FINAL REPORT

for

Habitat Monitoring and Evaluation of Working Lands for Wildlife: New England Cottontails

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February 12, 2016

SUMMARY BY STUDY OBJECTIVES

OBJECTIVE I -- DEVELOP A HABITAT MONITORING PROTOCOL FOR NEW ENGLAND COTTONTAILS THAT EVALUATES MANAGEMENT ACTIVITIES RELATIVE TO SUITABILITY AT THE SITE-SPECIFIC SCALE.

Approach: Generate habitat suitability index (HSI) equation using field data and expert opinion.

A manuscript on this approach has been accepted for publication by the Wildlife Society Bulletin (Appendix A).

OBJECTIVE II -- EVALUATE THE EFFECTS OF HABITAT MANAGEMENT AT THE LANDSCAPE SCALE USING POPULATION VIABILITY ANALYSES.

Approach: Use demographic information on New England cottontails and several scenarios on habitat management to explore the role of vital rates and habitat management in maintaining cottontail metapopulations.

INTRODUCTION

In response to the range-wide decline of New England cottontails (*Sylvilagus transitionalis* - NEC), several governmental (U.S. Fish and Wildlife Service, Natural Resources Conservation Service, and state fish and wildlife agencies within the current range of the New England cottontails) and nongovernmental organizations (e.g., Environmental Defense Fund, National Fish and Wildlife Foundation, National Wild Turkey Federation, Wildlife Management Institute, and local land trusts) are working in collaboration to create more habitat for this species (Fuller and Tur 2012). The management of habitat for NEC involves creating and maintaining patches of early-successional forests or shrubland habitats (Arbuthnot 2008). Restoration efforts are concentrated in focus areas to expand existing populations of NEC (Fuller and Tur 2012). For example, although NEC once occurred across much of southern Vermont and New Hampshire, and along the coast of Maine to Portland, habitat management is only occurring only in a few focus areas where NEC still occur (Fig. 1). This strategy, although intuitive, is untested. Metapopulation modeling offers an approach to evaluating its potential success. A metapopulation is a set of local populations that interact with one another via dispersal. Management focus areas will likely function as metapopulations where *source* and *sink* populations determine its viability (Fig. 2). A source population has high survival rates from which individuals frequently disperse to other populations. Sink populations, on the other

Figure 1. *The approximate historic northern extent of New England cottontails in northern New England, and the current management focus areas (Fuller and Tur 2012).*

hand, have low survival rates and rely on immigrants from source populations to remain occupied (Hanski 1998). The source-sink concept is particularly relevant to NEC because small habitat patches have been found to have lower survival rates (Barbour and Litvaitis 1993) and some of the metapopulations are declining because they are largely comprised of small patches (Litvaitis et al. 2006). Previous investigations of various plants and animals have examined the effects of habitat-patch size, quality, and spatial distribution of individual populations on metapopulation growth (Akcakaya et al. 2004). Modeling is commonly used in such efforts because it provides an opportunity to conduct simulations that would not be feasible otherwise. It would require immense resources and time to conduct a real experiment in which habitat availability was manipulated to determine the effects on population growth of NEC.

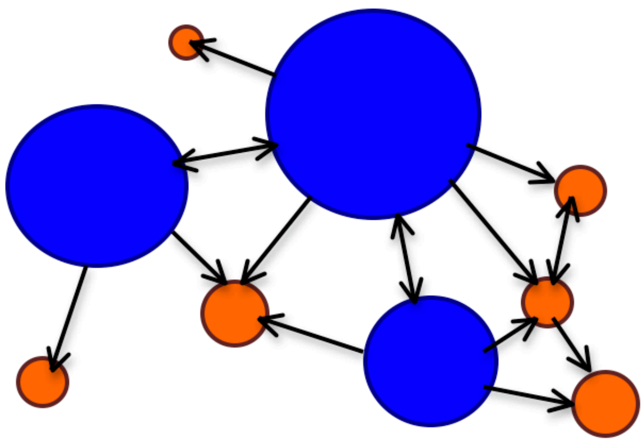

Figure 2. *Illustrated metapopulation composed of source patches (blue) and sink patches (orange), where the size of the circle represents carrying capacity. Source patches supply dispersing individuals that colonize sink patches, which are vulnerable to population decline and extinction.*

