Swamp Rabbit Distribution on the Northern Edge of their Range in Missouri

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Abstract - Sylvilagus aquaticus (Swamp Rabbit) is an imperiled species in Missouri that inhabits highly fragmented bottomland forested habitats in the southeastern portion of the state. Between 2010 and 2012, we conducted repeated, extensive presence–absence winter-latrine surveys in 15 counties to document their distribution. We compared our results to those of 2 previous winter-latrine surveys (2001–2002 and 1991–1992) conducted at the same sites. In addition, we used the Program MARK to estimate detection probability and site occupancy, and evaluate the influence of survey-site size on detectability and occupancy, and temperature at the time of the survey on detectability. We located 264 of 278 survey sites that were first surveyed in 1991, but could only survey 211. We detected Swamp Rabbits at 144 of 211 sites in 12 counties yielding a naïve occupancy estimate of 0.68. This estimate was higher than reported by both previous surveys: 0.53 in 2001–2002 and 0.40 in 1991–1992. Using occupancy modeling for the 2010–2012 survey, the estimated detection probability was 0.89 (SE = 0.02) and site occupancy was 0.70 (SE = 0.03). As expected, the size of a survey site influenced both detectability of and occupancy by Swamp Rabbits, and temperature influenced detectability. As the size of a site increased, both detectability and occupancy increased, and detectability increased as temperature decreased. Swamp Rabbits continue to occur in 13 counties and occupy fragmented, sometimes isolated blocks of bottomland forested habitat across the Mississippi River Alluvial Basin and along some Ozark Highlands streams.

Introduction

Loss and fragmentation of bottomland forested habitats have contributed to decreases in wildlife populations, including Sylvilagus aquaticus (Bachman) (Swamp Rabbit). These lagomorphs occur in 15 states across the southeastern US, where they inhabit bottomland forests, floodplains, marshes, swamps, and along the shores of lakes, rivers, and streams (Allen 1985, Chapman and Feldhamer 1981). Their global conservation status is considered of least concern and secure, but their distribution and abundance have declined, especially in states along the northern periphery of their range (IUCN 2017, NatureServe 2017).

Survey and monitoring programs are necessary to determine the conservation status of species, track changes in their distributions, and evaluate the effectiveness of management practices or other initiatives. To better understand the continuing threats to this imperiled species, we conducted repeated, extensive presence–absence winter-latrine surveys in 15 counties to document their distribution.
of management actions. These programs are especially important when the species of interest is of conservation concern on the edge of its range where these taxa are often classified as rare with scattered populations across less suitable habitat (Steen and Barrett 2015). Naïve occupancy estimates from surveys with only 1 visit to each survey site assume complete detectability, e.g., if the species is present it will be detected directly or indirectly via its sign. Wildlife species are rarely detected with perfect accuracy, and non-detection does not necessarily mean that a species was absent (Amstrup et al. 2005). The incorporation of occupancy modeling into monitoring programs helps to solve problems created by imperfect detection by using presence/absence information from repeated visits to each survey site to estimate detection probability (\(p\)) and occupancy (\(\Psi\); the probability that a species is present at a site or the proportion of sites occupied by a species). Information about site or survey characteristics (covariates) that could cause variation in either detectability or occupancy are incorporated into the models and inferences can be made about those covariates. Therefore, occupancy modeling is an improvement on naïve estimates of occupancy by incorporating detection probability and covariate information in order to derive more rigorous occupancy estimates and greater confidence in observed changes over time or responses to management activities.

