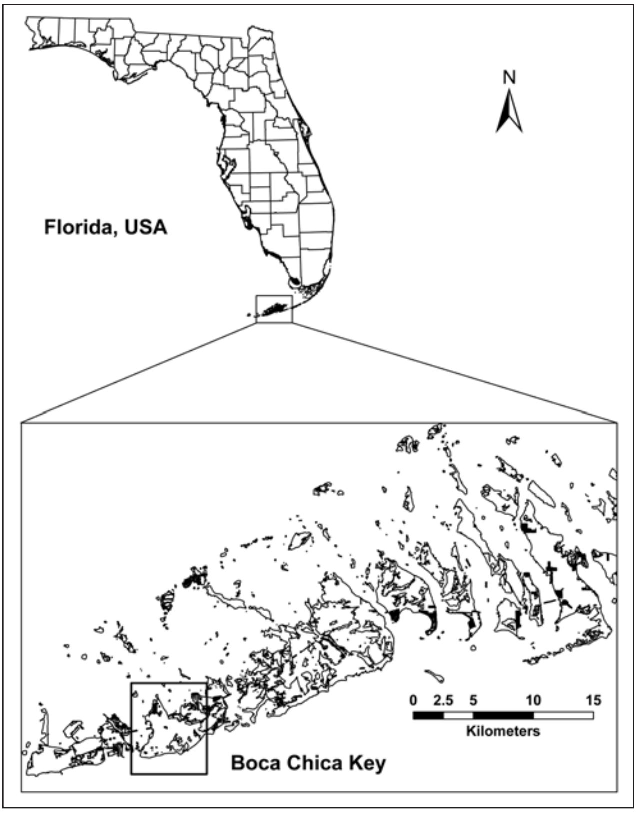

Figure 1. The island of Boca Chica Key located in the lower Florida Keys, Florida, USA.

serves as the main source population for rabbit translocations to other parts of the range. Increasing the extinction risk for this meta-population may greatly increase the extinction risk for the entire subspecies. When our research began, NAS was not in compliance with required airfield safety regulations set forth in U.S. Department of Defense, Naval Facilities, and Federal Aviation regulations. Compliance requires removal of woody vegetation within a designated airfield clearance zone and restoration of drainage canals that have become clogged with vegetation. Such actions may be prohibited under the Endangered Species Act of 1973 and, if taken, are likely to result in harm or death of marsh rabbits (Faulhaber 2005).

Initiation of the NAS runway clearance zone project triggered consultation with the U.S. Fish and Wildlife Service (USFWS) under Section 7(a)(2) of the Endangered Species Act (1973), which states that federal agencies shall "insure that any action they authorize, fund, or carry out is not likely to jeopardize the continued existence of a listed species." Therefore, NAS and USFWS were given the task of determining the likely impacts of proposed habitat modifications to meet clearance zone standards and to develop strategies to offset expected take of marsh rabbits. The extinction probability for the Boca Chica Key meta-population was previously estimated to be 1.0, with a time to extinction of 11 years or the year 2009. However, long-term monitoring has found this meta-population to be relatively stable (Forys 1995, Forys and Humphrey 1999*a*). Increasing survival rates by reducing cat predation was determined to be the most effective strategy for increasing long-term viability (Forys and Humphrey 1999*a*). Control of free-roaming cats was proposed as mitigation for expected take of marsh rabbits. Over 67% of patches were estimated to be below carrying capacity (Forys and Humphrey 1999*a*); however, the effects of habitat loss and restoration on marsh rabbit extinction rates was not previously evaluated.

Resource managers often face difficult decisions when confronted with the task of following multiple federal regulations, in this instance those of the Endangered Species Act and local airfield safety regulations. Conflicts may occur when the most likely mitigation measure for impacts to the marsh rabbit is control of free-roaming cats, which is a highly contentious and politicized issue. Population viability analysis can be a powerful conservation planning tool, allowing managers to evaluate activities that may allow human–wildlife conflicts to be avoided or reduced. Our objectives were to develop a spatially-explicit and stochastic, stage-structured matrix model of the marsh rabbit on Boca Chica Key (1) to determine the impact of 3 different airfield clearance scenarios on population viability, (2) to determine the impact of free-roaming cat control and habitat restoration on viability, and (3) to conduct a sensitivity analysis of model parameters.

