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RH: SWAMP RABBIT METAPOPULATION VIABILITY

Metapopulation viability of swamp rabbits in southern Illinois: potential impacts of habitat change

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Swamp rabbits (*Sylvilagus aquaticus*) in southern Illinois exist as a metapopulation due to fragmentation of the bottomland hardwood forests in which they live. This fragmentation makes their persistence in Illinois uncertain. We used population viability analysis (PVA) to estimate the probability of persistence of the swamp rabbit metapopulation in Illinois, using a habitat suitability map we created and life history parameters drawn from the literature. We varied the parameters used in our PVA from 50 to 150% of the initial value to compare their effects on extinction risk and to direct future management and research. We tested the effects of potential habitat loss and fragmentation by removing patches individually and in groups from the analysis, and by adding 60, 120, and 180 m to the edge of all patches. We also tested the potential effect of dispersal corridors by increasing dispersal between connected patches. Under baseline conditions, the model suggests a 0% chance of quasi-extinction (90% metapopulation decline) of swamp rabbits within 25 (or even 50) years. Changes in fecundity values and the effects of catastrophic flooding had the greatest effect on extinction risk, and changes in no other parameter yielded any appreciable impact. Removing the largest patches from the population increased the 25-year risk of extinction to 4%, whereas any other modifications to the habitat did not change the extinction risk. We suggest that managers focus on sustaining habitat quality, particularly upland habitats adjacent to occupied bottomland hardwood forests to improve the likelihood of swamp rabbit persistence in Illinois.

Key words: bottomland, corridors, dispersal, fragmentation, Illinois, metapopulation, model, population viability analysis, swamp rabbit, *Sylvilagus aquaticus*

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Habitat fragmentation can have immediate and long-term harmful effects ranging from the genetic level to the community level (Bowers et al. 1996; Dooley and Bowers 1998; Haag et al. 2010; Krauss et al. 2010). Habitat fragments are typically surrounded by a hostile matrix, which can act as a deterrent to dispersal attempts, reduce survival of individuals that do attempt to disperse, and provide suitable habitat for predators or competitors that may not have encountered the patch inhabitants otherwise (Rolstad 1991; Wilcove et al. 1997; Åström and Pärt 2013).

Habitat loss has affected many kinds of wildlife, including those inhabiting bottomland hardwood forests in the Mississippi River floodplain. Swamp rabbits (*Sylvilagus aquaticus*) are bottomland hardwood forest specialists (Allen 1985) found throughout much of the Mississippi River floodplain, making them an important indicator species for the integrity of bottomland hardwood forests in this area. They are classified as endangered in Indiana (Indiana Department of Natural Resources 2013) and rare in Missouri (Dailey et al. 1993; Scheibe and Henson 2003), and population declines have been noted throughout their range (Platt and Bunch 2000). Swamp rabbit abundance in Illinois has apparently declined since the 1970s, and swamp rabbits are now patchily distributed along the major rivers and some interior river drainages in the southern portion of the state (Kjolhaug et al. 1987; Barbour et al. 2001). Given this spatial structure, swamp rabbits are thought to exist as a metapopulation (i.e., a system of local populations connected by dispersing individuals—Hanski and Gilpin 1991), with small and large patches that may share dispersers scattered across the landscape (Woolf and Barbour 2002; Roy Nielsen et al. 2008).

Human activities substantially affect habitat quality for swamp rabbits, which predominantly prefer early-successional forests with close proximity to wooded wetlands (Scharine et al. 2009, 2011). Selective logging or burning can replace natural disturbances that create early-successional habitat (Lorimer 2001), leading to high-quality habitat in the long-term, but clear-cutting large areas of land can have the opposite effect of selective disturbance, decreasing the amount of high-quality habitat for swamp rabbits. Allen (1985) suggested that conversion of land to agricultural production is the most significant cause of swamp rabbit habitat loss, and considerable losses in swamp rabbit habitat have occurred throughout their range, most notably near the northern edge (Sole 1994; Zollner et al. 2000a; Fowler and Kissell 2007; Vale 2008).

Given the potential impact of past and future habitat alterations on swamp rabbits, managers are interested in predicting the fate of the species in Illinois under a range of possible action scenarios. Population viability analysis (PVA) uses quantitative models to assess the future status of a population or metapopulation, predict the success of potential recovery strategies, and identify aspects of a population (e.g., life history stages or demographic processes) that should receive the highest priority in research and management (Morris et al. 2002; Possingham et al. 2002; Ralls et al. 2002). Because PVAs are only as accurate as the parameters and assumptions used to create them, their use in management has been debated (Brook et al. 2002; Ellner et al. 2002). For instance, estimating parameters accurately can be troublesome for rare species, on which these analyses are typically performed (Holmes 2001; Ludwig and Walters 2002; Possingham et al. 2002; Ratcliffe et al. 2005), and most population viability analyses include stochasticity, incorporating demographic and environmental variances that can be even more problematic to estimate than average values (Beissinger and Westphal 1998; O'Grady et al. 2004). Although imperfect, population viability analyses can make useful comparisons between management tools (Starfield 1997; McCarthy and Broome 2000; Staples et al. 2004; Bakker and Doak 2009).

Population viability analyses have been implemented for swamp rabbits in the past, using field data collected through a number of studies in Illinois, Indiana, and Missouri. Woolf and Barbour (2002) and Roy Nielsen et al. (2008) both used spatially explicit stagestructured models and predicted slight negative trends in swamp rabbit populations over time. Woolf and Barbour (2002) predicted an 8.4% chance of the southern Illinois metapopulation falling below 1,000 individuals over 25 years, and Roy Nielsen et al. (2008) predicted a slight (< 10%) decline in patch occupancy over 25 years in Indiana. However, both assumed high (see below) maximum carrying capacities (1.5 rabbits / ha) based on localized trapping (Kjolhaug 1986). Woolf and Barbour (2002) also assumed that all patches within 200 m of each other were parts of the same modeled patch, and they used an average dispersal distance of 3 km; Roy Nielsen et al. (2008) also chose a high average dispersal distance of 1.5 km. These parameter choices may explain why their models yielded such optimistic results. More recent genetic evidence indicates that swamp rabbits in Illinois show limited success in dispersing (Berkman et al. 2015), with strong genetic differentiation among subpopulations separated by < 5 km. Also, a recent, extensive study of swamp rabbit home range size and overlap in southern Illinois suggests that typical densities are likely well below 1.5 rabbits / ha (Crawford 2014). Our 1st objective was to examine how these recent findings affect the prognosis for swamp rabbit persistence in southern Illinois. We also expanded on earlier PVAs by modeling specific changes to the habitat, including changes in fragmentation and the addition of dispersal corridors, with the goal of suggesting future management practices.