The northern range of the Swamp Rabbit extends along watersheds of the Mississippi and Ohio rivers. Extreme southwestern Indiana is the northern limit of their range and coincides with the northern limit of the southern swamp-forest community type (Allen 1985, Chapman and Feldhamer 1981). Here, and in other states on the northern edge of their range (Illinois, Kentucky, Kansas, and Missouri), the species’ decline has been associated with anthropogenic influences including habitat loss (i.e., draining of swampy areas, clearing of floodplains, damming of rivers), degradation, and fragmentation (Barbour et al. 2001, Dailey et al. 1993, Korte and Fredrickson 1977, Roy Nielsen et al. 2008, Scheibe and Henson 2003, Sole 1994, Terrel 1972). In Indiana, there has been a reduction in their range and a general decrease in population size; most Swamp Rabbits currently occur in 2 southwestern counties (Roy Nielsen et al. 2008, Terrel 1972, Whitaker and Abrell 1985). In Illinois, Swamp Rabbits were once distributed throughout most of the southern portion of the state but have a much more restricted, patchy distribution today (Barbour et al. 2001, Kjolhaug et al. 1987). Swamp Rabbits historically occurred in the western third of Kentucky and are still widely distributed throughout much of this range, but the species has been extirpated from parts of 13 counties and the overall population trend has been downward due to habitat loss (Sole 1994). Swamp Rabbits are considered species of conservation concern within these states and are listed as critically imperiled and state endangered in Indiana and vulnerable in Illinois and Kentucky (NatureServe 2017). They are probably extirpated from Kansas, where they historically occurred in the extreme southeastern portion of the state (DeSanty-Combes et al. 2002, Hibbard 1943, NatureServe 2017). Swamp Rabbits are still legally harvested in Illinois, Kentucky, and Missouri.

Southeast Missouri is on the northern periphery of the Mississippi River Alluvial Valley (MRAV), which includes the floodplain of the Mississippi River.
extending from just south of Cape Girardeau, MO, through portions of 7 states to
the Gulf of Mexico, and encompasses all or part of 10 Missouri counties (Fig. 1;
Nigh and Schroeder 2002). Prior to European settlement, bottomland hardwood
forests covered nearly 10 million ha of the entire MRAV landscape (King et al.
2006). Following widespread clearing of trees and draining of wetlands, primarily
for lumber, agriculture, and navigation projects, only about 2.8 million ha of mostly
highly fragmented bottomland forests remain today (King et al. 2006). Destruction
and modification of forested wetlands have been more extensive in the northern
sections of the MRAV compared to more southern sections (Heitmeyer et al. 1989).

In 1934, Swamp Rabbits were widely distributed throughout 21 southern Mis-
souri counties but were decreasing in number (Bennitt and Nagel 1937). Most
occurred within the Mississippi River Alluvial Basin of southeastern Missouri, but
they were also found in a few counties north along the Mississippi River and west
along southern Ozark Highlands streams. The Swamp Rabbit remained a locally
abundant and popular game species in the late 1950s (Toll et al. 1960), but by 1967
continued habitat loss had greatly reduced its range, and the small, localized popu-
lation in extreme southwestern Missouri was extirpated (Sadler 1969, K.C. Sadler,
Missouri Department of Conservation, Jefferson City, unpubl. data). Korte and
Fredrickson (1977) reported that the amount of suitable Swamp Rabbit habitat in 11
southeastern Missouri counties had declined from 850,000 ha in 1870 to <40,000 ha
in 1973. Just 10 counties and about half of the suitable habitat had Swamp Rabbits,
and only remnant populations remained in 5 of those counties. In 1974, the Swamp
Rabbit was listed as rare in Missouri (Missouri Department of Conservation and US
Department of Agriculture Soil Conservation Service 1974).

Extensive conversion of wetlands to agricultural and other uses over the last
100 years dramatically altered the southeast Missouri landscape; thus, the preva-
ience of bottomland forested habitats continued to decline, and Swamp Rabbits
remained listed as rare. The Missouri Department of Conservation (MDC) initiated
their first extensive winter-latrine survey (278 study sites in 15 counties) in 1991 to
determine the distribution of Swamp Rabbits and their habitat. Dailey et al. (1993)
reported that Swamp Rabbits occurred in 12 of those 15 counties and estimated that
45,218 ha of highly fragmented habitat suitable for Swamp Rabbits remained. Ten
years later, biologists from MDC and Southeast Missouri State University (SEMO)
resurveyed most of those same sites to document any changes in the distribution of
Swamp Rabbits and found sign in 11 of 15 counties (Scheibe and Henson 2003).