Study area

The Lower Florida Keys form the terminal portion of an archipelago of islands extending south and west from the mainland of Florida, USA, (Figure 1), and exhibit a subtropical climate due to the Gulf Stream and other maritime influences (Chen and Gerber 1990, Forys and Humphrey 1999*b*). There are distinct wet and dry seasons, with the dry season (November through April; Forys and Humphrey 1999*a*). Although elevation rarely exceeds 2 m, small variations in elevation result in distinct vegetation types. With increasing elevation, the vegetation community transitions from mangrove (*Rhizophora* spp.) swamps to salt marsh-buttonwood transition zones to upland hardwood hammocks and pine rocklands (McGarry MacAulay et al. 1994). In general, marsh rabbits occupy salt marsh-buttonwood transition zones dominated by salt-tolerant grasses and shrubs including seashore dropseed (*Sporobolus virginicus*), sea daisy (*Borrichia frutescens*), gulf cord grass (*Spartina spartinae*), marsh hay cord grass (*Spartina patens*), and salt marsh fringe-rush (*Fimbristylis castanea*), often with an open canopy of buttonwood (*Conocarpus erectus*) trees (Faulhaber 2003). This community occurs from approximately 1–3 m above sea level, is subject to tidal flooding, and occurs between the mangrove community and the upland hardwood hammocks or pine rocklands (Forys and Humphrey 1999*a*).

Subadult male Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*) taken at Boca Chica Key, Florida, USA. (*Photo by Neil Perry.*)

Methods

Model overview

We used the RAMAS-Metapop modeling program (Brook et al. 2000) to construct a demographic and spatial model of the Boca Chica Key marsh rabbit meta-population (Figure 2). Our model consisted of 3 demographic stages: juveniles, 1-year adults, and 2-year adults. We incorporated both demographic and environmental stochasticity into the model. We modeled demographic stochasticity by sampling from a binomial distribution and a Poisson distribution for the number of survivors and number of offspring, respectively (Akçakaya 1991). We modeled environmental stochasticity by randomly sampling mean survival and fecundity from the stage matrix and standard deviations from a "standard deviation matrix"

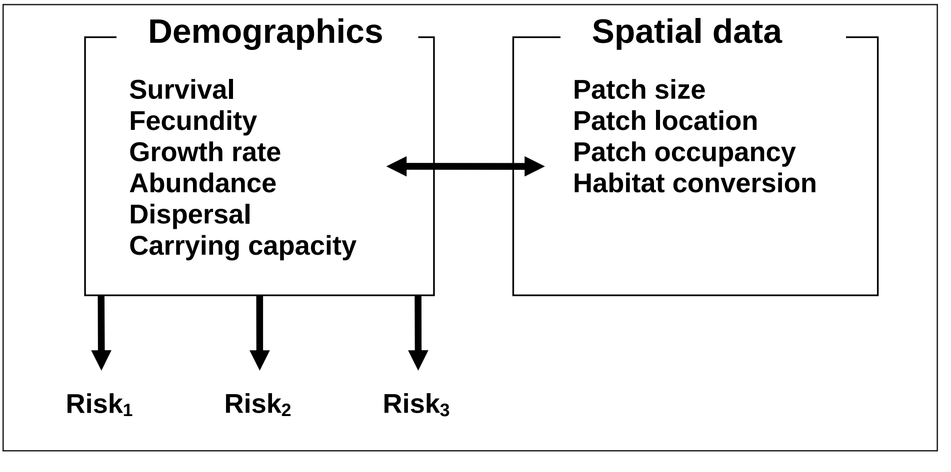

Figure 2. Conceptual diagram of our Lower Keys marsh rabbit population viability model on Boca Chica Key, Florida, USA. Our model consisted of both demographic and spatial data. When simulated with proposed U.S. Naval actions, it produced risk estimates. **Risk$_1$** represents a no-action scenario, used for comparison; **Risk$_2$** represents removal of all airfield vegetation with no conservation measures (Alternative 1). **Risk$_3$** represents removal of woody vegetation only, with conservation measures, such as conversion of mangroves to salt marsh (Alternative 2).