Further, a metapopulation model can be used for population viability analyses (PVA) to examine population growth and extinction probabilities in response to various management alternatives (Akçakaya et al. 2004, Blomberg et al. 2012). A PVA often includes population-specific vital rates and demographic/environmental stochasticity making it more realistic than population estimates based simply on habitat availability (Akcakaya et al. 2005). There are several examples of metapopulation models used to evaluate the effects of management on population viability that have implications for NEC. Notably efforts by Blomberg et al. (2012) that simulated responses by ruffed grouse (*Bonasa umbellus*) populations in response to different habitat-management strategies. These investigators found that fewer large patches resulted in a slower population decline (Blomberg et al.

2012). Modelling a hypothetical NEC metapopulation, Litvaitis and Villafuerte (1996) found that environmental correlation (e.g., snow conditions that are relatively uniform across a metapopulation affect individuals similarly) and habitat loss were important factors determining short-term extinction risk. Viability of a NEC metapopulation depended on the suitability of individual patches and the interactions among patches (Litvaitis and Villafuerte 1996).

To understand how restoration activities at the landscape scale will affect population growth and stability of NEC, we examined the effects of habitat management and environmental variation on two existing NEC metapopulations. Specifically, we examined the influence of three management scenarios (no management, creation of suitable habitat but no maintenance of habitats, and creation and maintenance of suitable habitats) on viability of two NEC metapopulations in established focus areas. We also evaluated the relative influence of demographic and environmental parameters on model output using sensitivity analyses. Combined, these results enabled us to critique current activities to restore existing NEC metapopulations.

METHODS

Study Areas

We modeled the Cape Elizabeth, Maine and Kittery-Berwick, Maine (Fig. 3) focus areas because there has been considerable information on NEC populations in those landscapes (Litvaitis et al. 2003, Fenderson et al. 2014).

The Cape Elizabeth focus area is coastal, contains a number of state parks and open areas as well as residential neighborhoods. It covers two towns, Scarborough and Cape Elizabeth, and totals about 15,000 hectares of which 262 ha are suitable (managed and unmanaged) for NEC (Table 1). The Kittery-Berwick focus area is actually two adjacent management focus areas, Kittery and Eliot-Berwick, and it includes inland and coastal areas, is more heavily forested, and covers 35,000 hectares, including 121 ha of suitable habitat (Table 1).