MATERIALS AND METHODS

Mapping suitable habitat and potential corridors.—Following methods used by LaRue and Nielsen (2008, 2011), we applied the analytical hierarchy process (AHP—Saaty 1980) to convert expert survey results into a habitat suitability map for the southern 28 counties of Illinois. This region largely consists of agricultural land and upland forests but has bottomland hardwood forests in the Cache, Kaskaskia, Saline, Mississippi, Ohio, and Big Muddy watersheds. The AHP hierarchy for identifying potential swamp rabbit habitat involved: the goal (suitable swamp rabbit habitat), factors, and attributes within the factors. We solicited expert opinion of the relative importance of habitat factors (landcover type, road type, waterbody classification, and percent canopy cover) and relative suitability of attributes within each factor (e.g., wetland forest within the "landcover type" factor; Table 1). We asked 12 researchers and managers familiar with swamp rabbit ecology to rate pairs of habitat factors in terms of relative importance and pairs of attributes in terms of relative habitat suitability for swamp rabbits, using a continuous rating scale from 1/9 to 9. For instance, when comparing the suitability of agriculture and upland forest attributes of the "land cover" feature, a rating of 1/6 would indicate that the expert considers agriculture to be one-sixth as suitable as upland forest, whereas a rating of 1 would indicate equal suitability. Six surveys were returned. Pairwise rating scores were made comparable by:

$$a_{ij}^{*} = a_{ij} \Big/ \sum_{k=1}^{n} a_{kj}$$

where a_{ij} is the raw score (relative importance or suitability) for attribute or factor i relative to attribute or factor j, a^{*}_{ij} is the normalized score, and n is the number of attributes or factors being compared (Kovacs et al. 2004). Then, weight (w_i) of each attribute or factor was calculated as follows:

$$w_i = \sum_{j=1}^{n} a_{ij}^{*}$$

Finally, these weights were averaged across the 6 experts who returned surveys.

We applied these weightings to assess the suitability of each 30 × 30-m pixel based on its attribute value for each habitat factor: land cover type (United States Geological Survey 2006, 2008), forest canopy cover (United States Geological Survey 2001), water bodies (United States Department of Commerce 2011), and roads (United States Department of

Commerce 2011). We modified some of the data layers for our analysis. Roads, streams, and water-bodies used in the habitat model were given a 0.25-km buffer. The road dataset contained 5 classes, but we combined "Primary highway with limited access" and "Primary road without limited access" into 1 class (Highways). Stream and water-body classes were grouped based on perennial/intermittent status and divided into streams, water bodies, or shorelines. The 2001 National Land Cover Dataset contained 30 classes, but we grouped similar classes into 8 categories thought to be important to swamp rabbit biology (Chapman and Feldhamer 1981). We also converted the canopy cover data from a continuous variable into 4 categories (Table 1). These geospatial data layers were then reclassified by multiplying attribute weights by the relevant factor weights. We summed weights over all attributes and factors for each pixel using the Raster Calculator in ArcGIS 10.1 (ESRI 2012) to generate a habitat suitability value for that pixel. We divided the observed range of habitat suitability values into 5 categories based on observed breaks in the data.

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We considered the highest 2 categories (highest 34% of values) to be suitable habitat for use in our model. We chose the 34% cutoff values based on an apparent break in the distribution of suitability values and because swamp rabbits in southern Illinois studied by Scharine et al. (2009) and Crawford (2014) tended to be located in these categories. Allen (1985) suggested that areas of contiguous habitat >100 ha are required to support a swamp rabbit population, but Scharine et al. (2009) located swamp rabbits in habitat patches < 25 ha. Due to the presence of swamp rabbits in patches far smaller than 100 ha (Kjolhaug 1986; Porath 1997; Scheibe and Henson 2003; Scharine et al. 2009), we included suitable habitat areas > 50 ha, as well as patches 25-50 ha that were within 2 km of a patch > 50 ha. We anticipated that swamp rabbits would rarely disperse as far as 2 km, but included such isolated patches to better evaluate how decreased fragmentation could influence the likelihood of persistence (discussed below). From these areas, we used those patches with confirmed swamp rabbit presence in the past 30 years (Kjolhaug 1986; Porath 1997; Woolf and Barbour 2002; Scharine et al. 2009; Crawford 2014) to run simulations.

Berkman et al. (2015) found limited genetic connectivity of swamp rabbit populations in the Cache River watershed of Illinois and suggested that forested corridors may improve metapopulation viability by increasing dispersal between populations. We used ArcGIS to conduct least-cost path analysis, to identify the most permeable portions of the Cache River watershed for potential dispersal (Singleton et al. 2002; Adriaensen et al. 2003; LaRue and Nielsen 2008). This analysis is based on simulating movement over a resistance map, in which each pixel is assigned a resistance to movement based on its habitat characteristics and cost is the total resistance encountered over the length of a path (Singleton et al. 2002; Wikramanayake et al. 2004; LaRue and Nielsen 2008). We employed the AHP to assign each pixel a resistance to dispersal using the same methodology, habitat factors and attributes, and experts as for the map of habitat suitability. We used the resulting resistance map to generate least-cost paths 1 pixel wide between occupied habitat patches.

Population viability analysis.—Like Woolf and Barbour (2002), we used a Lefkovitch matrix model (Caswell 2001) to simulate rabbit population dynamics in each patch. The model included a juvenile and adult stage with 1-year time steps and assumed a pre-breeding census, such that the juvenile class comprised individuals nearly 1 year old; therefore, fecundity parameters incorporated survival of individuals through their 1st year. This model also assumed a female-only population, and allowed patch carrying capacity to differ based on patch size and suitability.

We used the program RAMAS GIS, version 5.0 (Akçakaya 2005) to run all simulations for this study. We ran all simulations with 2,500 repetitions for 25 simulated years, and our primary outputs were the distribution of population sizes each year, as well as the probability (i.e., proportion of repetitions) of the total metapopulation abundance (i.e., number of female rabbits alive) dropping below our quasi-extinction threshold (Ginzburg et al. 1982), which we set at 10% of the total regional carrying capacity, within 25 years. We then compared these outputs between simulations run with varying parameter values (intermediate value versus 50 to 150% of intermediate value) and management scenarios (i.e., changes to the habitat suitability map based on possible interventions). Because the estimated quasi-extinction probability under intermediate parameter values was essentially 0% (see "Results"), we also examined the effects of simulated habitat management interventions using a fecundity value 40% lower than the intermediate value.