(Akçakaya 1991). We incorporated ceiling type density-dependence by including the carrying capacity of each subpopulation in the model. We based estimates of carrying capacity on both the area of a rabbit patch and the average core area that rabbits use because it has been shown that same-gender home ranges show little overlap (Forys and Humphrey 1996). We modeled density dependence so that when a patch reached carrying capacity dispersing individuals moved into a neighboring patch, which was within the maximum dispersal distance and below carrying capacity. If no patch was available, rabbits died.

We modeled females only, therefore, carrying capacity is based on the number of females that can fit in a patch. We summed patch carrying capacities to provide carrying capacity for the meta-population that we then entered into the model. We incorporated spatial information into the PVA model by mapping out the impacts from the airfield clearance scenarios in ArcGIS (version 8.3, Environmental Systems Research Institute, Redlands, Calif.), and integrating these impacts into RAMAS-Metapop as changes in carrying capacity. Only subadult marsh rabbits are known to disperse (Forys 1995); therefore, we based dispersal for subadult rabbits on a distance-function matrix, with dispersal between patches decreasing with increasing distance. Forys (1995) found the greatest dispersal made by a radio-collared rabbits was 2,500 m; therefore, we set the maximum dispersal distance at 3,000 m. We assumed a negative, exponential dispersal function with the average distance a dispersing rabbit travels was 300 m (Forys 1995).

Model parameterization

Baseline scenario. We estimated model parameters (Table 1) using pellet counts (2001–2002), radio tracking (1991–1992 and 2001–2005; $n = 75$ rabbits), as well as published and unpublished literature (Forys 1995, Cox et al. 1997, Forys and Humphrey 1999*a*, Bond et al. 2001, Faulhaber 2005, Faulhaber et al. 2006).

Table 1. Baseline model parameter estimations and data sources used in a population viability analysis of the Lower Keys marsh rabbit on Boca Chica Key, Florida. Fecundity is the number of offspring produced per female multiplied by the stage specific reproductive rate divided by two and only reflects female offspring. Survival estimates are an average of the cited estimates.

Parameter	Estimate	Source
Fecundity		
Adult 1-year-old	0.57 (SD = 0.07)	Forys 1995
Adult ≥2-year-old	0.09 (SD = 0.10)	
Survival		
Juvenile	0.52 (SD = 0.13)	Bond et al. 2001, Cox et al. 1997, Faulhaber et al. 2005
Adult 1-year-old	0.52 (SD = 0.09)	
Adult ≥2-year-old	0.25 (SD = 0.12)	
Initial abundance		
Baseline	Min-77, Max-162	Faulhaber 2005
Alternative 1	Min-39, Max-71	
Alternative 2	Min-64, Max-128	
Average dispersal		
Juvenile	300 m	Forys 1995
Maximum dispersal		
Juvenile	3,000 m	Forys 1995
Carrying capacity	Patch specific	Forys and Humphrey 1996

The Baseline scenario represents a "no action" scenario that we used to compare relative changes in viability due to the other scenarios.

Alternative 1 scenario. We parameterized Alternative 1 as above, but with simulated impacts from the airfield clearance project. Under this scenario, all vegetation is removed within the airfield clearance zone. Using ArcGIS, we estimated impacts of this action, which were integrated with RAMAS Metapop as a reduction in carrying capacity based on habitat lost to vegetation removal. This scenario contains no conservation measures for the marsh rabbit.