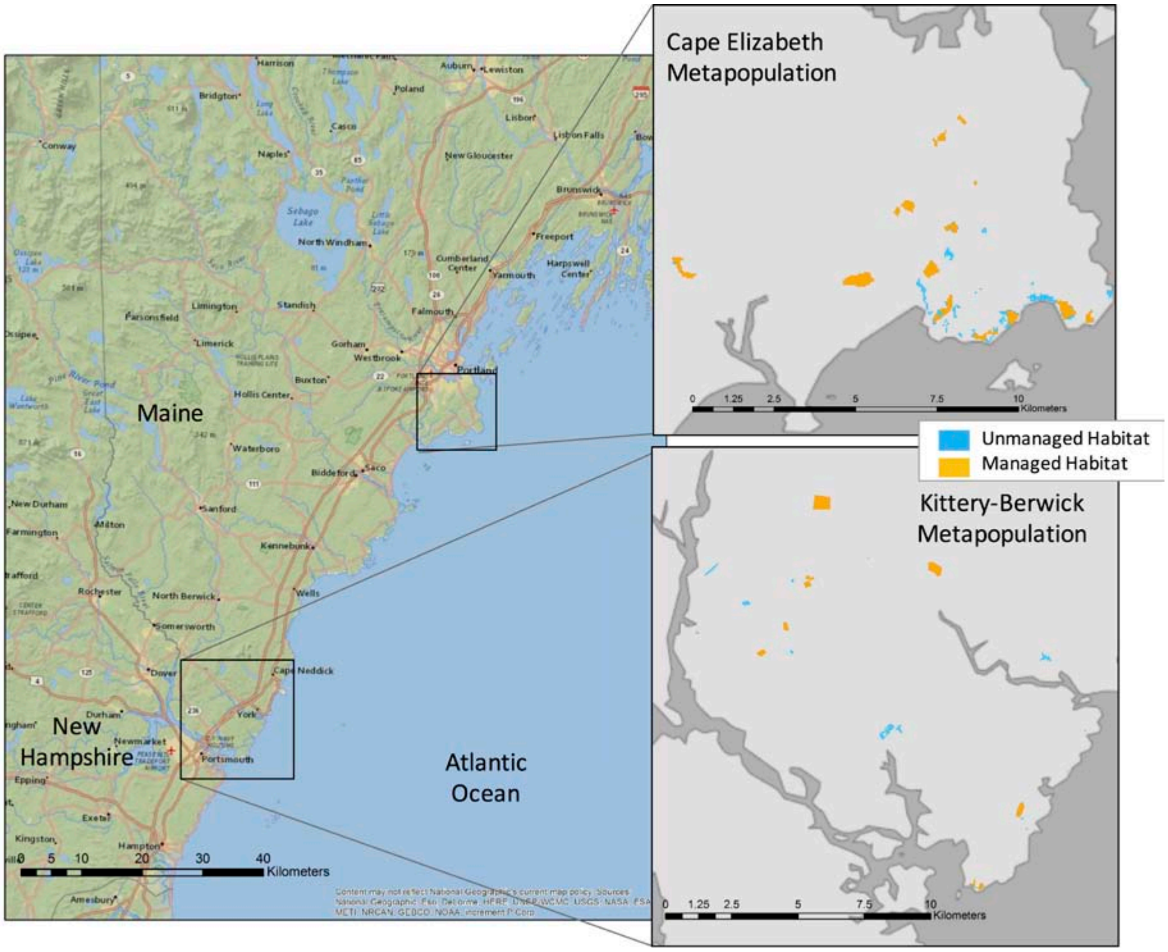

Figure 3: Habitat patches in the two focal areas, Cape Elizabeth and Kittery-Berwick, and the locations of the focal areas in Southern Maine. Managed habitat patches are shown in orange, and unmanaged patches in blue.

Table 1. Managed and unmanaged habitats suitable for New England cottontails in two focal areas in southern Maine.

Metapopulation	**Managed/Unmanaged habitat patches**		
	Number	**Mean size (ha)**	**Range (ha)**
Cape Elizabeth	16/17	10.2/5.8	1.2-28.7/0.7-30.5
Kittery-Berwick	8/15	11.1/2.1	3.8-32.0/0.1-10.5

Model Vital Rates

To simulate metapopulation dynamics, vital rates including annual survival, dispersal distances, and recruitment were estimated using existing literature and unpublished research (Table 2). The most comprehensive data set (using multiple sites and years) on survival rates of NEC came from H. Kilpatrick (Connecticut Department of Energy and Environment, personal communication). Information on juvenile survival rates is lacking. We assumed juvenile rates to be equivalent to those of adults as reported in studies of other lagomorphs (e.g., Gillis Elizabeth 1998, Zeoli et al. 2008, Kielland et al. 2010). Using information on litter sizes from the NEC captive breeding program at the Roger Williams Zoo (L. Perrotti, Roger Williams Zoo, Providence, RI; unpublished report) and literature reports (summarized in Chapman and Litvaitis 2003), we estimated per capita recruitment as: per capita reproductive rate x annual survival rate (Akcakaya and Root 2013). Adult females averaged 2.5 litters with 4.17 young/litter, so per capita (male or female) recruitment would be (2.5 x 4.16)/2 or 5.21 x annual survival rate.

***Table 2**. Estimated vital rates, carrying capacity, and dispersal distance for New England cottontails used to parameterize the metapopulation model.*