The maximum female carrying capacity ($K_{\max,i}$) of each patch (i) equaled the patch area divided by the mean size of swamp rabbit home ranges, as we assumed a uniform distribution of individuals. We used an intermediate home range size of 1.93 ha (2.54 ha with a 24% overlap, based on core areas (50% isopleths from fixed kernel utilization distributions) of n = 60 swamp rabbits—Crawford 2014). Depending on the relative amounts of patch i made up of suitable and highly suitable habitat, the intermediate carrying capacity (and initial abundance) of each patch (K_i) ranged from $0.8K_{\max,i}$ (all suitable) to $K_{\max,i}$ (all highly suitable). As per Woolf and Barbour (2002), we chose to model density dependence as a ceiling, in which the population in each patch (N_i) increases based on the density-independent matrix model until they reach or exceed K_i, at which point additional individuals above K_i are removed from the population (Akçakaya 2005). In intermediate-parameter runs, we kept K_i constant through time.

In RAMAS GIS, dispersal rates (m_{ij}) are calculated from each patch to all other patches based on a migration-distance function:

$$m_{ij} = a \cdot \exp\left(\frac{-D_{ij}^{c}}{b}\right) \text{ if } D_{ij} < D_{max}$$

$$m_{ij} = 0 \text{ if } D_{ij} > D_{max},$$

Equation 1

where m_{ij} is the proportion of animals in patch *i* that successfully disperse to patch *j* in each year, and D_{ij} is the shortest straight-line distance (km) between the edges of the two patches. D_{max} represents the maximum dispersal distance, and *a*, *b*, and *c* define the shape of the migration-distance curve: *a* is the maximum dispersal rate (i.e., maximum fraction of individuals from a patch that successfully disperse to any single other patch), *b* is the average dispersal distance (km) when $c = 1$, and *c* determines the shape of the curve.

Dispersal data for swamp rabbits are limited, but Forys (1995) found that the Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*) had an average dispersal distance of 300 m. However, marsh rabbits evolved in a naturally patchy habitat (Forys and Humphrey 1996) and cottontail rabbits (*Sylvilagus* spp.) do not typically disperse long distances (Shields 1960; Chapman and Trethewey 1972; Fenderson et al. 2014), which suggests 300 m is likely an overestimate for swamp rabbit dispersal. Genetic evidence also indicates limited successful dispersal of swamp rabbits within one watershed in Illinois (Berkman et al. 2015), so we used an average dispersal distance b=200 m. Since Akçakaya and Raphael (1998) suggested that only a small portion of individuals in a patch will actually disperse to a single neighboring patch, we set *a* equal to 0.1. We set the intermediate value of parameter $c = 1$ (exponential dispersal kernel). Despite their rarity, long-distance dispersers are generally more important than short-distance dispersers to the persistence and genetic mixing of a metapopulation (Johst et al. 2002; Trakhtenbrot et al. 2005). We therefore set $D_{max} = 4$ km, although dispersal in the model beyond 1.5 km was vanishingly rare based on the intermediate values of *a*, *b*, and *c*.

We used an intermediate annual survival rate of 0.3 based on survival analysis of 79 radiocollared swamp rabbits in southern Illinois (Crawford 2014). Swamp rabbits are legal game species in Illinois, and this estimate included mortality due to hunting. Due to a lack of data, we assumed that survival rates of juveniles (1 year old) and adults (>1 year old) were equal. Using values from Holler et al. (1963) and Sorensen et al. (1968), both from Missouri, we estimated average numbers of litters per female per year and offspring per litter per female from these studies as 2.8 and 3.2, respectively. These estimates yielded an estimate of 8.96 offspring per year per female, which is similar to estimates from other studies (Hunt 1959; Toll et al. 1960; Hill 1967). We used an all-female model, so we halved this value to 4.48 female offspring per year per female. Since we assumed equal survival rates regardless of age, the fecundity matrix element equaled 4.48 multiplied by the 0.3 survival rate, or 1.344 female recruits per female per year for both stages. In a simple 2-stage Lefkovitch matrix, these intermediate survival and fecundity values produce a baseline, deterministic estimate of the finite rate of increase: $\lambda = 1.644$.

Flooding can increase swamp rabbit mortality by predation, starvation, hunting, and drowning, as well as decrease their reproduction due to embryo resorption (Conaway et al. 1960; Platt and Bunch 2000; Zollner et al. 2000b). The quantitative effect of catastrophic flooding on rabbit populations is poorly understood. Hamilton et al. (2010) estimated that severe flooding reduced monthly survival of riparian brush rabbits (*Sylvilagus bachmani riparius*) by about 33%, from 0.90-0.96 to 0.61-0.64. Previous floods had greatly reduced the number of riparian brush rabbits trapped, but rigorous estimates of effects on abundance and survival were not available. Woolf and Barbour (2002) assumed a 60% decline in population abundance during a catastrophic flood, so we used this as our intermediate value of the effect of catastrophes. As catastrophes are rare by definition, we assumed a 10% annual occurrence rate for our intermediate value, and catastrophes occurred regionally, impacting all patches simultaneously. The value of 10% roughly corresponds to the frequency of major floods based on river stage data from the United States Geological Survey (2011) and the US Army Corps of Engineers (2011). These intermediate values for the effect and occurrence rate of catastrophic floods reduced deterministic λ to 1.545.

RAMAS GIS allows for both demographic and environmental stochasticity in modeling population growth. For demographic stochasticity, RAMAS selects the number of survivors per patch per year from a binomial distribution and the number of offspring per patch per year from a Poisson distribution. For environmental stochasticity, RAMAS samples each vital rate from a lognormal distribution (Akçakaya 2005); means and standard deviations for these distributions are set by the user. We estimated standard deviations by applying the coefficients of variation for fecundity and survival estimates of Lower Keys marsh rabbits to our values (Forys 1995; LaFever et al. 2008). The resulting standard deviations were 0.166, 0.076, and 0.051 for fecundity, juvenile survival, and adult survival, respectively.

Environmental conditions are typically more similar in nearby patches than in distant patches. We modeled spatial autocorrelation in survival and fecundity values between patches due to environmental similarities using the correlation-distance function:

$$\rho_{ij} = x \times \exp(-D_{ij}^{z}/y)$$

where ρ_{ij} is the coefficient of correlation between patches i and j, and D_{ij} is the distance (km) between the centers of the two patches. The parameters x, y, and z define the shape of the correlation-distance curve: x is the maximum correlation (as $D_{ij} \rightarrow 0$), y is the rate at which correlation declines with increasing distance, and z determines the shape of the curve. Woolf and Barbour (2002) found no significant difference in persistence probability caused by varying environmental correlation values so we used their intermediate values: $x = 1$, $z = 1$, and $y = 40$.