Alternative 2 scenario. We parameterized Alternative 2 identically to Alternative 1, but with only woody vegetation being removed within the airfield clearance zone and herbaceous vegetation left standing. Also, under this scenario, mangroves within rabbit patches were converted to marsh rabbit habitat (i.e., salt marsh) as a conservation measure. We estimated the impact of these actions in Alternative 2 scenario using ArcGIS. We integrated the actions with RAMAS Metapop as changes in carrying capacity from habitat lost to vegetation removal minus habitat created through conversion of mangroves to salt marsh.

Free-roaming cat control scenarios. Forys (1995) found that 52% of marsh rabbit mortality was due to free-roaming cats. We ran the 3 models (Baseline, Alternative 1, and Alternative 2) with 2 different cat-control scenarios. The direct relationship between control of free-roaming cats and marsh rabbit mortality is not known for our study area. We assume that cat control would decrease mortality of marsh rabbits as simulated. Therefore, we simulated scenarios where 50% and 75% of mortality due to predation was reduced, respectively. We calculated increases in survival (Table 2) due to these scenarios for each demographic stage, and reentered them into the model.

Table 2. Annual survival estimates used in population viability analysis for the Lower Keys marsh rabbit by age-class and percentage reduction in mortality associated with free-roaming cat control on Boca Chica Key, Florida, 2005.

	0%	**50%**	**75%**
Juvenile	0.520	0.647	0.710
Adult 1	0.520	0.647	0.710
Adult 2	0.255	0.424	0.551

Sensitivity analysis. Sensitivity analysis is an important part of conducting a population viability analysis (Parysow and Tazik 2002, McCleery et al. 2005) and can be directed toward identifying the parameters that, if known, would decrease uncertainty in the model with higher precision (Akçakaya and Sjogren-Gulve 2000). We investigated sensitivity of model parameters by varying each parameter by ±25% of the baseline estimate while holding all other parameters constant (Akçakaya 2000). We used terminal quasi-extinction risk as a measure of the effect of each parameter estimate on viability of the Boca Chica Key marsh rabbit meta-population. We subtracted absolute values of low estimates from absolute values of high estimates for this analysis.

Model use. Population viability analysis should be used to make relative predictions of extinction risk over short time frames (e.g., 10, 20, or 50 years; Noon and McKelvey 1996, Beissinger and Westphal 1998, Akçakaya and Sjogren-Gulve 2000, Reed et al. 2002). We evaluated the above scenarios in terms of marsh rabbit viability by running 1,000 iterations of the model for a 10-year period. We used 2 criteria to assess viability: terminal quasi-extinction risk and median time to extinction. We defined terminal quasi-extinction risk as the probability of the meta-population falling below a threshold of 10 individuals within 10 years. We measured median time to extinction in years, and we used quasi-extinction to account for potential Allee effects (Allee 1931, Groom 1998, Stephens et al. 1999).

Results

The Baseline scenario resulted in a terminal quasi-extinction risk of 0.584 (Figure 3) and a median time to quasi-extinction of 5.1 years (Figure 4). Quasi-extinction risk for Alternative 1 was 0.905 (Figure 3), while median time to quasi-extinction was 2.7 years (Figure 4). Quasi-extinction risk for Alternative 2 was 0.633 (Figure 3), and median time to quasi-extinction was 4.7 years (Figure 4).

