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Distribution Dynamics of Swamp Rabbits (Sylvilagus aquaticus) in Missouri

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DISTRIBUTION DYNAMICS OF SWAMP RABBITS (*SYLVILAGUS AQUATICUS*) IN MISSOURI

by

Kylie Bosch

B.S., Grand Valley State University, 2017

A Thesis
Submitted in Partial Fulfillment of the Requirements for the
Master of Science Degree

School of Forestry and Horticulture
in the Graduate School
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THESIS APPROVAL

DISTRIBUTION DYNAMICS OF SWAMP RABBITS (*SYLVILAGUS AQUATICUS*) IN MISSOURI

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A Thesis Submitted in Partial

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Master of Science

in the field of Forestry

Approved by:

Dr. Brent Pease, Chair

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Graduate School
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May 2, 2024

AN ABSTRACT OF THE THESIS OF

Kylie J. Bosch, for the Master of Science degree in Forestry, presented on May 2, 2024, at Southern Illinois University Carbondale.

TITLE: DISTRIBUTION DYNAMICS OF SWAMP RABBITS (*SYLVILAGUS AQUATICUS*) IN MISSOURI

Major Professor: Dr. Brent Pease

Swamp rabbits (*Sylvilagus aquaticus*) are a bottomland hardwood forest specialist undergoing contraction at the northern extent of their range. This decline is often attributed to the loss of bottomland hardwood forest and frequent, intense flooding. To mitigate this decline and inform decisions regarding the swamp rabbit's conservation status, there is a pressing need for long-term monitoring efforts. Although currently listed as imperiled (S2) in Missouri, shifts in occupancy trends may warrant a reassessment of the swamp rabbit's state rank. The Missouri Department of Conservation has conducted decadal surveys for swamp rabbits since 1991, and the work presented here describes the fourth iteration of this study – 2022-2023. Repeated latrine surveys at 176 previously surveyed sites were conducted from November 2022 – April 2023 across 16 counties in southeast Missouri. Dynamic occupancy models were then used to estimate occupancy, colonization, extinction, and detection probabilities and identify environmental factors driving distribution changes since 2012. Additionally, I examined the impact of including ground latrines in swamp rabbit detection histories for the 2022-2023 survey season in a comparative single-season occupancy analysis. This analysis aimed to evaluate how the incorporation of ground latrines, as opposed to restricting detections to latrines on elevated surfaces, influenced estimates of occupancy and detection probabilities. Swamp rabbits were detected at 148 sites in 15 counties in 2022-2023, with a noted increase in occupancy probability from 0.66 (SE = 0.01) in 2010-2012 to 0.79 (SE = 0.01) in 2022-2023. As expected, site isolation negatively impacted occupancy probability, but predictors for patch richness density, site area, flood frequency, and flood severity had varying levels of support. For example, occupancy probability was negatively influenced by patch richness density but positively influenced by site area, while colonization probabilities were high and positively influenced by both flood frequency and severity. Extinction probability was low but was negatively influenced by flood frequency. Models with occupancy, colonization, and extinction as a function of the proportion of bottomland hardwood forest at a site were not supported. Detection probability decreased from 0.90 (SE = 0.19) in 2010-2012 to 0.78 (SE = 0.13) in 2022-2023. The inclusion of ground latrines in analyses did increase detection (0.68 to 0.84) and estimates of occupancy probabilities (0.95 to 1.00) but the change in estimates of occurrence was not biologically meaningful. Despite concerns about decline at the northern edge of their range, swamp rabbit populations in southeast Missouri appear to be expanding, evidenced by the increased occupancy and promising colonization and extinction rates. While long-term monitoring efforts should continue, managers should consider changing the swamp rabbit's state rank from imperiled (S2) to vulnerable (S3).