We performed a sensitivity analysis to test the effect of changes in parameters that could be measured or estimated inaccurately, or affected by management efforts. We individually varied each parameter in 5% increments from 50 to 150% of the intermediate value (Table 2), and we ran all simulations with 2,500 replications each for 25 simulated years, using intermediate values for all other parameters. When varying mean survival and fecundity values, standard deviations (environmental stochasticity) changed accordingly, based on the coefficients of variation from Forys (1995) and LaFever et al. (2008). Although fecundity values incorporated survival to age 1, we kept the fecundity value constant when measuring sensitivity to survival rates. We also explored the effect of a trend in carrying capacity, such that the carrying capacity of each patch (*i*) changed linearly from the initial carrying capacity ($K_{0,i}$) to the new carrying capacity at year 25 ($0.5K_{0,i} \leq K_{25,i} \leq 1.5\, K_{0,i}$).

To identify which habitat patches may be most important to swamp rabbit viability in Illinois, we removed one patch at a time with replacement from the habitat map for each simulation, and also ran two simulations removing the largest and smallest 25% of patches by population size. To estimate the effect of habitat fragmentation, we reduced fragmentation by adding 60, 120, and 180 m to the perimeters of all patches, such that the initial test was used as a "high fragmentation" comparison. We separated the effect of habitat fragmentation *per se* from that of habitat amount by setting the initial abundance and carrying capacity of each expanded patch equal to that of the original patch or the sum of all original patches (initial test) the expanded patch incorporated (i.e., total carrying capacity of the landscape was not changed). We found intermediate model results were so optimistic that a positive change caused by the addition of dispersal corridors would not be detected, so we set fecundity at 60% of the intermediate test and compared results to the corresponding test from the sensitivity analysis.

We used the model to assess the benefit of improving dispersal along corridors identified by our least-cost path analysis. Because corridors would likely be used by the small number of individuals near the start of the corridor in each patch, we tested the effect of these dispersal corridors by adding 5% to the dispersal rate between patches connected by corridors (i.e. adding 0.05 to m_{ij} calculated via Equation 1), or in the case of one corridor that connected seven patches, by adding 0.0083 to the migration rate for each connected pair of patches. Because we were testing the use of corridors to improve dispersal between patches, we did not artificially join connected patches as a single patch in our model. As with the habitat fragmentation tests, we set fecundity at 60%, using the corresponding tests from the sensitivity analysis as a comparison.

RESULTS

Mapping suitable habitat and potential corridors.—Experts deemed that land cover was the most important factor for identifying suitable swamp rabbit habitat as well as resistance to dispersal (Fig. 1). Among land cover types (attributes), wetland forest was deemed most suitable for swamp rabbits and open water and developed/barren lands were most resistant to dispersal (Table 1). Canopy cover and water bodies were both deemed intermediate in importance (Fig. 1), with high canopy cover and perennial stream/ditch providing highest suitability and lowest resistance (Table 1). Roads were considered to be relatively unimportant (Fig. 1), and unpaved roads were considered most suitable and least resistant to dispersal (Table 1).

The resulting map of habitat in southern Illinois (Fig. 2a) consisted of 62 patches of suitable and highly suitable swamp rabbit habitat totaling just under 12,000 ha, with mean and median patch sizes of 193 ha and 86 ha, respectively (range = 25-3,818 ha). Of these patches, 19 patches were < 50 ha, 17 patches were 50-100 ha, and 26 patches were > 100 ha, and the initial metapopulation abundance was 5,577 individuals, resulting in a quasi-extinction threshold of 558 individuals. Least-cost path analysis identified 31 potential dispersal corridors, ranging from 0.7 km to 19.1 km long, linking suitable habitat patches in the Cache River watershed (Fig. 2b).

Population viability analysis.—The initial population viability analysis with intermediate parameter values predicted relatively little change in the swamp rabbit metapopulation of southern Illinois over the next 25 years, with a median final metapopulation abundance of 5,570 rabbits (0.13% decline; Fig. 3). The model estimated a 0% chance of the swamp rabbit metapopulation declining below 10% of the initial abundance (quasi-extinction) within 25 years (95% *CI*: 0-1.77%). Extending intermediate-parameter simulations to 50 years resulted in minuscule changes to median final abundance (5,564 rabbits) and quasi-extinction risk (0%).

Population growth and viability were most sensitive to changes in fecundity: the range of fecundity values we considered produced deterministic λ values ranging from 0.97 to 2.32, and a 50% reduction in fecundity caused the risk of quasi-extinction to exceed 75% (Fig. 4). Population growth and viability were moderately sensitive to changes in the effect of catastrophic flooding, resulting in a quasi-extinction probability as high as 40% (Fig. 4) despite deterministic λ only varying between 1.50 and 1.60). No other parameters, when changed, yielded an appreciable impact on the risk of quasi-extinction for the metapopulation (i.e. quasi-extinction risk exceeding the 95% *CI* from the intermediate test).

The removal of any single patch had no impact on the quasi-extinction risk of the overall metapopulation when compared to the original model (0%), nor did removal of the smallest 25% of patches, but removal of the largest 25% of patches (72% of the metapopulation abundance) increased the quasi-extinction risk to 4%. Simulations with fecundity reduced by 40% yielded a probability of quasi-extinction of 20% (95% *CI*: 18-22%), which we use as a baseline for comparing with simulated habitat or corridor manipuations. Adding 60, 120, and 180 m to the edge of all patches increased the total patch area to approximately 17,800 ha, 21,500 ha, and 24,600 ha, respectively, and adjusting for this increase in habitat area to isolate the effects of habitat fragmentation per se did not substantially affect the quasi-extinction risk for any of the three scenarios (21%, 20%, and 20%, respectively). Adding corridors also yielded no appreciable change in the predicted probability of quasi-extinction (21%).

Discussion

The swamp rabbit has high habitat specificity and the availability and abundance of swamp rabbit habitat have declined across its range, making an assessment of its viability in Illinois important to its conservation. Our findings suggest that swamp rabbit populations show no risk of extinction in Illinois in the next 50 years. The predicted extinction risk was most sensitive to changes in fecundity and the effect of catastrophes, and was relatively insensitive to changes in other parameter values. Our findings also suggest that efforts to increase connectivity, e.g., by adding dispersal corridors, will likely not benefit the overall metapopulation as much as efforts to increase the overall amount and quality of habitat.