Baseline quasi-extinction decreased to 0.10

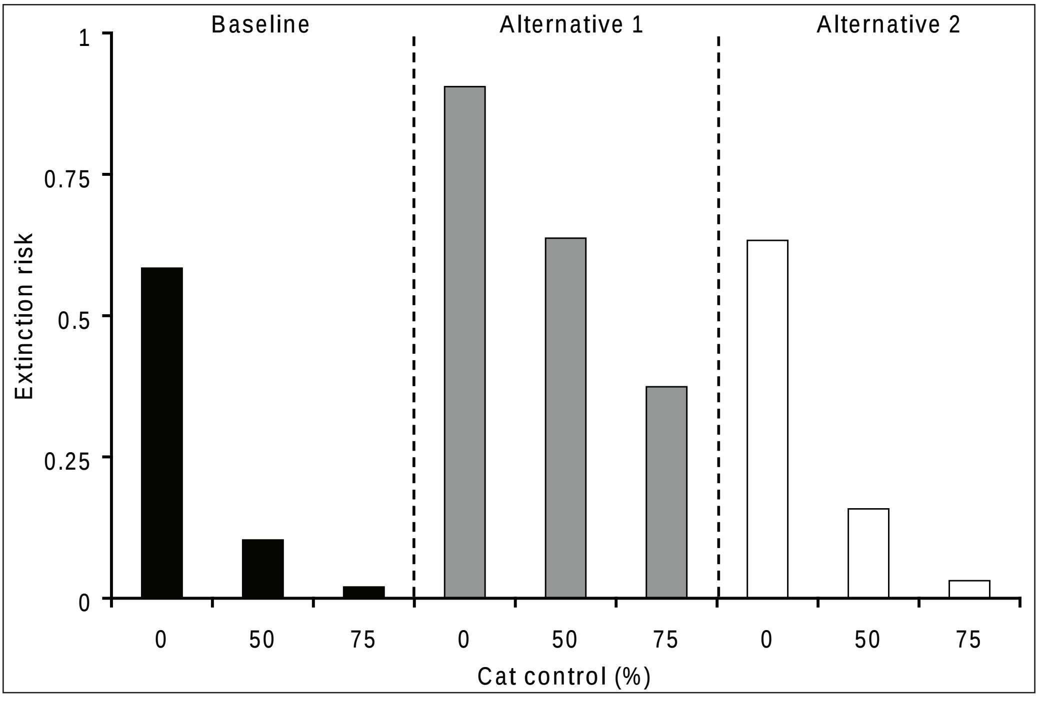

Figure 3. Terminal extinction risk (probability of quasi-extinction in 10 years) for the Lower Keys marsh rabbit on Boca Chica Key, Florida, under several management scenarios: Baseline is the no-action alternative, Alternative 1 is airfield vegetation clearance with no habitat improvement, and Alternative 2 is airfield vegetation clearance plus habitat improvement. Predator control is the percent reduction in Lower