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CHAPTER 1

INTRODUCTION

Anthropogenic landscape modification and climate change pose increasing risks to the survival of habitat specialists (Devictor et al., 2008; Travis, 2003). Understanding the long-term changes in species distributions therefore requires monitoring efforts that can detect changes over time. Swamp rabbits (*Sylvilagus aquaticus*) are habitat specialists that rely on bottomland hardwood (BLH) forest for forage and refugia, and avoid other cover types such as agriculture and urban areas (Chapman & Feldhamer, 1981; Zollner et al., 2000a; Crawford et al., 2018). The narrow range of environmental conditions under which they have evolved and the ease with which they can be routinely monitored have led to their classification as a potential bioindicator species for bottomland hardwood forests (Hillard et al., 2017) in the Mississippi Alluvial Valley (MAV). Changes in swamp rabbit populations should therefore reflect the conditions of the environments they occupy, and, by extension, the status of other bottomland hardwood forest species. Effective management of swamp rabbits, therefore, requires a comprehensive understanding of their habitat requirements and an assessment of long-term changes in occurrence.

A general decline in swamp rabbit populations has been observed along the northern edge of their range in Indiana, Illinois, Kentucky, and Missouri, where their conservation status ranges from critically imperiled to vulnerable (Barbour et al., 2001; Fantz et al., 2017; Roy Nielsen et al., 2008; Sole, 1994; NatureServe, 2023). By contrast, populations in the core range along the Gulf Coast are currently deemed secure (NatureServe, 2023). This difference highlights the urgency of targeted conservation efforts, emphasizing the need for adaptive management strategies (Walters, 1986) to safeguard swamp rabbit populations facing environmental challenges in the areas most affected by change.

Several studies over the past 85 years have assessed swamp rabbit distribution in southeast Missouri. In 1937, swamp rabbits were reported in 21 southern Missouri counties within the Mississippi Alluvial Valley, the Ozark Highlands, and north of the MAV (Bennitt & Nagel, 1937). By 1977, swamp rabbits occurred in only 10 counties (Korte & Fredrickson, 1977), and as a result the Missouri Department of Conservation formally began decadal occupancy surveys for swamp rabbits in 1991. Dailey et al. (1993) reported swamp rabbits at 104 of 260 sites (40%) across 12 counties in southeast Missouri. In 2001-2002, swamp rabbits were detected at 120 of 226 sites (53%) in 11 counties (Scheibe & Henson, 2003). While it appears that swamp rabbit occurrence increased between the first and second surveys, this could be due to increased survey effort in the 2001-2002 season. Most recently, Fantz et al. (2017) conducted the 2010-2012 decadal survey, instituting a survey protocol of three visits to each site to account for imperfect detection in the modeling procedure. During the 2010-2012 survey, swamp rabbits were detected at least once at 144 of 211 sites (68%) in 12 counties. Because of the differences in survey protocols, all three surveys could not be compared directly. Any apparent increase in occurrence during the third survey may simply be a result of increased survey effort. Common across all three surveys, however, was the suggestion that habitat loss is the primary driver of swamp rabbit decline, and because swamp rabbits are listed as a Species of Greatest Conservation Need in the state (MDC, 2015), this is a problem.

Several biotic and abiotic factors determine a species' distribution, and these factors can vary from the core of their range to the edge (Hardie & Hutchings, 2010). Populations at the edge of their range are at a heightened risk of extinction due to lower genetic variability, reduced population size, and isolation as compared to core populations (Hardie & Hutchings, 2010). Because swamp rabbits are habitat specialists and the Missouri population is near the northern extent of their range, habitat loss is, therefore, a major conservation concern (Fig. 1). Indeed, the loss and degradation of bottomland hardwood forests are believed to be the primary drivers of declining swamp rabbit populations across several states (Korte & Fredrickson, 1977; Scharine et al., 2009; Terrel, 1972; Whitaker & Abrell, 1986). Of the estimated 850,000 hectares (ha) of BLH forest in Missouri in 1870, only 11% (92,000 ha) remained in 1970 (Korte & Fredrickson, 1977). What currently remains of these forests are fragmented patches with reduced connectivity, potentially limiting Missouri swamp rabbits to metapopulations at risk of isolation and the possibility of undergoing repeated extinction and colonization events (Robinson et al., 2016; Roy Nielsen et al., 2008). A genetic analysis of swamp rabbit populations in Illinois, which experience similar fragmentation issues as Missouri populations, indicated higher levels of genetic drift when compared with sympatric eastern cottontails (*Sylvilagus floridanus*) in the same area. Greater genetic drift is likely an indicator of population substructure and low habitat connectivity (Berkman et al., 2015). Thus, some of these populations may function as sinks (Fantz et al., 2017), reliant on continuous immigration from other areas to sustain themselves, underscoring the need for greater restoration efforts.