Our model suggests a 0% chance of quasi-extinction within 50 years, with a median percent decline of < 1%. Similarly to Woolf and Barbour (2002), our model was sensitive to few of its parameters. The model was most sensitive to changes in fecundity, and the fecundity value we used was estimated based on two studies of captive individuals from Missouri conducted over 40 years ago. The rabbits in these studies may have reproduced less than they would have in the wild due to high stress resulting from limited space in the enclosure, as crowding can lead to higher than normal rates of litter resorption (Conaway et al. 1960; Holler et al. 1963; Sorensen et al. 1968), which suggests that our fecundity value may be an underestimate yet still resulted in a 0% chance of extinction. Other studies have reported similar reproductive rates in captive and free-living *Sylvilagus*, however (e.g, Kirkpatrick and Baldwin 1974). Kjolhaug (1986) estimated an 18% annual survival rate for swamp rabbits in Illinois, which would not increase the likelihood of extinction based on our sensitivity analysis. However, when this new survival value was used to calculate fecundity, the risk of extinction increased to about 20%, suggesting that accurate estimates of both demographic rates are very important to achieve reliable estimates of absolute extinction risk.

Catastrophes also had a large impact on the risk of quasi-extinction. We based the occurrence rate of catastrophes on flood gauge measurements, but the actual occurrence rate of catastrophic floods that affect swamp rabbits in southern Illinois is unknown, and climate change models predict an increase in the occurrence of flooding events around the Mississippi River (Pinter et al. 2006) and at the global scale (Bouwer 2011; Wilby and Keenan 2012). Although the occurrence rate of catastrophes appeared to have no impact on extinction risk, the frequency of catastrophes would amplify the impact the effects catastrophes have on the population. The model was more sensitive to the effect that catastrophic floods have on swamp rabbit populations than occurrence rate, but the value for the effect of catastrophic floods was assumed with little empirical data to support it, suggesting more research is needed to determine their impacts. Severe flooding in 1976 and again in 1997 appeared to nearly eradicate the only known (at the time) population of riparian brush rabbits (United States Fish and Wildlife Service 1998), and Hamilton et al. (2010) estimated that a severe (but apparently brief) flood reduced survival rate of riparian brush rabbits by approximately 30%. However, the impact of flooding is likely to vary strongly with local topography as well as flood duration. Crawford (2014) reported that swamp rabbits in some but not all sites within the Cache River National Wildlife Refuge, Illinois, were able to find refuge from a severe and persistent flood event. Combined, these observations reinforce the need to ensure that upland refugia remaining near fragmented populations vulnerable to flooding are given conservation priority.

The model appeared to be relatively insensitive to changes in home range area (which determined carrying capacity) and the trend in carrying capacity, but our simulations showed that the total metapopulation abundance tended to stay at approximately the total carrying capacity of the landscape. Thus, home range area and temporal changes in suitability are likely to influence the overall abundance of the species in Illinois. Removal of any single patch had no appreciable impact on the extinction risk for the metapopulation as a whole, suggesting that individual patches are not crucial to metapopulation persistence, concurring with the results of our dispersal and connectivity tests. However, removal of the largest 25% of patches did yield a negative effect, pointing out that further habitat loss and degradation can reverse the current prediction of low extinction risk. Conversely, our results confirm that increasing the amount and suitability (and therefore local carrying capacity) of habitat can further increase the total swamp rabbit metapopulation size (i.e., number of rabbits).

Swamp rabbit persistence in the model was relatively insensitive to changes in average dispersal distance or maximum dispersal rates, as well as to the shape of the dispersal kernel (parameter *c*). Decreased fragmentation per se and addition of dispersal corridors also had little effect on model results, especially when compared to the effect of habitat loss, again suggesting that habitat quality and quantity is more important to manage than habitat connectivity. Although this seems contrary to the logic behind a metapopulation, the intermediate parameter values resulted in very rare dispersal between patches at the average nearest neighbor distance of 2.09 km. Rare dispersal coupled with the strong baseline population growth rates meant that in situ population dynamics were much more important for persistence than metapopulation dynamics. Akçakaya et al. (2003) obtained similar results for metapopulation viability of California least terns (*Sterna antillarum browni*): where strong in situ population growth resulted in essentially zero near-term risk of extinction under intermediate parameter values, and greater sensitivity to demographic rates than dispersal parameters. In contrast, Medici and Desbiez (2012) found that dispersal was crucial for persistence of fragmented populations of lowland tapirs (*Tapirus terrestris*), whose maximum population growth rates were much lower than we estimate for swamp rabbits. Frequent dispersal also enables persistence of American pikas (*Ochotona princeps*) in a metapopulation occupying a complex of small mine tailing patches (Moilanen et al. 1998; Smith and Nagy 2015), a system that differs from ours in that dispersal is frequent and extinction rates are very high because most patches typically only support a few individuals. We would expect connectivity to play a larger role for swamp rabbits over longer timescales (with increased probability of extinction), but the amount and distribution of habitat as well as flooding regimes are likely to change dramatically over longer time horizons.

Our findings are based on several assumptions that require further validation. The habitat suitability map we used to build our models assumed a clear dichotomy between suitable and unusable habitat in southern Illinois, although swamp rabbits have been found in lower quality or smaller areas than the cut-off we chose (Rubert 2007; Scharine et al. 2009, 2011). Empirical validation or participation by a greater number of experts would improve confidence in habitat suitability values. Also, we treated patches separated by > 30 m as 2 separate patches, even though the patches may have been separated by a river or a lower quality wooded area. Small areas such as these that did not register as suitable habitat may not act as a barrier for a swamp rabbit in reality, suggesting our map may represent an artificially fragmented landscape. We also assumed that all patches identified were fully occupied at the start, although this is likely a false assumption (Kjolhaug 1986; Barbour et al. 2001). However, our results indicate that predicted persistence was much more sensitive to demographic parameters than to the amount or connectivity of suitable habitat. Even removing the patches containing most of the simulated rabbits in the model only increased the predicted probability of extinction to 4%. Our findings point to refining estimates of those demographic rates rather than estimates of habitat suitability as the most important avenue to increasing confidence in PVA results.

There has been much debate about whether the primary approach of species conservation should be to increase connectivity or to conserve existing habitat (Simberloff and Cox 1987; Simberloff et al. 1992; Beier and Noss 1998). Enhancing connectivity can increase genetic variability, decrease local extinctions, and increase abundance in patches with smaller populations (Fahrig and Merriam 1985; Dunning et al. 1995; Haddad and Baum 1999). However, our models suggest that efforts to improve dispersal amongst swamp rabbit populations in southern Illinois will have less impact on their overall persistence in the state than improvements in patch habitat quality. This conclusion is in concordance with the outcome of agent-based simulation models of Ye et al. (2013), who found that long-term abundance of habitat specialists in heterogeneous environments depended mainly on the size and quality of suitable habitat patches whereas that of generalists was more strongly influenced by patch isolation. Thus, while habitat quality is obviously important for demographic parameters and population persistence of all species, it may be particularly crucial (relative to connectivity) for habitat specialists with low vagility.