Vital rate	**Mean (SD)**	**Supporting literature**
Annual survival rate on patches ≥3 ha (source populations)	0.13 (0.3)	H. Kilpatrick (pers. comm.), Brown and Litvaitis (1995), Villafuerte and Litvaitis (1996)
Annual survival rate on patches <3 ha (sink populations)	0.065 (0.15)	H. Kilpatrick (pers. comm.), Barbour and Litvaitis (1993), Villafuerte and Litvaitis (1996)
Carrying capacity	1 rabbit/0.5 ha	Barbour and Litvaitis (1993), Villafuerte and Litvaitis (1996)
Recruitment per capita on patches ≥3 ha (source populations)	0.68 (0.22)	Chapman and Litvaitis (2003), L. Perrotti (unpublished report)
Recruitment per capita on patches <3 ha (sink populations)	0.34 (0.11)	Chapman and Litvaitis (2003), L. Perrotti (unpublished report), Barbour and Litvaitis (1993)
Maximum dispersal distance	3 km	Litvaitis and Villafuerte (1996)
Maximum annual growth rate (λ)	2.0	Keith and Windberg (1978), Litvaitis and Villafuerte (1996)

Model Structure

*R*AMAS GIS (Version 6, Akcakaya and Root 2013) provided the framework for developing a metapopulation model. Habitat availability, vital rates, demographic and environmental stochasticity, and environmental correlation were components of the model. Stochasticity included variation in annual survival, recruitment, and carrying capacity because these rates are affected by changes in weather, predation, and other factors. Based on the last 40 years of weather data from Portland, Maine, we found that 1 in 10 winters had >100 days with snow on the ground. NEC mortality is strongly influenced by long winters (Brown and Litvaitis 1995), so our model included a 10% annual probability of a catastrophe (severe winter) in which 90% of adults and juveniles die. In non-catastrophe years, the model adjusted vital rates based on a normal probability curve that is supported by snow-cover data that were normally distributed.

Environmental correlation is the concept that habitat patches close together will be similarly affected by events such as weather. NEC experience high environmental correlation(Villafuerte and Litvaitis 1996), as their vital rates are affected by weather and the metapopulations in northern New England are not large enough to experience significantly different weather events. Inputs of habitat availability were modified to create three scenarios (described below). For each scenario, we used a 15-year simulation that was replicated 1,000 times for both focus areas. Simulations more than 15 years may be unrealistic due to the ephemeral nature of the habitat and rapid life cycle of NEC. Metapopulation simulations generated two useful outputs: a population-growth trajectory and extinction risk. The trajectory showed an average abundance of NECs over time (increase or decline) whereas extinction risk was the proportion of the 1,000 simulations for a specific management scenario that fell below a specific threshold of abundance.

Habitat Availability

Spatial information on unmanaged but suitable habitats was derived from known occupied habitat patches surveyed by Fenderson et al. (2014). Information on managed habitats was obtained from the Natural Resources Conservation Service, U.S. Fish and Wildlife Service, and Maine Department of Inland Fisheries and Wildlife. The amount and location of managed habitats was projected over the next 15 years based on the assumption that NEC habitats are ephemeral and require 7 years to become suitable after intensive management (e.g., clearcuts) and remain suitable for 10-12 years without further management (Aber 1979, Fig. 4). For each patch included in our models, we considered the initial condition, schedule of management actions, and the prescribed management activity, and then created maps of estimated suitable managed habitat for 4 time steps: the years 2015, 2020, 2025 and 2030. Based on field surveys (Fenderson et al. 2014), occupied patches did not need intensive management and were considered suitable at start of our simulations. Unmanaged and managed habitats were assumed to decline at a rate of 10% per year over the course of the simulation due to succession.

Management Alternatives

We compared three management scenarios for each focus area.

No management: Only unmanaged habitat patches, based on known occupied sites, are considered suitable. This is representative of no action being taken to conserve NEC.

Current management: Managed patches are added to the unmanaged patches over time, but no maintenance is invoked so habitat abundance declines with time. This scenario demonstrates the effects on NECs if the initiative to create and maintain habitat were to discontinue, causing a gradual decrease in available habitat.

Maintained management: all managed and unmanaged habitat patches are considered suitable for the duration of the simulation to represent continuous management of all patches. This represents the continued close monitoring and maintenance of managed patches, if NEC habitat programs and funding continue for the foreseeable future.