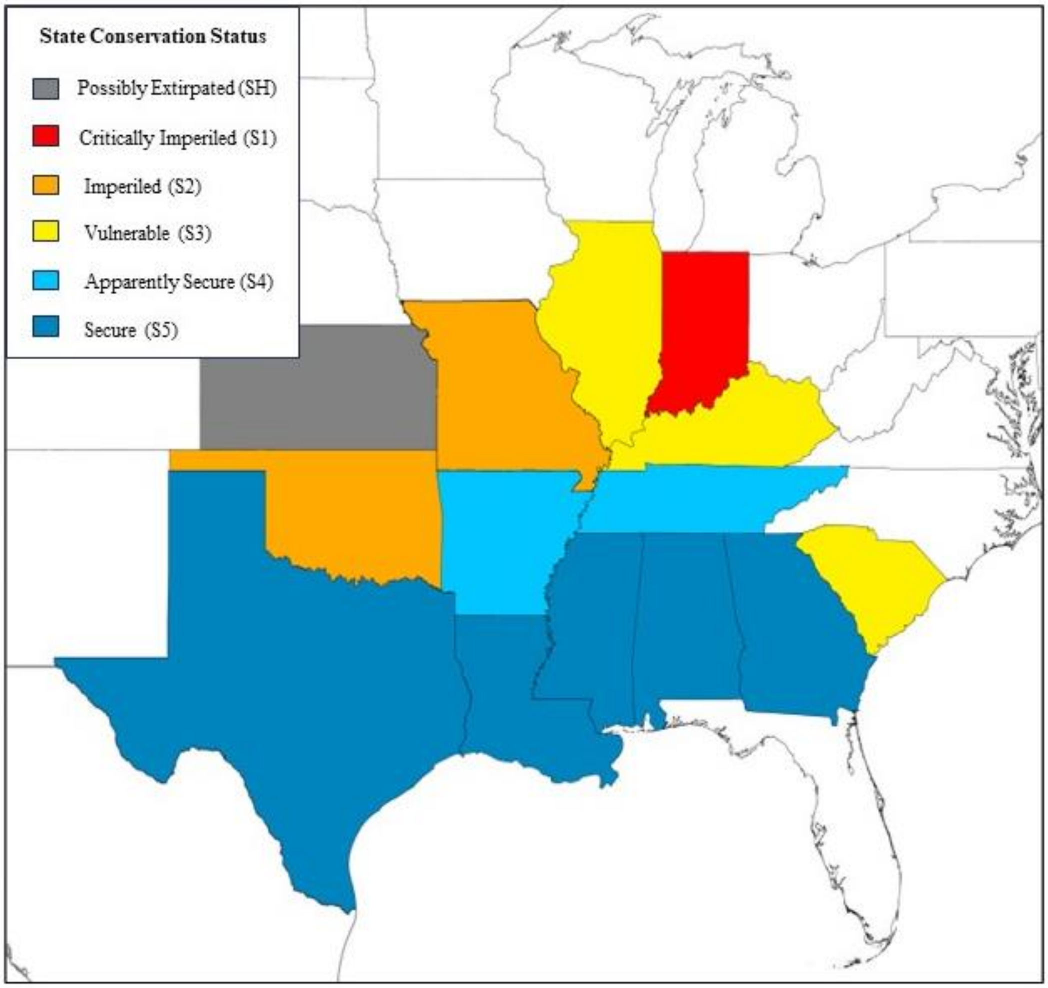

Figure 1. Swamp rabbit conservation status across their range (NatureServe, 2023).