This study suggests some potential changes to management practices that would help swamp rabbit population in Illinois and will likely have similar positive effects in other fragmented areas in the northern portion of the swamp rabbit range (e.g. Indiana—Roy Nielsen et al. 2008), as well as for other species occupying similar habitats. Wildlife managers working to conserve individual species are often torn between improving and expanding existing habitat (Hobbs 1992; Beier and Noss 1998; Hoctor et al. 2000). Woolf and Barbour (2002) and Scharine et al. (2009) suggested that maintaining quality of existing patches, particularly upland areas adjacent to the bottomland hardwood forests currently occupied, should be a major goal in swamp rabbit conservation, and our results agree. High-quality upland habitat (e.g., with thicker understory growth for food and protection) provides a refuge from flooding without high predation (Kjolhaug et al. 1987), which will decrease the effect of floods on survival and population abundance, and increase reproduction during flooding periods. We also identified further research to improve our knowledge of swamp rabbit persistence in southern Illinois and create more accurate models of swamp rabbit population dynamics in the future. Most important are better estimates of fecundity of swamp rabbits in Illinois and the effect of floods on swamp rabbit populations. These 2 parameters had the greatest effect on extinction risk in the model and are the least studied in swamp rabbits range wide.

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FIGURE LEGENDS

Fig. 1. Mean importance weights with standard deviations calculated using the analytical hierarchy process (Saaty 1980), representing the relative importance of each factor in the habitat suitability model (solid bar) and the dispersal cost model (hatched bar) for swamp rabbits (*Sylvilagus aquaticus*) in southern Illinois. A mean weight of 1 (dotted line) indicates equal perceived importance relative to other factors.

Fig. 2. Maps of a) habitat patches (*n* = 62) identified as suitable or highly suitable and with confirmed swamp rabbit (*Sylvilagus aquaticus*) presence in southern Illinois (inset) in 1983-1985, 1995-1997, 2006-2007, or 2009-2011, and b) dispersal corridors (in black) connecting suitable habitat patches with confirmed swamp rabbit presence (in gray) in the Cache River watershed, southern Illinois.

Fig. 3. Minimum (circles), 5th percentile (squares), and median (50th percentile; diamonds) simulated metapopulation abundance as percentage of initial metapopulation size for swamp rabbits (*Sylvilagus aquaticus*) in southern Illinois over 50 years, based on intermediate parameter values.

Fig. 4. Probability of quasi-extinction for swamp rabbits (*Sylvilagus aquaticus*) in southern Illinois within 25 years following detrimental changes in fecundity (decreased fecundity; diamonds) and effect of catastrophes (increased impact on populations; squares). Dashed line represents the upper 95% confidence interval around the probability of quasi-extinction (0%) from the initial test using all intermediate values.

Table 1. Importance of habitat characteristics for swamp rabbits (*Sylvilagus aquaticus*), calculated from expert surveys using the analytical hierarchy process (Saaty 1980). Values are mean weights (± *SD*), representing the relative suitability of each attribute within the factors used in mapping habitat suitability and dispersal resistance for swamp rabbits in southern Illinois. Bold indicates the attribute with highest suitability or dispersal resistance within each factor.

Factor	Attribute	Suitability	Dispersal resistance
Land cover	Open water/barren/developed	0.16 ± 0.02	**2.68 ± 0.49**
	Agriculture	0.24 ± 0.06	1.75 ± 0.58
	Upland forest	0.39 ± 0.11	0.88 ± 0.07
	Upland shrub/scrub	0.54 ± 0.08	0.83 ± 0.22
	Upland herbaceous	0.50 ± 0.18	1.15 ± 0.47
	Wetland forest	**2.26 ± 0.63**	0.23 ± 0.07
	Wetland shrub/scrub	2.11 ± 0.57	0.20 ± 0.05
	Wetland herbaceous	1.80 ±0.49	0.29 ± 0.10
Canopy cover	0-25%	0.24 ± 0.06	**1.93 ± 0.81**
	26-50%	0.91 ± 0.50	0.89 ± 0.35
	51-75%	1.36 ± 0.36	0.64 ± 0.60

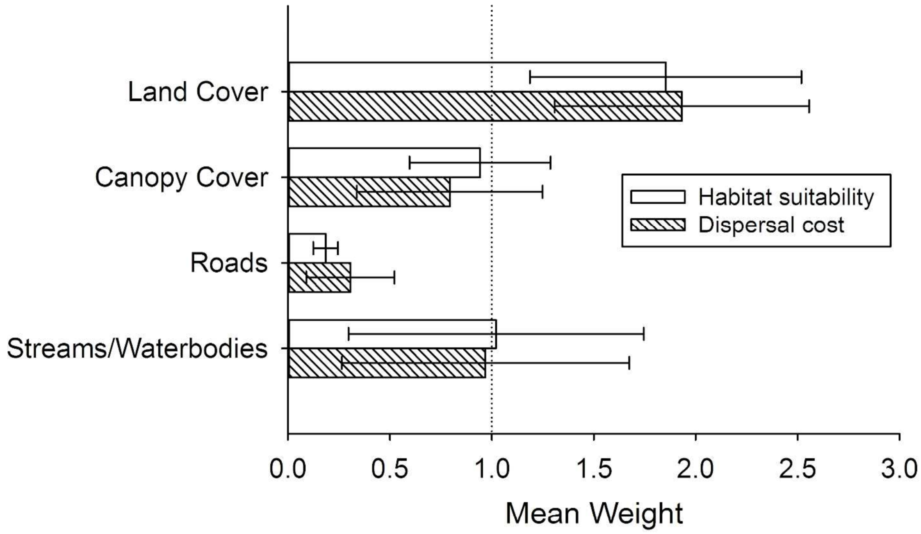
	76-100%	**1.49 ± 0.75**	0.54 ± 0.37
Streams and water bodies	Intermittent shoreline	0.58 ± 0.48	1.16 ± 0.64
	Perennial shoreline	1.14 ± 0.56	0.89 ± 0.57
	Intermittent stream/ditch	0.64 ± 0.31	1.01 ± 0.54
	Perennial stream/ditch	**1.58 ± 0.44**	0.81 ± 0.50
	Intermittent lake/pond	0.76 ± 0.50	**1.25 ± 0.65**
	Perennial lake/pond	1.31 ± 0.88	0.87 ± 0.94
Roads	Highways	0.22 ± 0.05	**1.81 ± 0.79**
	Secondary	0.45 ± 0.07	0.96 ± 0.28
	Local/rural	0.82 ± 0.18	0.64 ± 0.20
	Unpaved	**2.50 ± 0.20**	0.59 ± 0.92

Table 2. Parameter values used in the initial population viability analysis (intermediate values) and sensitivity tests for swamp rabbits (*Sylvilagus aquaticus*) in southern Illinois. Effect of catastrophe values are the percent of patch abundance lost in a flood, and trend in carrying capacity values are year-25 carrying capacity (K_{25}) as a percentage of K_0.