Today, the Swamp Rabbit is listed as a Missouri imperiled species of conserva-
tion concern and a species of greatest conservation need in the southeast Missouri
wetland natural communities (MDC 2015, 2017) where an estimated 40,000 ha
of suitable habitat remains as mostly small, fragmented patches (Warwick 2003).
In 2010, the MDC and SEMO continued their long-term monitoring commitment
and resurveyed the Swamp Rabbit study sites, but incorporated repeated visits to
individual sites and occupancy modeling. The objectives of this survey were to (1)
compare current occupancy of the survey sites to the results from the 1991–1992
and 2001–2002 surveys, (2) estimate detectability and occupancy for the 2010–
2012 survey, (3) determine if survey site area influences occupancy by Swamp Rabbits and if survey site area and temperature influence detectability, and (4) update the Missouri Swamp Rabbit range map.

**Field-Site Description**

We located 264 of the 278 southeast Missouri study sites identified prior to the 1991–1992 survey (Fig. 1). We found that 14 of the original sites, varying from 17.9 ha to 70.5 ha, were either cleared for agricultural use or homes, or could not be identified based on their previous site descriptions. Criteria for identifying the original 278 survey sites included: bottomland hardwood forests with ≥25% canopy cover of woody vegetation, hydric soils, periodic flooding, and an area of ≥16.2 ha in 1989 (Dailey et al. 1993). Researchers chose a minimum size of 16.2 ha based on input from federal and state natural resources agencies staff who speculated at that time that forest blocks as small as 16.2 ha could sustain Swamp Rabbits. Sites varied from 16.2 ha to 4609.2 ha and totaled 34,812 ha, with site boundaries based on presence of barriers that would diminish a Swamp Rabbit’s ability to travel (e.g., rivers, major highways, and large crop-fields). The smaller sites were mostly privately owned, and the largest sites were mostly publicly owned (Table 1). Most sites were isolated by crop fields.

We differentiated survey sites from habitat patches or forested blocks, and defined a patch or block as a continuous, unbroken area of potential Swamp Rabbit habitat and a site as a discrete parcel of land we surveyed. Some forest blocks represented 1 site, whereas some of the larger blocks were divided into multiple sites. We used ArcGIS 9.3 to estimate the total area of a site (ESRI 2008). Elevation at survey sites varied from 73 m to 274 m.

Two hundred and three sites were within the Mississippi River Alluvial Basin ecological section. Sites varied in size from 16.3 ha to 4609.2 ha and totaled 29,169 ha. The topography of the area is gently undulating to flat, with low ridges rising a few meters above the plains. Elevation at survey sites varied from 73 m to 122 m. Formerly, most of this area was a vast forested swamp of *Taxodium distichum* (L.) (Bald Cypress), *Liquidambar styraciflua* L. (Sweetgum), and associated plants (Nigh and Schroeder 2002). Extensive timber harvest in the mid- to late 1800s followed by land drainage and flood-protection projects in the early 1900s resulted in an extensive network of diversion channels, drainage ditches, levees, and catch-basins; virtually the entire Basin was converted to cropland. The remaining bottomland forests were mostly mixed *Quercus* spp. (oak) and *Carya* spp. (hickory)

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**Table 1.** Total number of 2010–2012 Missouri Swamp Rabbit survey sites grouped by size and ownership (public or private). Size categories are based on survey methodology.

