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Persistence of a Swamp Rabbit Metapopulation: The Incidence Function Model Approach

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ABSTRACT

We evaluate the status and distribution of swamp rabbits (Sylvilagus aquaticus) in Missouri using the Incidence Function Model and logistic regression in an effort to assess the long term viability of the Missouri metapopulation. We used results of latrine surveys performed in 1992 and 2001 to estimate the likelihood of persistence of swamp rabbits over periods of 9 to 1000 years. Under current conditions, more than 50% of the patches are predicted to contain rabbits after 1000 years. Logistic regression revealed that both patch area and patch isolation were significantly related to patch occupancy, and play key roles in the incidence of swamp rabbits.

Keywords: *Sylvilagus aquaticus*, metapopulation, incidence function model, Missouri.

Mathematics Subject Classification: 62J02, 62P12

Computing Classification System: Q.570

1. INTRODUCTION

As a consequence of habitat loss and fragmentation, swamp rabbits in Missouri (USA) now exist as a metapopulation linked through dispersal. Although the species is listed in Missouri as imperiled (very vulnerable to extirpation; Missouri Department of Conservation, 2009) it is still hunted, presumably because its conservation status at the core of its range is secure. The species occupies bottomland hardwood forest with dense understory vegetation, refugia such as logs and stumps, and standing water (Dailey et al., 1993). Although these habitats were once abundant in southeast Missouri, most wetland areas have been converted to agricultural uses. In fact, between 1870 and 1973, more than 810,000 ha of lowland habitat were converted to agricultural and other uses (Dailey et al., 1993). Because Missouri represents part of the distributional limit of swamp rabbits, there is concern about persistence of this species in Missouri.

Nielsen et al. (2008) performed a population viability analysis (PVA) on the swamp rabbit metapopulation in Indiana, part of the northernmost edge of the swamp rabbit distribution. Their model included demographic data that enabled them to predict occupancy dynamics. It was determined that, while the population of swamp rabbits in Indiana remains stable, their numbers are few. Extinction of the Indiana population is not likely, even considering a worst-case scenario. However, these models hold true only if current habitat conditions remain the same or improve; if conditions deteriorate, there is substantial risk of extirpation of *S. aquaticus* in Indiana.

In Missouri, the question of whether swamp rabbits should remain classified as an S2 species (imperiled) or reclassified is important to both conservation groups and hunters (Henson, 2002). In this paper, we assess whether swamp rabbits are likely to persist in both the short and long-term, given current conditions of the metapopulation in southeast Missouri. We compare patch occupancy data from 1992 and 2001 together with patch area and isolation to predict if swamp rabbits persist in a given area. We assume the metapopulation in southeast Missouri is not connected to any other metapopulations. We use a logistic regression model to determine whether area and isolation influences the occurrence of swamp rabbits. Isolation is described as a function of distance from one of 2 core population centers: Mingo National Wildlife Refuge and Donaldson Point Conservation Area. These centers represent locations that are likely source populations for swamp rabbits. Also, the Incidence Function Model (Hanski, 1994; Hanski et al., 1995; Wahlberg et al., 1996) is used to predict whether swamp rabbits are likely to persist over the long term.

2. METHODS

2.1. Study Area and Data

Swamp rabbits occur in 15 southeast Missouri counties: Bollinger, Butler, Cape Girardeau, Dunklin, Jefferson, Mississippi, New Madrid, Oregon, Pemiscot, Perry, Ripley, Scott, Ste. Genevieve, Stoddard, and Wayne Counties. Across these counties, Scheibe and Henson (2003) identified 278 potential habitat patches. We obtained patch occupancy data for swamp rabbits in 1992 and 2001 from Henson (2002) and the Missouri Department of Conservation.

2.2. Data Transformation

We determined the location, section, range and township of each habitat patch using original field notes and maps from the 1992 and 2001 surveys (Henson, 2002). These locations were converted to an (x, y)-coordinate system using Google Earth (http://www.google.com/ earth/index.html, accessed 5 Jan 2009) and Clark's Earthpoint system (2008). We obtained latitude and longitude coordinates for the approximate center of each habitat patch, error not exceeding 2 degrees. An origin point was chosen arbitrarily as 36° N 91.3°W. Using Mississippi State University's Agricultural and Biological Engineering Department (http://www.abe.msstate.edu/ Tools/Calculator/gps.php, accessed 5 Jan 2009) Global Positioning System (GPS) calculator, we were able to obtain distances between the origin and each latitude and longitude coordinate point, under the assumption the earth is spherical.

All calculated distances and (x,y) coordinates were in kilometers, and area estimates were converted to km^2.