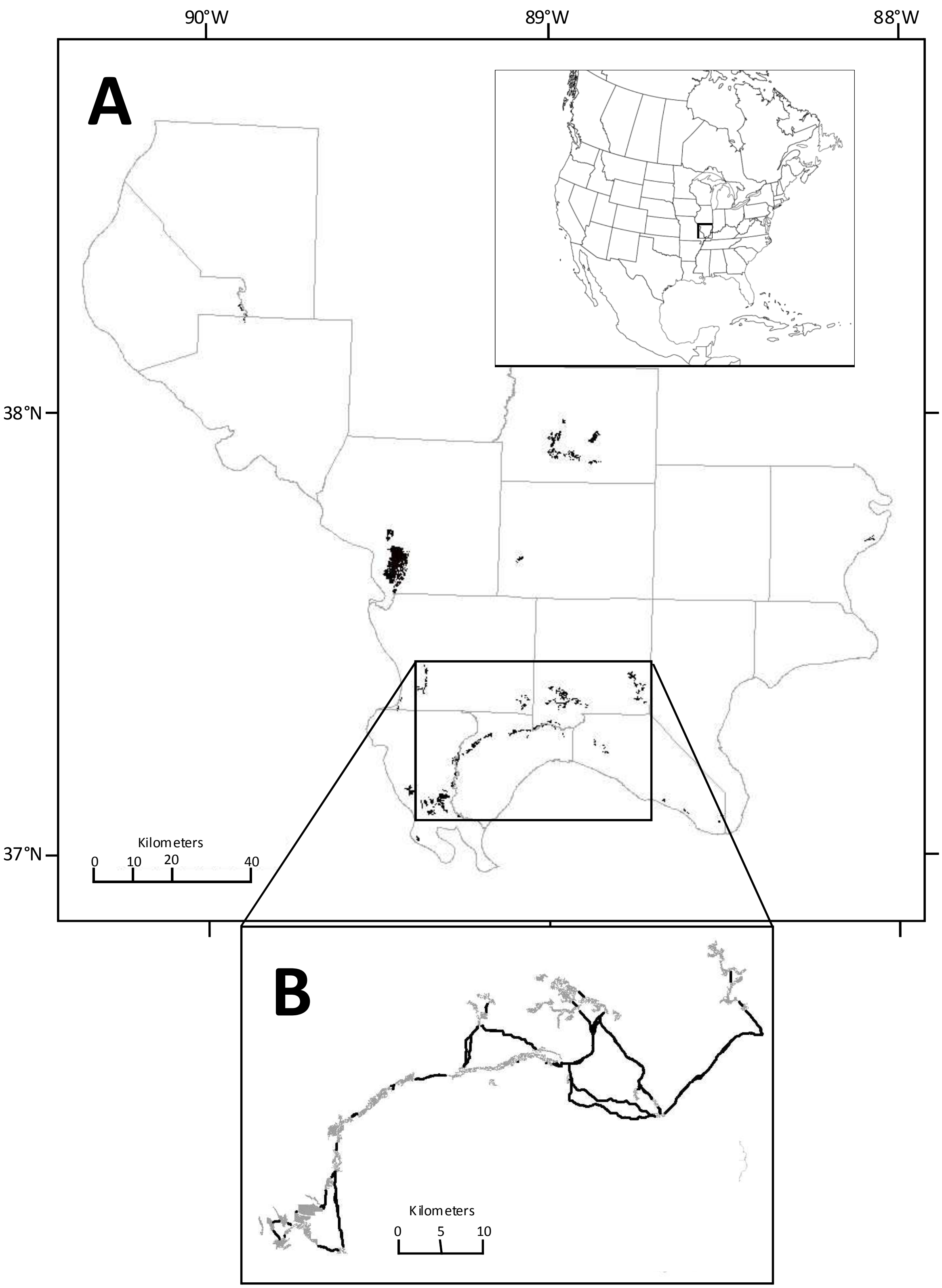
Parameter	Minimum	Intermediate	Maximum
Home Range (ha)	0.965	1.93	2.895
Survival	0.15	0.3	0.45
Fecundity	0.672	1.344	2.016
Occurrence Rate of Catastrophes	5%	10%	15%
Effect of Catastrophes[a]	30%	60%	90%
Average Dispersal Distance (m)	100	200	300
Maximum Dispersal Rate	5%	10%	15%
Dispersal Parameter *c*	0.5	1	1.5
Trend in Carrying Capacity[b]	50%	100%	150%