In addition to landscape conversion to agriculture, climate change also influences environmental conditions (Mantyka-Pringle et al., 2012; Williams et al., 2022), and its impacts on swamp rabbits remain an unanswered question. In the past twelve years, southeast Missouri has experienced several severe floods (MDPS, SEMA, 2011, 2015a, 2015b, 2017, 2019), as well as severe droughts (NIDIS, 2023) and several EF2+ tornadoes (Springfield News-Leader, 2023) which may have altered forest structure. The environmental impacts of severe flooding are widespread and varied. Floods can cause major damage and even death for many trees. Flood waters transport large amounts of sediment, creating depressions that trap and redirect water, altering the volume and composition of soil, which can then impact tree species assemblages and soil drainage (Broadfoot & Williston, 1973; Cosgriff et al., 2007). Heat stress, ice storms, and windthrow can also all directly damage or kill trees. These disturbances can reduce canopy cover, releasing the understory, and creating a more early-successional environment, which may benefit swamp rabbits (Barbour et al., 2001). And while snowstorms are not common in southeast Missouri (Decker & Guinan, 2011), Hillard et al. (2018) reported that swamp rabbit mortality in Southern Illinois increased on snow-covered days, primarily due to predation. The expected near elimination of snow cover in their northern range paired with expected temperature increases (Demaria et al., 2016) may improve swamp rabbit survival and potentially expand their range if southern forests migrate northward. Thus, the cumulative effects of predicted climate changes may positively impact swamp rabbit populations in Missouri.

However, there is still much uncertainty in predicted climate changes and species responses to these changes. Bottomland hardwood forests are among the most vulnerable to projected climate changes, especially when already stressed by altered hydrology, high levels of erosion, or fragmentation (Swanston et al., 2018). Many climate models have projected an increase in both extreme precipitation events and total rainfall in Missouri, with more of the annual rainfall occurring during these extreme events, which are expected to increase runoff and peak flow in the winter and spring seasons (Swanston et al., 2018; Andersen & Shepherd, 2013; Winkler et al., 2014). In turn, excessive flooding and erosion are likely to increase both in magnitude and frequency (Swanston et al., 2018; Andersen & Shepherd, 2013). Hillard et al. (2021) reported that swamp rabbits in southern Illinois selected sites farther from inundated cover types (open water, wooded wetlands) and closer to bottomland hardwood forests with 6-10 month dry periods. If human development continues in these already fragmented landscapes, it could push swamp rabbits towards more undesirable habitats that are experiencing increased flooding and erosion and longer annual wet periods. Robinson et al. (2016) reported that catastrophic flood events had a strong effect on the risk of quasi-extinction of swamp rabbit populations in Illinois, though the relationship between the occurrence and frequency of these events on swamp rabbit occurrence is not well understood. Understanding how swamp rabbits respond to the effects of a variety of climate changes is, therefore, imperative.

When weighing all of these influential climate change events, there are three important factors to consider: 1) climate changes may alter the flood regime and, in turn, forest and soil composition (Cosgriff et al., 2007; Hodges, 1997; Mikac et al., 2018), 2), altering forest and soil composition could subsequently alter the flood pattern (Hümann et al., 2011) and, 3) permanent loss of forest due to the increasing frequency and severity of climate events could preclude swamp rabbit occurrence. Of additional concern is the belief that the frequency of catastrophic weather events is increasing in response to climate change (Bouwer, 2011; Ummenhofer & Meehl, 2017). Thus, over several decades, repeated disturbance events could completely change a bottomland hardwood forest floodplain system, and as a result, swamp rabbit distribution may vary over time.