2.3. Isolation Index

Within the logistic regression model we used an index for isolation (Frick, 2007) that measured the shortest distance between two points. We computed isolation of a habitat patch in relation to 2 probable source populations (Scheibe and Henson, 2003): Donaldson Point Conservation Area and Mingo National Wildlife Refuge. Donaldson Point supports large stands of bottomland hardwoods, giant cane, pools, and seasonal flooding from the Mississippi River. Mingo National Wildlife Refuge lies in the historic channel of the Mississippi and has been hydrologically maintained since approximately 1944 (http://www.fws.gov/Refuge/Mingo/about/history.html, Accessed 27 April 2009). We measured isolation of habitat patches from these locations because both wetland sites support relatively large populations of swamp rabbits. Because swamp rabbits occupy wetland habitats, and because movements greater than 2 km from water are not likely (Nielsen et al., 2008), we computed intermediate steps between habitat patches. To calculate isolation from a given habitat patch and Donaldson Point or Mingo, the location of the patch is important (Figure 1). Patches were classified as left side, right side, or neck, with patch 60 central to left, right, and neck patches. Isolation from the source populations depends on where (left, right, and neck) the patch of interest lies. For example, isolation (distance) between a patch in the neck and Mingo is computed as the distance from Mingo to patch 60, and then from patch 60 to the neck patch. This is because travel between patches must follow appropriate habitat corridors. Because the range of values for both patch area and isolation was large, all data were log transformed.

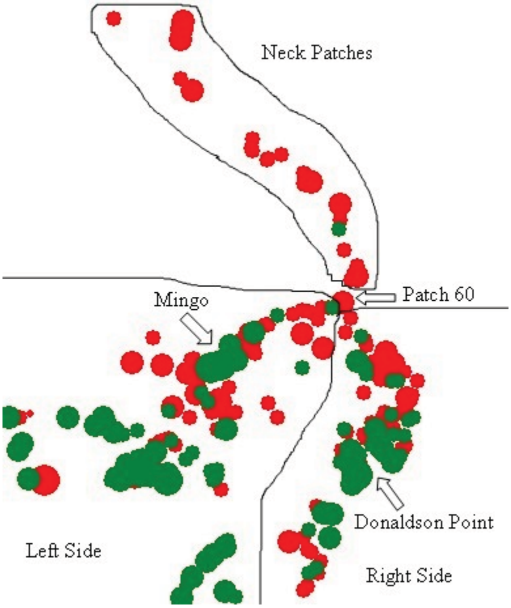

Figure 1. Patch classifications and the relative locations of Donaldson Point and Mingo National Wildlife Refuge

2.4. Incidence of Swamp Rabbits

For both 1992 and 2001, absence or presence of swamp rabbits in a patch was denoted as 0 (absence) or 1 (presence). Sites that were not surveyed because of flooding, lack of permission from the landowner, or construction on the site were assigned a value of -1 because the presence/absence of swamp rabbits is unknown. Sites that had been cleared or suffered a loss of suitable habitat during a particular survey were assigned a value of 0 because no animal was found at the location. Locations that were missing data for both years were omitted from the analysis. Also, when analyzing just 1992 data, patches that received a value of -1 for incidence were omitted, bringing the total number of patches with incidence data for 1992 to 253 patches. Similarly, for the 2001 dataset, the number of patches with incidence data was 226. Overall, for both 1992 and 2001, there were 216 patches that included data for both years.

2.5. Modeling

We used 2 modeling approaches. The first was a logistic regression analysis with patch occupancy treated as a dependent indicator variable (empty patch = 0, occupied patch =1), and patch area, patch isolation, and interactions between area and isolation as independent variables. Second, we developed an incidence function model using SPOMSIM (http://www.helsinki.fi/science/metapop/Software.htm#_SPOM, Accessed 20 October 2008), again using patch occupancy as an indicator variable. SPOMSIM was developed by Moilanen (2004), and was used to parameterize the IFM based on Hanski's original IFM model (1994). Initial simulations were performed using the 1992 data set, and executed over 9 years to predict occupancy for 2001. These results were compared with the field observations made in 2001, and were then used to simulate patch occupancy 25, 50, 100, 400, and 1000 years after 1992 and 2001.

2.6. Logistic Regression Model

Because the response variable is binary, we used logistic regression to determine the influence of area and isolation on the probability of patch occupancy by swamp rabbits (Frick, 2007). The fitted logit response function followed the form

$$\pi' = g_0 + g_1 X_1 + g_2 X_2 + \cdots + g_{r-1} X_{r-1},$$

where r is the number of parameters, $\pi' = \log_e\left(\frac{\pi}{1-\pi}\right)$ by a logit transformation, and

$$\pi = \frac{\exp(g_0 + g_1 X_1 + \cdots + g_{r-1} X_{r-1})}{1 + \exp(g_0 + g_1 X_1 + \cdots + g_{r-1} X_{r-1})}.$$

The X_i's represent area, isolation, and the interaction terms and g_i's are parameter coefficients (estimated using SAS®). The probability that incidence equals 1 was modeled using maximum likelihood estimates for parameter coefficients.