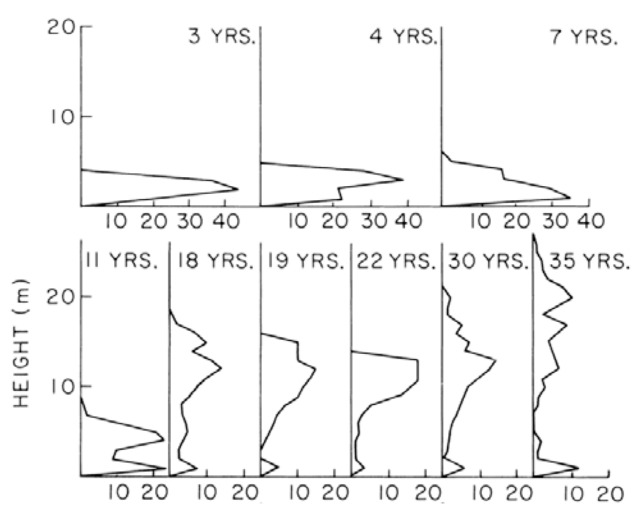

Figure 4. Vegetation regeneration in a hardwood forest after a clearcut (from Aber 1979). By 18 years after management, the bulk of the vegetation is no longer in the understory and the habitat is unsuitable for NEC.

Sensitivity Analysis

To examine the relative influence of specific model parameters on model output, values were modified by -50%, -25%, -10%, +10%, +25%, and +50% of the initial input value to measure the effects of these changes on the probability of falling below 50 individuals during the simulation (extinction risk). The values chosen were: mean survival and recruitment rates, standard deviations of the survival and recruitment rates, proportion of the population that disperses to another patch, and probability of an environmental catastrophe (severe winters).

RESULTS

Simulations

Overall abundance of NEC was higher in the maintained management scenario as compared to no management in both focus areas (Fig. 5 and 6). The current management scenario was generally higher than no management as well, but cottontail abundance declined during the 15-year projection. Similarly, the extinction risks were lower in the maintained management scenarios (Table 2). The Cape Elizabeth focus area had higher abundances and generally lower extinction risks than the Kittery-Berwick focus area.

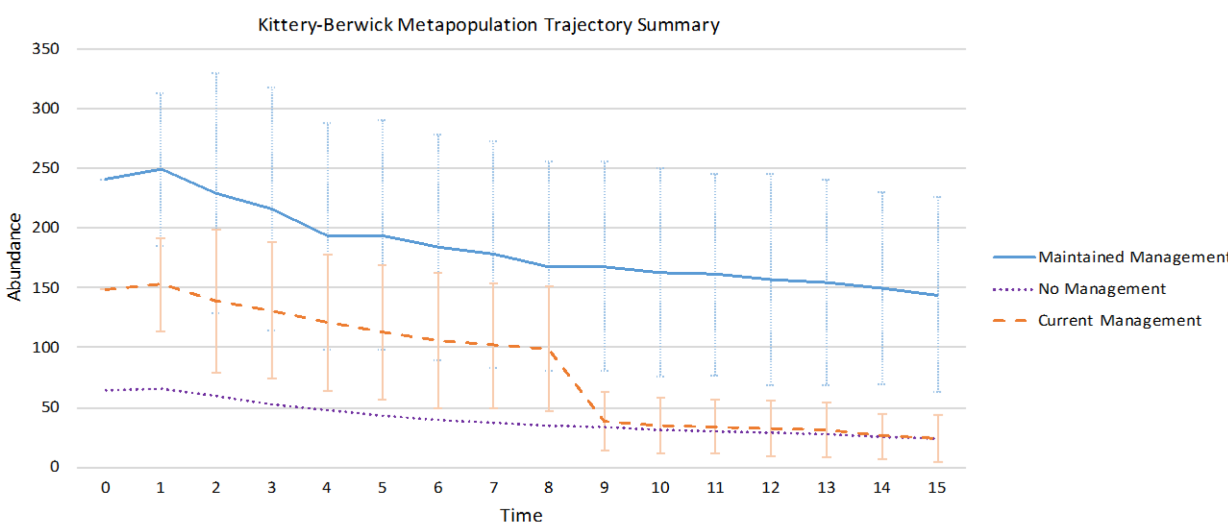

Figure 5. *Average abundance (and standard deviations) of New England cottontail metapopulation in the Cape Elizabeth focus area in response to three management scenarios.*