<table>
<thead>
<tr>
<th>Ownership</th>
<th>≤40.5 ha</th>
<th>&gt;40.5 ha and &lt; 405 ha</th>
<th>≥405 ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Public</td>
<td>11</td>
<td>39</td>
<td>10</td>
</tr>
<tr>
<td>Private</td>
<td>110</td>
<td>65</td>
<td>6</td>
</tr>
</tbody>
</table>
Figure 1. Study-site locations and results for the 2010–2012 Missouri Swamp Rabbit survey (n = 264 survey sites). + = Swamp Rabbit or sign was detected at that site, x = indicates that Swamp Rabbit or sign was not detected at that site, and o = no survey was conducted at that site. Major streams are identified. The dark solid line separates the Ozark Highlands and Mississippi River Alluvial Basin ecological sections.
interspersed with Bald Cypress and *Nyssa* spp. (tupelo) swamps and mixed emergent marshes, or fragmented mixed Riverfront forest.

Thirty-five sites were within the Ozark Highlands ecological section along the Mississippi River north of the Mississippi River Alluvial Basin, with sizes varying from 16.2 to 451.9 ha (total area = 2865 ha) and elevations varying from 98 m to 168 m. Pre-settlement vegetation included both timber and wet prairie, but most was cleared and replaced with row crops (Nigh and Schroeder 2002). A fragmented mixed Riverfront forest remained. Only the lowest, wettest areas and those unprotected by levees had small, isolated patches of natural vegetation.

The remaining 26 sites were within the Ozark Highlands ecological section west of the Mississippi River Alluvial Basin mostly along the mid- to lower reaches of major streams, with sizes varying from 17.8 to 1176 ha (total area = 2778 ha) and elevations varying from 98 m to 274 m. Sites were dominated by a mixed oak and Sweetgum bottomland forest along the St. Francis River, and mixed oak and *Acer saccharum* Marsh. (Sugar Maple) bottomland forests along the Current, Eleven Point, and Black rivers (Nigh and Schroeder 2002).

**Methods**

**Field sampling**

We modified the previous survey protocols in order to estimate detection probability and incorporate occupancy modeling (MacKenzie et al. 2002, 2006; Scheibe and Henson 2003). Unlike the previous 2 surveys, where sites were visited only once, we surveyed each site 3 times to minimize the effects of imperfect detection which can cause some sites to appear to be unoccupied when they are truly occupied.

Between 15 October and 15 March (2010–2011and 2011–2012), we surveyed 211 out of 264 sites for the presence of fecal pellets deposited on down logs or stumps. Some sites were inaccessible because of flooding or if the landowner refused access to the property. Winter-latrine surveys work especially well for rare or cryptic species such as the Swamp Rabbit. Swamp Rabbits prefer dense cover, which makes them difficult to locate, and they are not easily detected in roadside counts or captured in live traps (Schauber et al. 2008). Fortunately, they defecate large discoidal fecal pellets mostly on logs (frequently ones that are broad, moss-covered, and in advanced decay), but also on stumps and other non-log sites (e.g., elevated sandy mounds covered with moss) (Zollner et al. 1996). Zollner et al. (1996) reported that in Arkansas, Swamp Rabbits deposited >91% of their pellets on logs. These latrine sites are conspicuous, especially in winter, and latrine surveys and pellet counts are used across their range to determine presence and abundance (Roy Nielsen et al. 2008).

We visited each site 3 times within a 10-day period to meet the occupancy assumption of closure and to increase the probability that environmental conditions would remain relatively constant during the site-specific survey period (MacKenzie et al. 2006). Three independent observers assessed each site 1 time within the 2-y study period. To ensure reasonable independence between site observations, the observers did not communicate with each other between visits about the
presence or absence of sign at that site. We followed the 2001–2002 survey protocol for length of search time within a survey site. For sites ≤40.5 ha, an observer searched a site for up to 1 h. At larger sites (>40.5 ha and <405 ha), if sign was not detected after 1 hour, the observer moved to a different area of the site and searched up to 1 additional hour (up to 2 h total). At the largest sites (≥405 ha), if observers did not detect sign after 1 hour, they moved to a different area of the site and searched up to 1 additional hour. If no sign was detected after 2 h, the observer moved to another area of the site (different from the other 2) to survey for up to 1 additional hour (up to 3 h total). Each surveyor determined the area(s) within the site that would be searched. If a latrine was detected, the observer immediately left that survey site and the entire site was classified as occupied. Surveyors recorded the observer’s name, the temperature at the beginning of the site visit, detection histories (whether Swamp Rabbits were detected or not), UTM coordinates for latrines, and number of downed logs (<5 or ≥5) determined to be suitable for use by Swamp Rabbits as latrine sites. Taking care to leave some pellets are each latrine site, observers also collected a sample of the pellets for visual species confirmation by J.S. Scheibe. We waited for 3 days after a snow event to conduct our surveys.