Significance of parameter coefficients in the logistic regression model was assessed using the Wald Test, with α = 0.05 (Kutner, et al., 2005). Given significance of the parameter coefficients, the odds-ratio, where

$$\text{Odds Ratio} = \hat{R} = \exp(g_i),$$

determines the odds of the swamp rabbit being found given the indicator variable(s) used in the model.

To determine if all fitted coefficients are equal to zero, the likelihood ratio test was used. Here, the test statistic was

$$G^2 = -2\log_e\left[\frac{L(R)}{L(F)}\right],$$

where $L(R)$ is the likelihood function of the reduced model (with q parameters), and $L(F)$ is the likelihood function of the full model. By the theory of large numbers, when sample size n is large, $G^2 \sim \chi^2(r-q)$, where $df_R = n - q$ and $df_F = n - r$. The decision rule for this test is(Kutner, et al., 2005)

$$\begin{aligned}&\text{if } G^2 \le \chi^2(1-\alpha; r-q), \text{conclude } H_0\\&\text{if } G^2 > \chi^2(1-\alpha; r-q), \text{conclude } H_a\end{aligned}$$

2.7. Incidence Function Model

The IFM uses only a few observations about a metapopulation to predict future incidence. In our model, the only necessary information is area, location and occupancy state of all individual patches. The purpose of the IFM is to predict whether the species will be present at some future time. It provides no assessment of population size or structure. However, occupancy data are central in any management plan designed to assure long-term persistence. Some general assumptions for the IFM (Hanski, 1994; Hanski, 1997b; and Hokit et al., 2001) include; 1) All patches within the metapopulation must be at a dynamic equilibrium in terms of colonizations and extinctions, 2) Local (within-patch) demographic processes occur quickly relative to regional dynamics and may be ignored, and 3) The presence or absence of a species must be able to be determined in discrete intervals. Additionally, Hanski (1997b) noted that 1) Patches must be able to support local breeding populations in which there is a possibility for local extinctions and local colonizations and 2) Habitat patches must be able to be delineated from the rest of the surrounding habitat. Moreover, the area of these patches must only be a portion of the entire area studied.

The second assumption enables us to ignore shapes of the patches and thus distance between any two distinct patches may be measured from the center coordinates of one patch to the other (Hanski et al., 2000). Moreover, the distance between center points can be determined by the Euclidean distance between the 2 points (Hanski, 1997b). Using a spherical distance measurement will not affect this study in a meaningful way. Thus, all patches were treated as circular, with larger circles denoting a patch with a larger area and smaller circles denoting a patch with a smaller area. A full description of the underlying mathematical model is presented in Appendix A.

For simplicity, we assumed no regional stochasticity, where regional stochasticity is spatially correlated environmental stochasticity that affects the quality of many or all patches simultaneously (Hanski, et al., 1996; Moilanen, 1999). Therefore, it is possible to parameterize the model using nonlinear regression within SPOMSIM. Also, we included the rescue effect and the improved connectivity function (A.1), as discussed in Appendix A. We use an independently estimated turnover rate of 6.6 years (Martinson, et al. 1961; Missouri Department of Conservation, http://mdc4.mdc.mo.gov/applications/mofwis/, Accessed 28 Jan 2009). A population turnover rate of 6.6 years is approximately 0.151515 events per year. Thus, we wish to optimize the parameter θ (the measure of dispersal) as well as parameters associated with the intrinsic extinction probability (u, x), the connectivity function (*b*) and the colonization function (*y*).

Nielsen et al. (2008), MacKenzie et al. (2003), and Pellet et al. (2007) expressed concerns with how the IFM treats false zeros: a patch is labeled as empty when an animal is actually present. Nielsen et al. (2008) circumvented this problem by using a population viability analysis when testing for occupancy of swamp rabbits. MacKenzie et al. (2003) required that detection/non-detection data be collected in addition to animal presence in order for false zeros to be accounted for. Pellet et al. (2007) state that by not accounting for errors in data collection, the Markovian assumption may be violated in that occupancy at time $t+1$ may not depend solely on time t. This results in overestimation of extinction probabilities and dispersal values (Moilanen, 2002). For simplicity, we assumed that sampling always produced the actual occupancy of swamp rabbits. The effect of this potential bias will be addressed in future work.

3. RESULTS AND DISCUSSION

3.1. Logistic Regression

We considered 4 possible logistic regression models for each survey year (1992 and 2001): Area Only, Isolation Only, Area and Isolation, and Area, Isolation and the Area by Isolation interaction term, where isolation was calculated as the distance of a habitat patch from either of the major swamp rabbit source populations (Donaldson Point or Mingo National Wildlife Refuge). Data were log transformed in all cases to minimize variance. Parameter estimates, odds-ratio estimates, the Wald Test, and Likelihood Ratio Test results are given in Table 1.