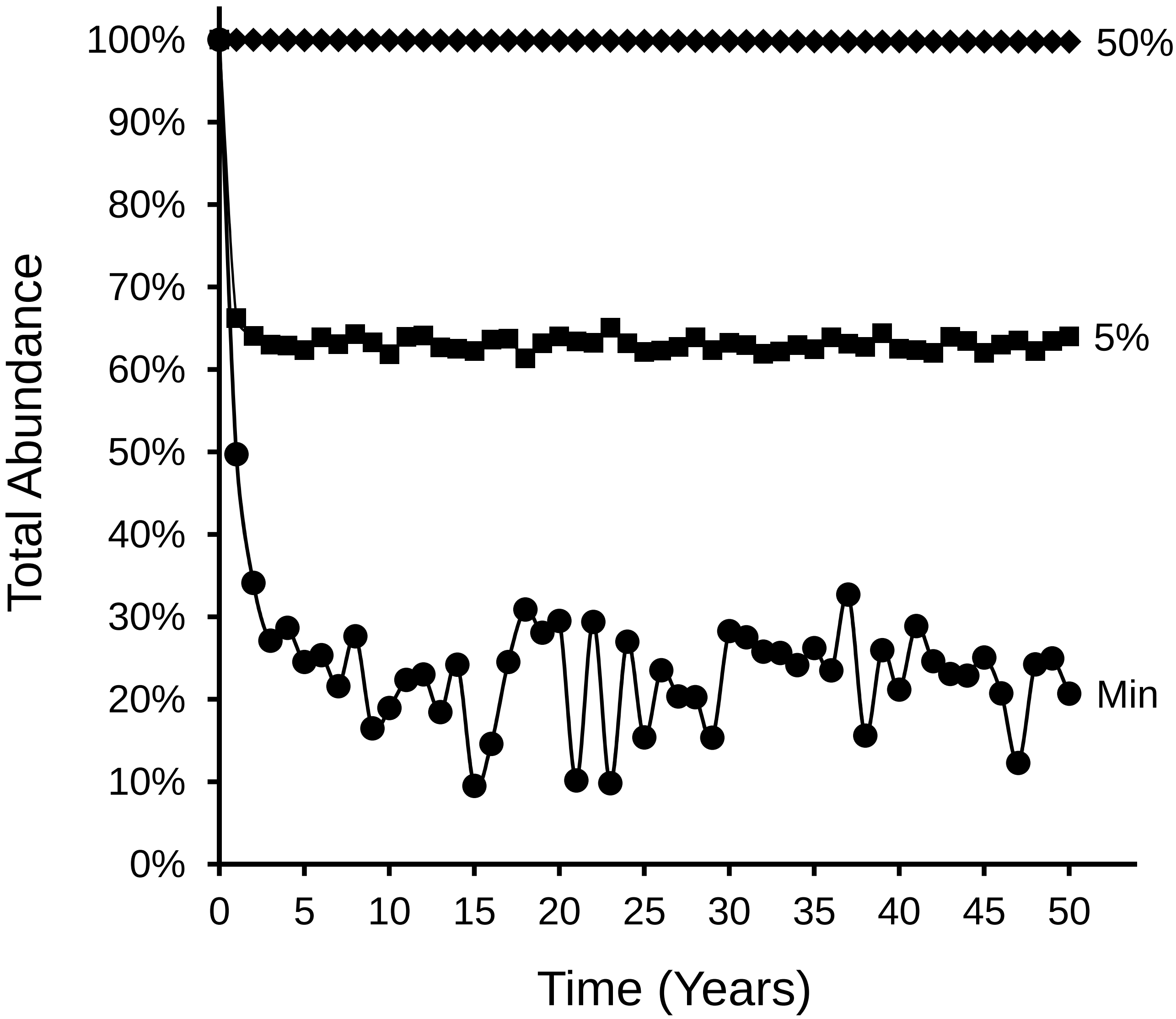
[a]Percentage of patch population lost during flood.

[b]Values indicate carrying capacity in year 25 as a percentage of carrying capacity in year 0. 100% indicates no trend.

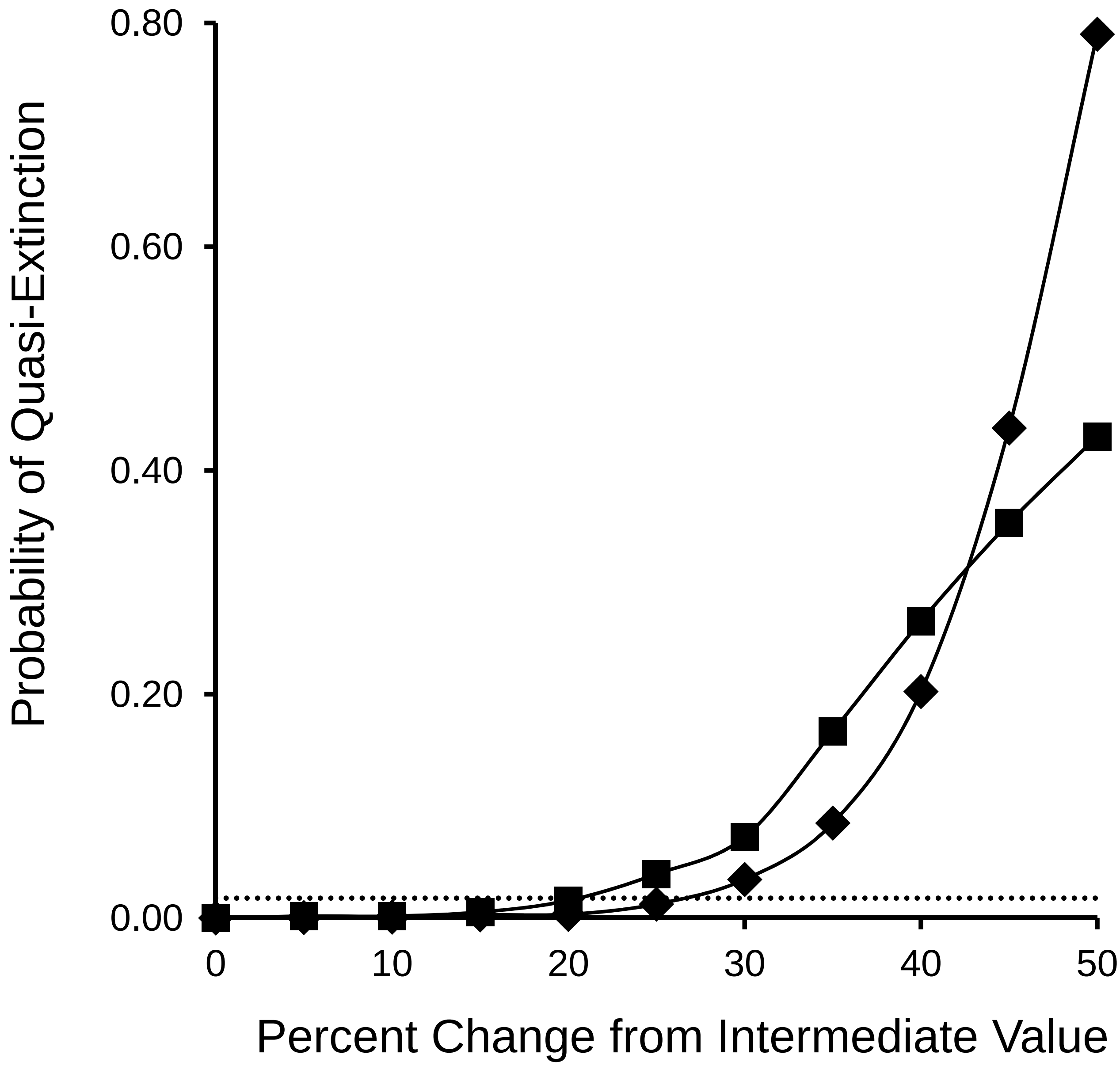


278x215mm (300 x 300 DPI)


90°W
89°W
88°W
38°N
37°N
A
Kilometers
0 10 20 40
B
Kilometers
0 5 10



100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Total Abundance
0
5
10
15
20
25
30
35
40
45
50
Time (Years)
50%
5%
Min


0.80
0.60
0.40
0.20
0.00
Probability of Quasi-Extinction
0
10
20
30
40
50
Percent Change from Intermediate Value