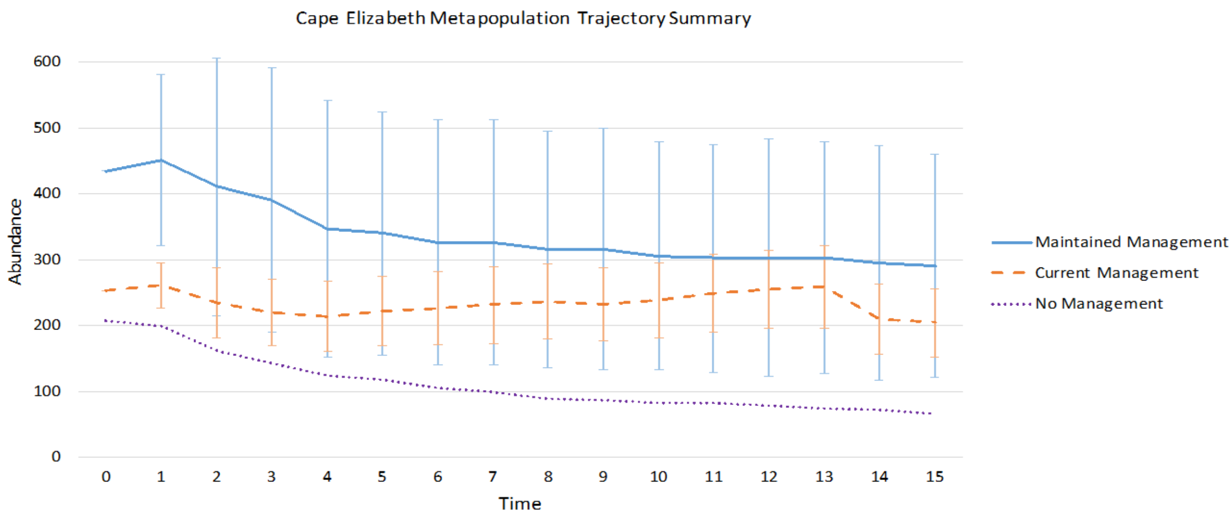

Figure 6. *Average abundance (and standard deviations) of New England cottontail metapopulation in the Kittery-Berwick focus areas in response to three management scenarios.*

Table 2. *Probabilities of two New England cottontail metapopulations falling to specific abundance thresholds in response to three management actions.*

Metapopulation	**Action**	**Probability of reaching specific thresholds**			
		200	**100**	**50**	**0**
Cape Elizabeth	No management	0.934	0.766	0.543	0.189
	Current management	0.488	0.011	0	0
	Maintained management	0.341	0.127	0.038	0
Kittery-Berwick	No management	1.000	0.998	0.883	0.079
	Current management	1.000	0.999	0.896	0.046
	Maintained management	0.766	0.347	0.111	0

Sensitivity Analysis

Altering mean survival and recruitment rates had little influence on the metapopulation extinction risks. However, increasing the variation (standard deviations) of these values and the probability of catastrophe (exceptionally snowy winter) had a substantial influence (Fig. 7). These results suggested that populations were more responsive to demographic and environmental variation than to changes mean vital rates and the proportion of dispersing individuals.