Patch area was significantly and positively related to occupancy during both survey years, but isolation alone was significant only during the 2001 survey, and then only with respect to Mingo National Wildlife Refuge. Similarly, when considered with patch area,

Table 1: Logistic regression results for the 1992 and 2001 surveys. Competing regression models are presented at left. Oc = occupancy (0, 1), A = area, I_{DP} = isolation from Donaldson Point, I_{mnwr} = isolation from Mingo National Wildlife Refuge. The Wald test assesses significance for each regression parameter, and the Likelihood Ratio test indicates overall model significance. Although estimates of the intercepts are not given here, in each case the parameter estimate was greater than its standard error.

Model	Parameter Estimates 1992 / 2001	1992 Wald Test $\left(\Pr > \chi^2\right)$	1992 Likelihood Ratio $\left(\Pr > \chi^2\right)$	2001 Wald Test $\left(\Pr > \chi^2\right)$	2001 Likelihood Ratio $\left(\Pr > \chi^2\right)$
Oc = A	0.5111 / 0.7789	<0.0001	<0.0001	0.0350	0.0280
Oc = I_{DP}	-0.0492 / -0.0980	NS	NS	NS	NS
Oc = I_{MNWR}	0.1905 / 0.6324	NS	NS	0.0004	0.0002
Oc = A + I_{DP}	0.5136 / 0.3035 -0.0653 / -0.1138	<0.0001 NS	0.0001	0.0330 NS	NS
Oc = A + I_{MNWR}	0.5194 / 0.3661 0.2346 / 0.6739	<0.0001 NS	<0.0001	0.0137 0.0001	<0.0001
Oc = A + I_{DP} + (A * I_{DP})	1.0299 / -0.0699 -0.1166 / -0.0795 -0.1128 / 0.0849	NS NS NS	0.0003	NS NS NS	NS
Oc = A + I_{MNWR} + (A * I_{MNWR})	0.9761 / 1.5192 0.2128 / 0.6272 -0.1116 / -0.2941	NS NS NS	0.0001	0.0223 0.0023 NS	<0.0001

isolation of a patch from a source population was significant only during the 2001 survey, and only with respect to Mingo National Wildlife Refuge. Although the overall models for 1992 (Mingo and Donaldson Point) and 2001 (Mingo only) were significant, the isolation term was significant only for Mingo NWR in 2001.

When area, isolation and the isolation by area interaction terms were incorporated into the models, isolation from Donaldson Point did not appear to be important. The overall model incorporating isolation from Donaldson Point was significant for 1992, but none of the regression coefficients was significant at the .05 level. In 2001, overall models incorporating isolation from Mingo NWR were significant, but individual regression coefficients were significant only for the 2001 model. Here, Area and Isolation were significant, but not the area by isolation interaction term. These results demonstrate that patch area and isolation of a patch from Mingo NWR are key predictors of patch occupancy for swamp rabbits in Missouri.

The portion of occupied patches was greater in 2001 than in 1992 (64% vs. 43%) and this may have contributed to the apparent stronger relationship between Log Area and occupancy for 1992. In 2001, patches with a small area were more likely to contain swamp rabbits. Moreover, in 1992, there were 109 occupied patches, but in 2001 there were 145. Because more patches were occupied in 2001, patch area would not necessarily have to be large to contain swamp rabbits. This may explain the decreasing odds of finding swamp rabbits between 1992 and 2001. For example, in the Area only model, the odds of finding a swamp rabbit decreased from 66.7% to 34.8% as Log Area changed between 1992 and 2001 respectively. Thus, variation in patch size may not be as important in 2001 as in 1992.

Log Isolation was important only with respect to isolation from Mingo National Wildlife Refuge in 2001. This may be a consequence of greater connectivity between habitat patches along the Mississippi River and consequently, less isolation from Donaldson Point, and/or greater fragmentation of habitats near Mingo NWR. Because Mingo NWR is hydrologically maintained, habitat quality in this area may influence incidence of swamp rabbits. No estimates of habitat quality were made in this study. Incorporation of habitat quality in the model may improve estimates of the odds of incidence in the logistic regression model. Occupancy of neck patches (see Figure 2) may play a role in the importance of Log Isolation. These patches were occupied in 2001 but not 1992. Again, this may be a consequence of greater connectivity of habitat patches along the Mississippi River.