Estimating detection probabilities and occupancy modeling

We included Swamp Rabbit detection histories from 208 survey sites to estimate detection probabilities and occupancy. As specified in the first objective, comparison between surveys was of foremost importance. Therefore, we analyzed information for only those sites that were also surveyed during at least 1 of the previous 2 surveys (208 instead of 211 sites).

Based on previous survey results, we predicted that Swamp Rabbits would be more likely to occupy larger sites compared to smaller sites (Root and Laatsch 2003, Scheibe and Henson 2003, Warwick 2003) and that detectability would be influenced by the size of a site. Environmental factors or survey conditions might also be important in detecting Swamp Rabbits. Winter temperatures in southeast Missouri can vary widely (temperatures during our study were as low as -11 °C and as high as 29 °C) and we also hypothesized that temperature might influence detectability. We originally planned to incorporate information about the presence or absence of suitable latrine logs into our models, but 99% of the site visits with latrine data had ≥5, so those data were not included. Thus, there are 2 covariates; size of the site (ha) and temperature at the time of the search (in °C).

We employed the Occupancy Estimation procedure in Program MARK to determine detection probability, occupancy, and covariate parameter estimations, as well as model comparisons using an information-theoretic approach (Burnham and Anderson 2002, White and Burnham 1999). For our analysis, we used the natural log of the area of a site because the large variation in the site sizes (16.2–4609 ha) caused the distribution of site size to be highly positively skewed. There were 6 sites that covered more than 809 ha each. In a regression analysis (including logistic regression), these values would be points of strong influence that may not represent the entire dataset. Taking the natural log of the total area had the desired
effect of reducing variance and minimizing the influence of a few points (Neter et al. 1985).

We considered models in which occupancy was assumed to be constant for all sites (Ψ(.)) or varied among sites according to site area (Ψ(LnHa)). Detection probability was either constant for all sites (p(.)), different among surveys (p(t)), or varied among sites according to site area (p(LnHa)) or temperature (p(temp)). We fitted to the data 6 candidate models with and 2 without covariates and ranked them according to Akaike’s information criterion (AIC; Table 2). There were 72 different observers with varying skill levels across both years, so adjusting detection by observer would be problematic especially with the lack of variation in detection histories (Table 3).

The first 2 surveys estimated occupancy from a single visit and assumed a detection probability of 1. This assumption makes comparisons between surveys problematic because the most recent survey had 3 visits for each location. Specifically, changes in observing Swamp Rabbit sign at a specific site could either be due to true changes in occupancy or a detection issue. Therefore, we made no attempt to estimate colonization or extinction rates using program MARK. As mentioned above, we compared overall changes in estimated occurrence to the previous 2 studies.