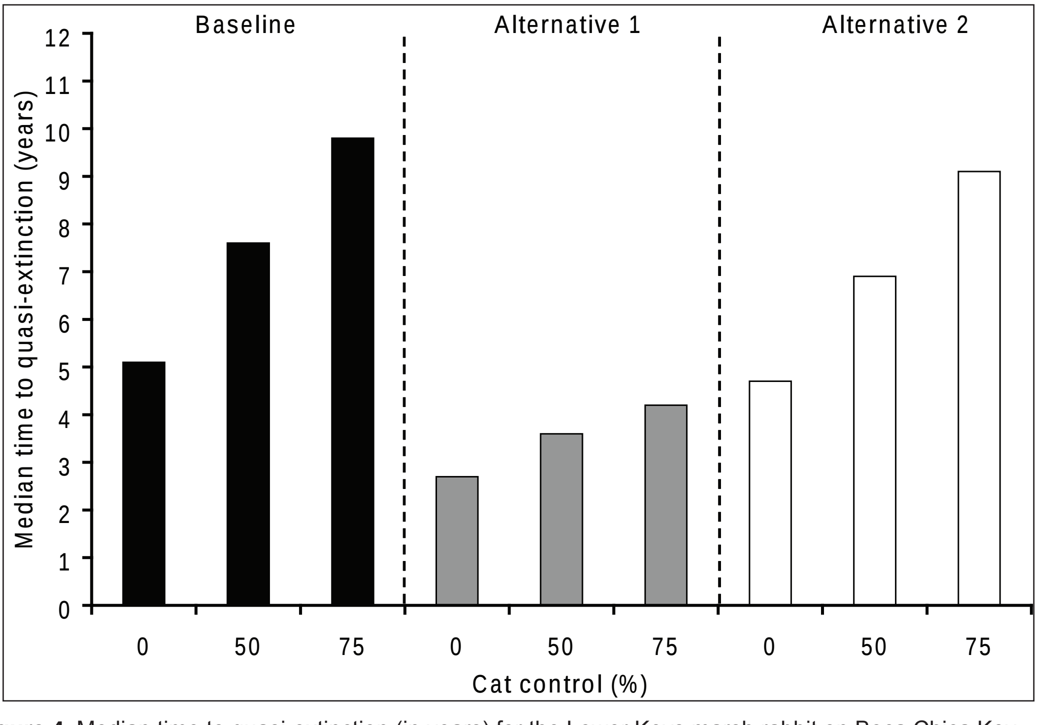

Figure 4. Median time to quasi-extinction (in years) for the Lower Keys marsh rabbit on Boca Chica Key, Florida, under several management scenarios: Baseline is the "no action" alternative, Alternative 1 is removal of all airfield vegetation with no habitat improvement, and Alternative 2 is removal of woody airfield vegetation plus habitat improvement. Predator control is the percentage reduction in Lower Keys marsh rabbit mortality due to removal of free-roaming cats.

and 0.02 (Figure 3), and median time to quasi-extinction increased to 7.6 and 9.8 years (Figure 4) with 50% and 75% cat control, respectively. Both alternatives, coupled with cat control, decreased the quasi-extinction risk (Figure 3) and increased median time to extinction (Figure 4). Quasi-extinction risk was virtually eliminated under both the Baseline and Alternative 2 scenarios, with 75% cat control (Figure 3). The 3 most sensitive parameters for terminal extinction risk were initial abundance, juvenile survivorship, and 1-year-old adult fecundity (Figure 5).

Discussion

Marsh rabbit viability

Overall, the outlook for the marsh rabbit meta-population on Boca Chica Key, without future conservation actions, is dismal. Extinction is predicted in 10 years if no action is taken to bring the NAS into compliance with federal safety regulations (i.e., Baseline scenario). Extinction is predicted in 4.3 years if the necessary vegetation removal to achieve regulatory compliance is executed without conservation measures (Figures 3 and 4). Reducing marsh rabbit mortality due to predation through management of free-roaming cat populations will greatly improve the viability of marsh rabbits on Boca Chica Key in the near future. Conservation measures are essential to mitigate the impacts of establishing and maintaining runway clear zones and to increase the likelihood of marsh rabbit persistence on Boca Chica Key.

Conservation implications

Modeled effects of conservation measures such as free-roaming cat control and creation of marsh rabbit habitat reveal scenarios that can improve the likelihood of persistence of the Boca Chica Key marsh rabbit meta-population. All 3 scenarios with free-roaming cat control improved the persistence time and decreased the extinction risk. These results reinforce those found by Forys and Humphrey (1999*a*). Under their Baseline scenario, they found an extinction risk of 1.00 in 11 years but found an extinction risk of 0.46 with 33 years to extinction when all