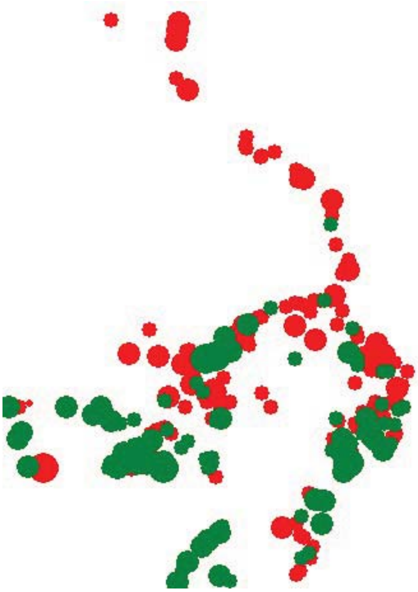

Figure 2. Network in 1992 which includes all possible habitat patches. Green circles represent areas where swamp rabbits were found. Red circles indicate where the rabbits were not present. Circle sizes are proportional to their respective areas.

3.2 Incidence Function Model

The IFM was parameterized initially using only patch locations from the 1992 survey (Table 2). Here, parameters *u,* and *x* for the extinction probability function, *y* for the colonization probability, *b* for the connectivity function and θ describing the dispersal kernel are given in Table 2, and described more fully in the Appendix. Under this parameterization, the population of swamp rabbits was simulated to go extinct after 2 years, although the observed Missouri metapopulation persisted through 2001. Consequently, the model was modified by removal of some peripheral habitat patches located far from other more tightly clustered patches. The removed patches were the neck patches shown in Figures 2 and 3. The subsequent parameter values for the model with neck patches removed are shown in Table 2. No dispersal distances are published for *S. aquaticus*, and thus we used estimates for *Sylvilagus palustris*, the marsh rabbit (Bowman et al., 2002; Nielsen et al., 2008). Thus our estimated θ of about 0.04 provides a maximum distance of about 25 km, which seems to be a reasonable assumption.

Table 2: Parameter estimates for the Incidence Function Model. Here, ***θ*** is the dispersal kernel, and *b and y* are parameters for the connectivity and colonization functions respectively. The extinction probability function is defined using parameters *u* and *x.* The reparameterization for 1992 was based on removal of neck patches. Subsequent surveys in 2010 and 2011 suggest swamp rabbits have been extirpated from the neck patches.

Parameter	Initial Parameterization for 1992	Reparameterization for 1992	Reparameterization for 2001
Dispersal Kernal: *θ*	0.04166104	0.03966842	0.04
b	0.5667602	0.2226194	0.1665934
y	32.61398	544.7305	9.8728
u	4.753427	0.0004259	21.33202
x	0.2216994	0.7007647	1.300078

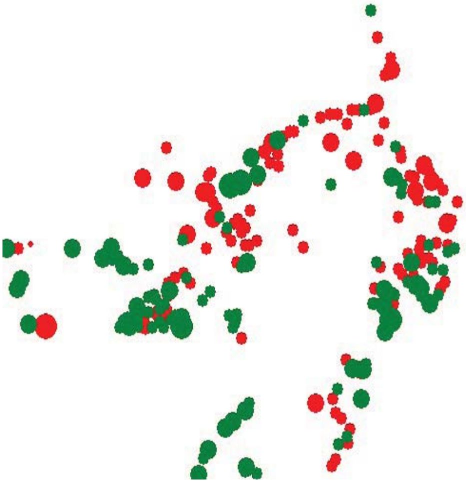

Figure 3. Deleted Patch Network in 1992. Green circles represent occupied patches and red circles represent empty patches.

We used the same approach to parameterize the 2001 model. Originally, these data were parameterized using all available patches (226). However, this resulted in an estimate for θ equal to 0, indicating an infinite dispersal distance. Because *S. aquaticus* is unlikely to disperse more than 25 km, we modified the model in the same manner as the 1992 model; the new parameter values are provided in Table 2. However, even under this regime, the dispersal distance is about 1566 km. Thus, we fix theta at 0.04 giving a dispersal distance of 25 km.

We simulated the metapopulation over 9 years using all data from 1992, but using the parameter estimates based on exclusion of the neck patches. In this way, it was possible to determine how the proportion of occupied patches and area differed between the predicted and observed values for 2001. The results are shown in Table 3 and Figures 4 and 5. Predicted occupancy for 2001 was smaller than observed occupancy. This may be a consequence of greater sampling intensity during the 2001 study (Henson, 2002; Scheibe and Henson, 2003). Also, sites located in the neck that were initially classified as containing swamp rabbits were later reclassified as empty based on pellet mass, that is, the pellets were produced by a non-target species (Henson, 2002). At the same time, predicted proportion of occupied area was within 2 standard deviations of the observed 2001 value. While the proportion of occupied patches did not fall within these bounds, predicted proportion of occupied area fell within acceptable limits.