### Table 2. Model-selection results for detection probability (p) and occupancy (Ψ) for the 2010–2012 Missouri Swamp Rabbit survey. LnHa = the natural log of site area (ha), temp = temperature in °C at the time of the search, AICc = Akaike’s information criterion corrected for small sample size, ΔAICc = the difference between the model’s mean AICc value and the mean AICc value of the best fit model, K = the number of parameters estimated, and Weight = the weight of evidence for the model.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ψ(LnHa) p(LnHa+temp)</td>
<td>5</td>
<td>544.408</td>
<td>0.000</td>
<td>0.9905</td>
</tr>
<tr>
<td>Ψ(LnHa) p(temp)</td>
<td>4</td>
<td>553.739</td>
<td>9.331</td>
<td>0.0093</td>
</tr>
<tr>
<td>Ψ(α) p(temp)</td>
<td>3</td>
<td>561.337</td>
<td>16.929</td>
<td>0.0002</td>
</tr>
<tr>
<td>Ψ(LnHa) p(LnHa)</td>
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<td>570.189</td>
<td>25.780</td>
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<tr>
<td>Ψ(LnHa) p(α)</td>
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<td>584.212</td>
<td>39.804</td>
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<tr>
<td>Ψ(LnHa) p(t)</td>
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<td>43.703</td>
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</tr>
<tr>
<td>Ψ(α) p(α)</td>
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<td>591.719</td>
<td>47.310</td>
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</tr>
<tr>
<td>Ψ(α) p(t)</td>
<td>4</td>
<td>595.577</td>
<td>51.169</td>
<td>0.0000</td>
</tr>
</tbody>
</table>

### Table 3. Detection histories for Swamp Rabbits by visit (3 total visits per site) during the 2010–2012 Missouri survey. 1 = detection, 0 = nondetection, and NS indicates no survey for that visit.

<table>
<thead>
<tr>
<th>Visit 1</th>
<th>Visit 2</th>
<th>Visit 3</th>
<th>Number of sites</th>
</tr>
</thead>
<tbody>
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<td>1</td>
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<td>110</td>
</tr>
<tr>
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<td>0</td>
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</tr>
<tr>
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</tr>
<tr>
<td>0</td>
<td>0</td>
<td>NS</td>
<td>1</td>
</tr>
</tbody>
</table>
**Range estimation**

We used information from all 3 Swamp Rabbit surveys plus other smaller surveys, extant locations in the Missouri Natural Heritage database, harvest records, and input from conservation professionals to update the estimated range of the Swamp Rabbit in Missouri.

**Results**

**Comparison between surveys**

We surveyed sites initially identified in 1991 in order to make comparisons between surveys and found that most sites were consistently occupied or unoccupied over the 3 survey periods (Table 4). We detected Swamp Rabbits at 144 of 211 sites in 12 counties in 2010–2012, yielding a naïve occupancy estimate of 0.68 (Fig. 1). This estimate was higher than both previous surveys; 120 of 226 sites (0.53) in 11 counties in 2001–2002, and 104 of 260 sites (0.40) in 12 counties in 1991–1992. Had we made only 1 visit (instead of 3) to each site during the 2010–2012 survey (as in the previous 2 surveys), we would have documented Swamp Rabbits at 126 sites yielding a naïve occupancy estimate of 0.60 (Table 3). Of the 175 survey sites visited during all 3 surveys, Swamp Rabbit sign was found at 102 sites (naïve occupancy estimate = 0.58; detection only at first site visit) in 2010–2012, 93 sites (naïve occupancy estimate = 0.53) in 2001–2002, and 76 sites (naïve occupancy estimate = 0.43) in 1991–1992 (Table 4). We found Swamp Rabbit sign at 115 sites (naïve occupancy estimate = 0.66) during the 2010–2012 survey, when detection was positive for any of the 3 visits to a site.

**Occupancy modeling**

The best-fit model (99% of the weight) was for the model where Ψ varied across sites according to the site area and p varied across sites according to site area with additive temperature effects (Table 2). Estimated detection probability was 0.89 (SE = 0.02) when using averaged area and temperature, and site occupancy was 0.70 (SE = 0.03) when using averaged area. We did not conduct model averaging because the top model represented 99% of the weight. No other model showed strong evidence of support (ΔAIC<sub>c</sub> < 2) but the second best-fit model also indicated that site area influenced Ψ and temperature influenced p. The untransformed coefficients of covariates

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<tbody>
<tr>
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<tr>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
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</table>

Table 4. Detection histories for Swamp Rabbits at 175 sites that were visited during all 3 Missouri Swamp Rabbit surveys (1991–1992, 2001–2002, and 2010–2012). Total number of sites include detection histories from the 2010–2012 first site visit only. 1 = detection and 0 = nondetection.
estimated by MARK for $p$ was 0.528 (SE = 0.177) for log area and -0.104 (SE = 0.021) for temperature, and for $\Psi$ was 0.473 (SE = 0.172) for log area.