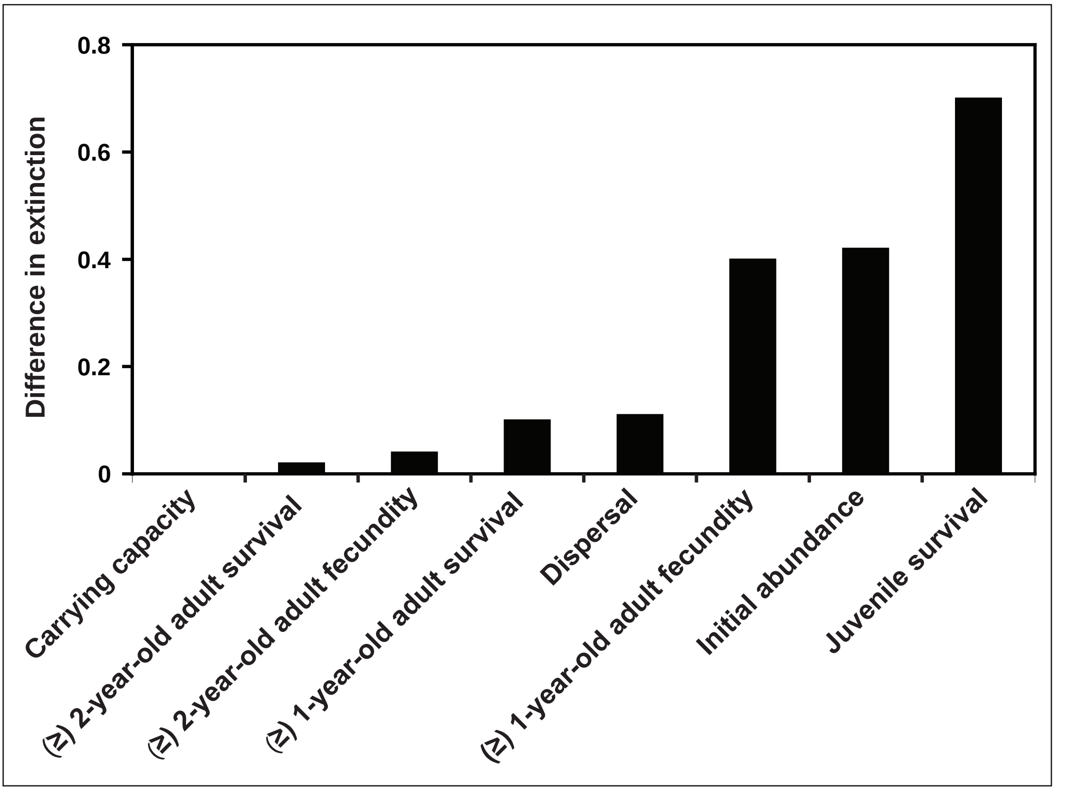

Figure 5. Sensitivity analysis (differences in terminal extinction risk between high and low parameter values) of model results for the Lower Keys marsh rabbit on Boca Chica Key, Florida, USA. Parameter values were varied ±25% from baseline estimate.

free-roaming cat mortality was removed. Free-roaming cats have been found to be the cause of biodiversity extinction on islands throughout the world (Whittaker 1998). Subsequent eradication programs have been successful on many islands, particularly those <5 km^2 and uninhabited by people (Nogales et al. 2004). Although total eradication of free-roaming cats from Boca Chica Key was unlikely, due to social constraints, a reduction of 50–75% of mortality due to predation increased the viability of the marsh rabbit. Over-abundant populations of native predators, such as raccoons (*Procyon lotor*) may exacerbate predation pressures from free-roaming cats, particularly for nestling rabbits (Garrott et al. 1993). Current sources of mortality rates for marsh rabbits are from radio-collared adult rabbits; sources of mortality rates for juvenile and nestling rabbits is less well-known (Forys 1995). From 50% to 75% reductions in marsh rabbit mortality rates is more achievable if all sources of predation are treated, including control of raccoon populations.

Improving and restoring salt marsh habitats also will benefit marsh rabbits. However, habitat management is costlier and more difficult, and conservation benefits are not always immediate. Control of free-roaming cat populations is operationally easy to implement and likely to cost less and conservation benefits will likely be realized sooner. Mitigation measures, such as free-roaming cat control, are imperative if the marsh rabbit is to persist into the future. A concomitant environmental education program should be implemented in order to alleviate public displeasure with such programs.

Sensitivity analysis

Our analysis indicates that initial abundance, juvenile survivorship, and adult fecundity (1–2-year-old adults) are the most sensitive parameter estimates in our model. This suggests that model uncertainty can be improved if better estimates for these parameters are obtained. Within the bounds of limited resources for research, we suggest field efforts focus on initial abundance estimates for rabbit subpopulations on Boca Chica Key. To improve estimates of survivorship and fecundity, radiotelemetry would be necessary, but radiotelemetry is a relatively invasive and labor-intensive technique. Initial abundance estimates can be obtained by surveying for fecal pellets, which does not necessitate capturing rabbits (Wood 1988, Forys and Humphrey 1997, Prugh and Krebs 2004). An updated estimate of rabbit abundance also is needed to improve the accuracy of our model and to help with conservation planning for the marsh rabbit.

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