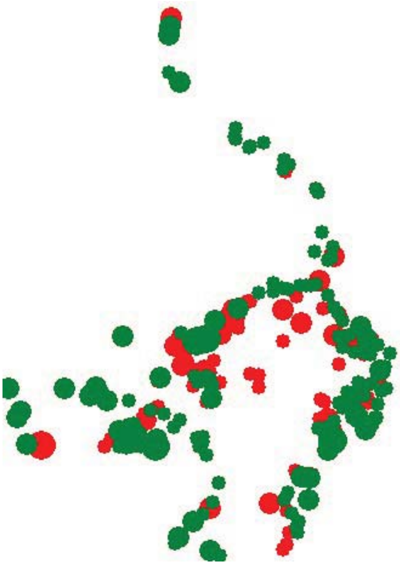

Figure 4. 2001 Actual Occupancies. Green circles represent patches that are occupied. Red circles represent patches that are empty.

Table 3: Proportion of patches occupied in 1992, and the predicted and observed values for 2001. Standard deviation of the estimate is given in parentheses.

	1992 actual	2001 estimated	2001 actual
# patches	253	253	226
Proportion of Patches Occupied	0.43083 (0.03113)	0.537 (0.03135)	0.641593 (0.03190)
Proportion of Area Occupied	0.67245 (0.02951)	0.731 (0.02788)	0.759862 (0.02841)

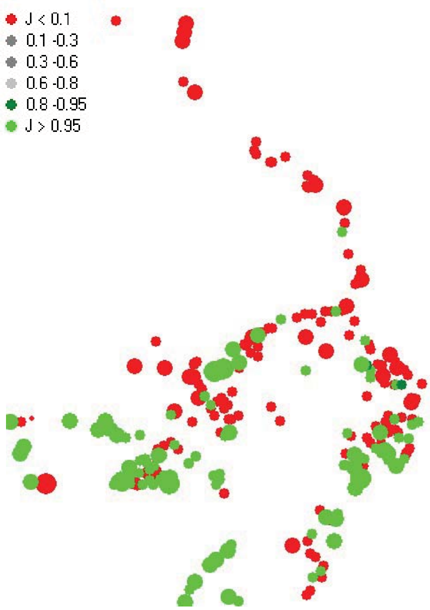

Figure 5. 2001 Estimated Occupancies. Green circles represent patches that have a higher probability of occupancy. Red patches represent patches with a low probability of occupancy.

Next, we used only patches that were sampled in both years to compare predicted 2001 occupancy with observed occupancy (Table 4). Here, 57% of the 216 patches showed a match between predicted and observed occupancy. Of the patches that did not match, 73% were predicted to be empty but were actually occupied and 27% were predicted to be occupied but were empty (see Table 4). Thus, the model underestimated the number of patches that should be occupied. Again, this may be a consequence of the increased sampling effort employed for the 2001 survey.

Table 4: Comparison of observed and estimated patch occupancy for 2001.

Observed 2001 vs Estimated 2001	
Total Same:	124
Total Changed:	92
Total Patches	216
Proportion Stayed Same:	0.574
Proportion Changed:	0.426
Patches that were the same between 2001 estimated and 2001 actual	
Number Occupied:	71
Number Empty:	53
Proportion Occupied:	0.573
Proportion Empty:	0.427
Total Patches	124
Patches that were different between 2001 estimated and 2001 actual. 0 = empty; 1 = occupied	
Number Changed from 0 to 1:	67
Number Changed from 1 to 0:	25
Proportion 0 to 1:	0.728
Proportion 1 to 0:	0.272
Total Patches:	92

We used SPOMSIM, to study the system over periods of 25, 50, 100, 400, and 1000 years, beginning from both 1992 and 2001. In each case, the system persisted over the 1000 year interval (Figures 6 and 7), although predicted occupancies were different. The simulation that began in 2001 resulted in occupied swamp rabbit patches clustered around Mingo National Wildlife Refuge and Donaldson Point (see Figure 1 for locations of Mingo NWR and Donaldson Point). Again, this may be a consequence of greater sampling effort during the 2001 survey, but suggests too that swamp rabbit incidence may have been underestimated in 1992.