**Missouri distribution**

Swamp Rabbits continue to occur in habitat patches across the Mississippi River Alluvial Basin, especially along the St. Francis River, Mississippi River, and The Floodway ditches, on land in both public and private ownership (Fig. 2). They also continue to occur within riparian corridors along some Ozark Highlands streams.

**Discussion**

This study provides insights into Missouri Swamp Rabbits, especially over the last 20 years. Swamp Rabbits continue to occur in 13 counties and occupy fragmented, sometimes isolated blocks of bottomland forested habitat across the Mississippi River Alluvial Basin and along some Ozark Highlands streams. Unfortunately, these habitats continue to be susceptible to anthropogenic modifications (e.g., clearing for crop land or houses) and stochastic events (e.g., record flood events).

Figure 2. Estimated Missouri Swamp Rabbit range following the 2010–2012 Swamp Rabbit survey. Information from all 3 Swamp Rabbit surveys plus other smaller surveys, extant locations in the Missouri Natural Heritage database, harvest records, and input from conservation professionals were incorporated. Three core subpopulations within large blocks of bottomland forest centered around (1) Mingo National Wildlife Refuge and Duck Creek Conservation Area, (2) Donaldson Point Conservation Area, and (3) Coon Island Conservation Area are identified.
Pajda-De La O et al. (2013) described Missouri Swamp Rabbits as a metapopulation: disjunct subpopulations linked through dispersal with other areas of suitable habitat that are subject to localized extinction events and recolonization. We identified 3 core subpopulations within large blocks of bottomland forest centered around (1) Mingo National Wildlife Refuge and Duck Creek Conservation Area, (2) Donaldson Point Conservation Area, and (3) Coon Island Conservation Area. These larger tracts of public land likely function as source populations which help ensure the species’ persistence in the midst of anthropogenic disturbances.

Our results imply greater site occupancy when compared to the previous 2 surveys but this apparent growth may be the result of increased survey effort rather than a true increase in occupied habitats. We visited each site 3 times during the 2010–2012 survey versus only once in previous surveys. There were more detections in 2001–2002 when compared to 1991–1992, possibly because more time was spent within survey sites, especially in the larger blocks, or 2 major flooding events between 1992 and 2001 may have facilitated Swamp Rabbit dispersal (Scheibe and Henson 2003) or enhanced the habitat by killing overstory trees and creating canopy gaps important for Swamp Rabbits. Southeast Missouri experienced 2 additional major flooding events in 2002 and 2008 prior to the 2010–2012 survey.

Korte (1975) suggested that Missouri Swamp Rabbits utilize small habitat patches but require relatively large tracts of suitable habitat (≥100 ha) to maintain viable populations. Scheibe and Henson (2003) reported that Swamp Rabbits were detected in relatively small forest tracts, but data from their work and the 1991–1992 survey indicated that the chance of encountering Swamp Rabbit sign increased as forest-patch size increased. In addition, Root and Laatsch (2003) and Pajda-De La O et al. (2013) compared occupied versus unoccupied habitat patches for the 1991–1992 and 2001–2002 surveys and concluded that occupied patch area was significantly and positively related to occupancy. Warwick (2003), in a separate Missouri study, also reported that Swamp Rabbit presence was more likely as the area of the forested patch increased. Warwick (2003) reported that Missouri Swamp Rabbits preferred natural forest remnants with >20% forest cover when compared to agroforestry plantings and strip cover, and that these natural forest remnants often are the largest habitat patches remaining in southeast Missouri. In addition, these natural forest remnants contained more *Arundo donax* L. (Giant Cane), a plant used by Swamp Rabbits for food and cover, and a greater density of latrine logs when compared to agroforestry patches and strip cover. Our results suggest that both occupancy and detectability increase as the size of a survey site increases, and Swamp Rabbits appear to be more abundant on the larger tracts. It is important to note that detection probability can vary among sites not only in response to measurable covariates, but also due to variation in abundance among sites (Royle and Dorazio 2008), i.e., the more individuals in an area the more likely the species will be detected.