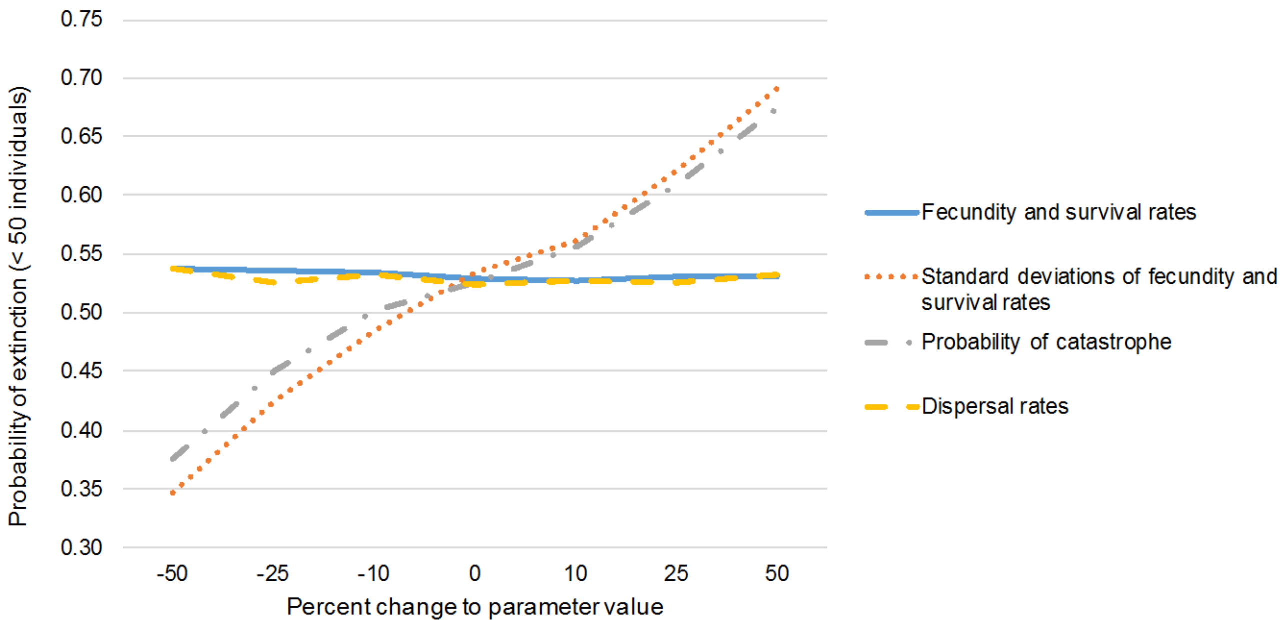

Figure 7. *A sensitivity analysis of four model parameters: recruitment and survival rates, standard deviations of recruitment and survival rates, probability of catastrophe (representing severe winters), and dispersal rates (the proportion of the population that disperses to another patch).*

MANAGEMENT IMPLICATIONS

Comparing the two focus areas was useful for evaluating how management activities may affect metapopulation growth and stability. The Kittery-Berwick is a larger area with fewer occupied habitat patches with few, large managed habitats. Based on our simulations, higher density of managed and unmanaged patches supported a greater abundance of NEC on Cape Elizabeth and with lower extinction risks, suggesting the focus area approach may be effective by placing habitat restoration efforts near occupied and other management sites. In both focus areas, there was reduction in extinction risk and an increase in abundance with the maintained management scenario because suitability declined on all patches with forest succession. Because NEC habitats lack regular forms of natural disturbance (e.g., fires) and suburban developments are likely to further reduce available habitats, management of habitats will need to continue to maintain these existing metapopulations.

The sensitivity analysis has implications for future research and habitat management. Because environmental and demographic variation (simulated by changes in the standard deviation associated with parameters) and probability of a catastrophe were more influential than changes in average parameter values, monitoring of existing populations will be essential. However, factors affecting juvenile survival are unknown and may prove influential once identified.

Climate change studies indicate that weather will likely become increasingly variable, with more frequent, intense precipitation events, and in fact we are already seeing these effects today (e.g., American Association for the Advancement of Science 2014, Intergovernmental Panel on Climate Change 2014). This could have multiple impacts on NEC metapopulation growth and stability. Sensitivity analysis showed that the extinction risk of a metapopulation is highly sensitive to the probability of catastrophic mortality events (i.e., severe winters), as well as variation in annual survival and fecundity rates. As vital rates become more variable due to climate (meaning very high and low annual rates become more common), and as catastrophic mortalities become more probable, the risk of metapopulation extinction is higher. When a large percentage of the individuals in a metapopulation die, as is likely for NEC in a particularly long, snowy winter (Brown and Litvaitis 1995), it is less likely that the now-vacant patches will be re-colonized by neighboring populations. There may also be an increase in average winter temperatures, which could reduce the average number of days per year with snow, benefitting NEC somewhat; however, we hypothesize that NEC metapopulation extinction is influenced more by environmental variability and the frequency of severe snowy winters, that could increase with climate change, than by small increases to average survival rates. To mitigate that effect, populations of NEC and habitat should be closely monitored so that managers can intervene when needed by introducing captive bred rabbits to vacant patches and maintaining suitable habitat through management.

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Appendix A

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