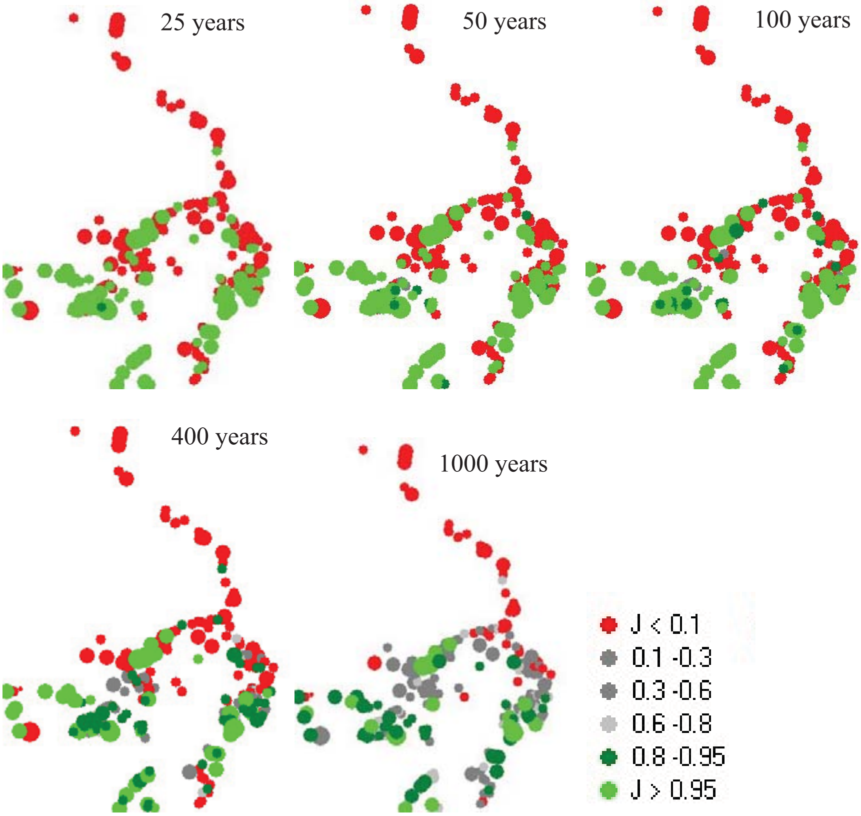

Figure 6. Patch Incidences 25-, 50-, 100-, 400-, and 1000- years after 1992. Incidence is color coded, as shown in the key at lower right.

The average proportion of patches occupied 1000 years after 2001 is stable over the time interval, with approximately 70%, occupancy fluctuating between 60 and 80%. This result differs markedly when the 1000 year simulation begins in 1992. Here the initial occupancy was 43% and increased steadily over 1000 years to about 50%. If the 1992 incidence values were underestimated, the increased proportion of patches occupied may have reached an equilibrium. The 2001 simulation results suggest the system was at or near equilibrium at the start.

4. CONCLUSIONS

We modeled the incidence of swamp rabbits using 2 approaches: logistic regression and the incidence function model. Both models estimate the incidence of swamp rabbits and both can be used to predict where swamp rabbits are likely to occur. The best logistic regression model for predicting the incidence of swamp rabbits in 1992 included Area and isolation from Mingo NWR. For

2001 the best model included the interaction of Area and isolation from Mingo NWR. While the logistic regression model incorporated only 2 explanatory variables the incidence function model took into account the distance between any 2 patches, the area of each habitat patch, and extinction and colonization rates. In addition, the IFM was able to predict incidence for each patch from 1992 to 2001, and over an interval of 1000 years. Overall, the IFM makes it possible to conclude that swamp rabbits will persist in Missouri for a long time if conditions of patch size and dispersion remain constant.

Our IFM did not include regional stochasticity, or spatially correlated environmental stochasticity affecting the quality of many or all patches simultaneously (Moilanen, 1999). To account for this, parameterization using a Monte Carlo estimation that includes regional stochasticity and the equilibrium assumption may improve parameter estimates leading to greater accuracy.

It is important to consider false zeros, or the possibility that an animal was present in the patch but the patch was marked as empty. MacKenzie et al. (2003) discussed the importance of incorporating this measure into the incidence function model, or the model will likely underestimate occupancy and deliver biased estimates in relation to colonization and extinction probabilities. Also, the incidence function model should incorporate some measure of habitat quality. Because SPOMSIM is able to include this component, it would be valuable to incorporate habitat quality data, perhaps derived from GIS models, in future simulations of this system.

Finally, we assumed that all habitat patches were incorporated in the analysis. This is unlikely to be true, and in fact recent reports to the Missouri Department of Conservation suggest possible occupied habitat patches in St. Louis Co. Also, more patches of swamp rabbits exist in nearby states including Indiana, Illinois and Arkansas. Data from these areas should be incorporated to further improve the models, and improve parameter estimates.

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Appendix A: Incidence Function Model Mechanics

From the assumptions of this model, it is possible to measure the presence or absence of a species in discrete time intervals, by denoting the first year by time t and the next successive year by time $t+1$. Each individual time will have its own respective colonization and extinction probabilities, represented by C_i and E_i, where i is any patch within the metapopulation. For example, if a population is occupied in time t, then it has a probability of extinction of E_i in time $t+1$. Assuming that the probabilities of colonization and extinction are constant, this is an example of a linear first-order Markov chain with the states of present or absent (Hanski, 1994; Hanski, 1997b; Hanski et al., 1996; Moilanen, 1999).