Swamp Rabbits also used some of the smallest sites that we surveyed. These small forest blocks may act as sink populations, yet they might be important for
dispersal when adjacent to larger blocks of suitable habitat. Unfortunately, there continue to be losses of these smaller, mostly privately owned forest blocks, and management options for bottomland species are limited on those small parcels. Dailey et al. (1993) stated that most private land within Missouri’s Swamp Rabbit range is unsuitable for Swamp Rabbits partly because of small size but also because of inferior forested habitat or lack of suitable habitat on adjacent land (e.g., absence of woody corridors, presence of row crops), or both.

Most of the largest remaining habitat patches in southeast Missouri are publicly owned and are managed for bottomland hardwood forest and other wetlands, but a few are privately owned and managed for commercial timber. If private landowners continue to convert bottomland forests to agricultural or other land uses, Swamp Rabbits may become confined to mostly public lands and narrow, forested riparian corridors along some Ozark Highlands streams. Fortunately, there are public–private partnerships through government incentive programs, most notably the USDA Wetland Reserve Program and Conservation Reserve Program, that encourage removal of marginal farmland from agricultural production, reforestation of bottomland habitats, and restoration of wetlands.

Detectability may also be related to characteristics of a survey on a particular day, such as weather conditions. Identifying the optimal survey conditions for detection should increase the reliability of survey data and occupancy estimates, and better guide management actions. For example, our data indicate that as temperature decreased, our detection of Swamp Rabbit latrines increased. There are several plausible explanations for this increase: the senescence of lush vegetation as temperatures decreased makes pellets more visible; pellets decompose slower and persist longer in colder temperatures; and decaying logs often contain abundant populations of insects that consume feces, and these populations are less abundant and active during colder weather (Cochran and Stains 1961, Zollner et al. 1996).

Detection probabilities, occupancy estimates, and habitat characteristics that influence occupancy and detectability, including site area, have been reported for other states on the northern edge of Swamp Rabbit range. In Illinois, Porath (1997) reported that unoccupied sites were smaller (mean = 307.7, min–max = 29–1491 ha) than occupied sites (mean = 654.8, min–max = 23–3904 ha) (P = 0.059). Scharine et al. (2011) live-trapped 27 early-successional bottomland forests (agricultural lands recently afforested via federal farm programs) for Swamp Rabbits in southern Illinois and reported 71% of sites occupied and a detection probability of 0.12 (SE = 0.03). Canopy closure and site area had the most influence on detection probability; canopy closure positively influenced detection, but site area negatively influenced detection. Our survey sites did not include recently afforested land but these habitats do exist in southeast Missouri, and some should be incorporated into future survey efforts. In Indiana, Roy Nielsen et al. (2008) conducted latrine surveys and reported that patches occupied by Swamp Rabbits were significantly larger than unoccupied patches. Averaging over all models, occupancy was estimated to be 0.35 (95% CI = 0.14–0.63) and detection probability was 0.70 (95% CI = 0.40–0.89).
The results of this survey support the continued use of winter-latrine surveys with multiple site visits for monitoring this species and its habitats to detect changes over time and adjust management activities if needed. The incorporation of additional environmental factors and microhabitat characteristics into occupancy models are essential to determine key habitat components ecologically important for Swamp Rabbits inhabiting fragmented habitat patches on the northern edge of their range.

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Literature Cited