Now, let J_i be the incidence of stationary probability that patch i is occupied, where $J_i = \dfrac{C_i}{C_i + E_i}$ and C_i is the colonization probability of patch i and E_i is the extinction probability of the same patch i. To calculate the extinction probability of a patch i, it must be assumed that all patches have the same quality (Hanski, 1994). Because the patches have the same quality, then they must also have the same equilibrium density of a specific species. Now, extinction probability likely depends on population size, so extinction probability is a function of the area of the patch. Hence,

$$E_i = \frac{u}{A_i^{\,x}}, \quad \text{if } A_i > u^{\frac{1}{x}}$$

and

$$E_i = 1, \quad \text{if } A_i \le u^{\frac{1}{x}},$$

where $u \,\text{and}\, x$ are constants, and A_i is the area of patch i. The parameter x explains how extinction risk depends on patch size, which, in turn, explains its dependence on population size (Hanski, 1994). To further simplify the extinction probability when the parameters are unknown, it is necessary to take the minimum of the two values for the extinction probability. In other words,

$$E_i = \min\left(\frac{u}{A_i^{\,x}}, 1\right)$$ (Hanski, 1997a,b; Hanski et al., 1996).

The colonization probability depends upon the number of individuals that migrate to the population per year, which will be denoted by M_i. Complications arise in the computation of M_i because every year the number of immigrants into the patch will vary. However, this variation will be small and thus can be ignored in the calculations of M_i. Therefore, treat M_i as a constant in the calculation of the colonization probability (Hanski, 1994). In addition, it is also necessary to assume that immigrants will interact with each other; if no interaction were assumed, then new populations would be established every time an individual emigrated from the original population. Hence,

$$C_i = \frac{M_i^{\,2}}{M_i^{\,2} + y^2}$$

calculates the colonization probability as an S-shaped curve between 0 and 1. In this equation, M_i is as stated above and y is a parameter that will determine how fast the colonization probability reaches 1.

Now, the number of immigrants into a population depends on how well that particular patch is connected to the rest of the patches in the metapopulation. If a patch is not well connected, that means that there will be a smaller number of immigrants to that patch. Similarly, if a patch is well connected to other patches, then there will be a larger number of immigrants that will arrive in that patch. If the connectivity of a patch is denoted by S_i, then

$$M_i = \beta S_i ,$$

where β is a product of "the (constant) density of individuals in the patches, the rate of emigration (the fraction of individuals leaving their natal patch), and the fraction of emigrants moving from patch j in the direction of patch i" (Hanski, 1994) and

$$S_i = \sum_{j \neq i} p_j \exp\left(-\theta d_{ij}\right) A_j .$$

It is important to note that the sum in the above equation is taken over all patches where patch j does not equal patch i. Also, p_j equals 0 when the patch is not occupied in year t and p_j equals 1 when the patch is occupied in year t, d_{ij} is the shortest distance between two patches i and j where $i \neq j$, A_j is the area of patch j, and θ is a constant that determines the survival rate of the individuals migrating from patch i to patch j.

To help improve the quality of this model, it can be refined by taking into account the rescue effect "for a metapopulation with moderate or high turnover" (Moilanen, 1999). A rescue effect occurs when the immigration rate is high, thereby reducing the extinction rate. Moreover "a high immigration rate also will have a statistical effect in reducing the apparent extinction rate simply by decreasing the probability that a given species will be absent during any census" (Brown and Kodric-Brown, 1977). Thus

$$J_i = \frac{C_i}{C_i + E_i - C_i E_i} ,$$

where $C_i E_i$ is the rescue effect.

Therefore, by all of the above assumptions, the incidence of a patch i is given by

$$J_i = \left(1 + \frac{uy'}{S_i^{\ 2} A_i^{\ x}}\right)^{-1},$$

where $y' = \left(\frac{y}{\beta}\right)^2$. All of the parameters of this model are able to be estimated with a “snapshot of patch occupancies” (Hanski, 1998; Hanski et al., 1996; Wahlberg et al., 1996). That is, it is possible to take information about patch occupancies in a single survey to estimate the parameter values.

Moilanen and Niemienen (2002) made the interesting point that the connectivity function can be enhanced by adding the effect of a focal patch. This additional measure scales immigration with the focal patch area by parameter b, and hence, connectivity becomes

$$S_i(t) = \sum_{i \neq j} p_j(t) \exp(-\theta d_{ij}) A_j^b \quad \text{Eq. (A.1).}$$

Moilanen and Hanski (2001) and Moilanen and Nieminen (2002) improved the connectivity measure further by adding a constant that scales emigration with focal patch area: parameter c. By using this information, accuracy of the measurement of patch connectivity can be improved. Thus, the connectivity function is

$$S_i(t) = A_i^c \sum_{i \neq j} p_j(t) \exp(-\theta d_{ij}) A_j^{\ b}.$$

For the purposes of this study, we used (A.1) for the measure of connectivity so there is less error introduced in having to calculate the value of an additional parameter.

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