Although swamp rabbit occurrence has been surveyed in Missouri for three consecutive decades, no survey has examined long-term changes in parameters such as occurrence, colonization, extinction, and detection probabilities. The effects of forest change, forest patch isolation and contrast, flooding, weather conditions, and other factors, have therefore not been related to these parameters for more than a single season. My study provides managers with more detailed information on the status of swamp rabbit occurrence in Missouri, poses explanations for how and why it has changed over the decades, and provides predictions on the direction of swamp rabbit response to potential future climate and habitat changes.

The primary objective of my study was to enhance management strategies for swamp rabbits in southeast Missouri. This was achieved by (1) using dynamic occupancy models to estimate probabilities of occupancy, colonization, extinction, and detection of swamp rabbits in southeast Missouri, and (2) identifying the environmental factors driving changes in their distribution. The secondary objective of my study was to investigate the influence of the inclusion of ground latrines on swamp rabbit detection and occupancy probabilities for the 2022-2023 decadal survey. I had three principal hypotheses regarding swamp rabbit distribution dynamics. First, I hypothesized that detection probability would be influenced by search effort, fluctuations in weather and time of year (Hunt, 1959; Zollner et al., 1996), site area (Fantz et al., 2017), and survey year. Second, I hypothesized that occupancy probability would be influenced by the landscape heterogeneity of a site (Dumyahn et al., 2015; Zollner et al., 2000a), site area (Fantz et al., 2017), and isolation from other BLH forest patches (Robinson et al., 2016). Third, I hypothesized that colonization and extinction probabilities would be influenced by flooding activity at a site (Barbour et al., 2001; Crawford et al., 2018; Robinson et al., 2016), change in BLH forest at a site (Crawford et al., 2018, Robinson et al., 2016), and change in site isolation (Robinson et al., 2016). Additionally, I hypothesized that including ground latrine detections in the survey method would increase occupancy and detection probabilities.

CHAPTER 2

METHODS & MATERIALS

2.1 Study Area

Sites for the initial decadal survey in 1991-1992 were determined using historical evidence of swamp rabbit occupancy from landowners and state and federal agency personnel as well as aerial imagery (Dailey et al., 1993). Ultimately, sites meeting specific criteria, including ≥ 25% canopy cover, hydric soils, flooding on an average of 2 of every 5 years, and a minimum size of 16 ha were selected (Dailey et al., 1993). These ranged in size from 16.2 ha to 4609.2 ha with an average of 129.3 ha and a median of 38 ha, totaling 34,272.2 ha (Dailey et al., 1993). Agricultural fields isolated most sites, with smaller sites mostly privately owned and most larger sites publicly owned. Survey site elevation ranged from 73 m to 274 m (Fantz et al., 2017).

Southeast Missouri has a continental climate with average January temperatures ranging from -2.4-7° Celsius and average July temperatures ranging from 21.2-31.8° Celsius (NWS, 2024). Winters are cold and rainy with an average of 70 days of freezing temperatures, a mean of 52 inches of precipitation, and on average < 25 centimeters of snowfall (Decker & Guinan, 2011). The growing season lasts from April to October (Decker & Guinan, 2011).

The study area included sixteen counties in southeast Missouri that were surveyed in the past three decadal surveys (Bollinger, Butler, Cape Girardeau, Dunklin, Jefferson, Mississippi, New Madrid, Oregon, Pemiscot, Perry, Ripley, Scott, Stoddard, St Charles, Ste Genevieve, Wayne). Of the original 278 sites selected by Dailey et al. (1993), 211 sites were re-surveyed in the 2010-2012 study, incorporating a new survey protocol to explicitly account for imperfect detection. An additional 21 sites were added in 2011 by Fantz et al. (2017), which were identified as potential swamp rabbit dispersal corridors or locations of suspected swamp rabbit activity. During the 2022-2023 survey a total of 176 of both the “original” and “new” sites were resurveyed (Fig. 2).

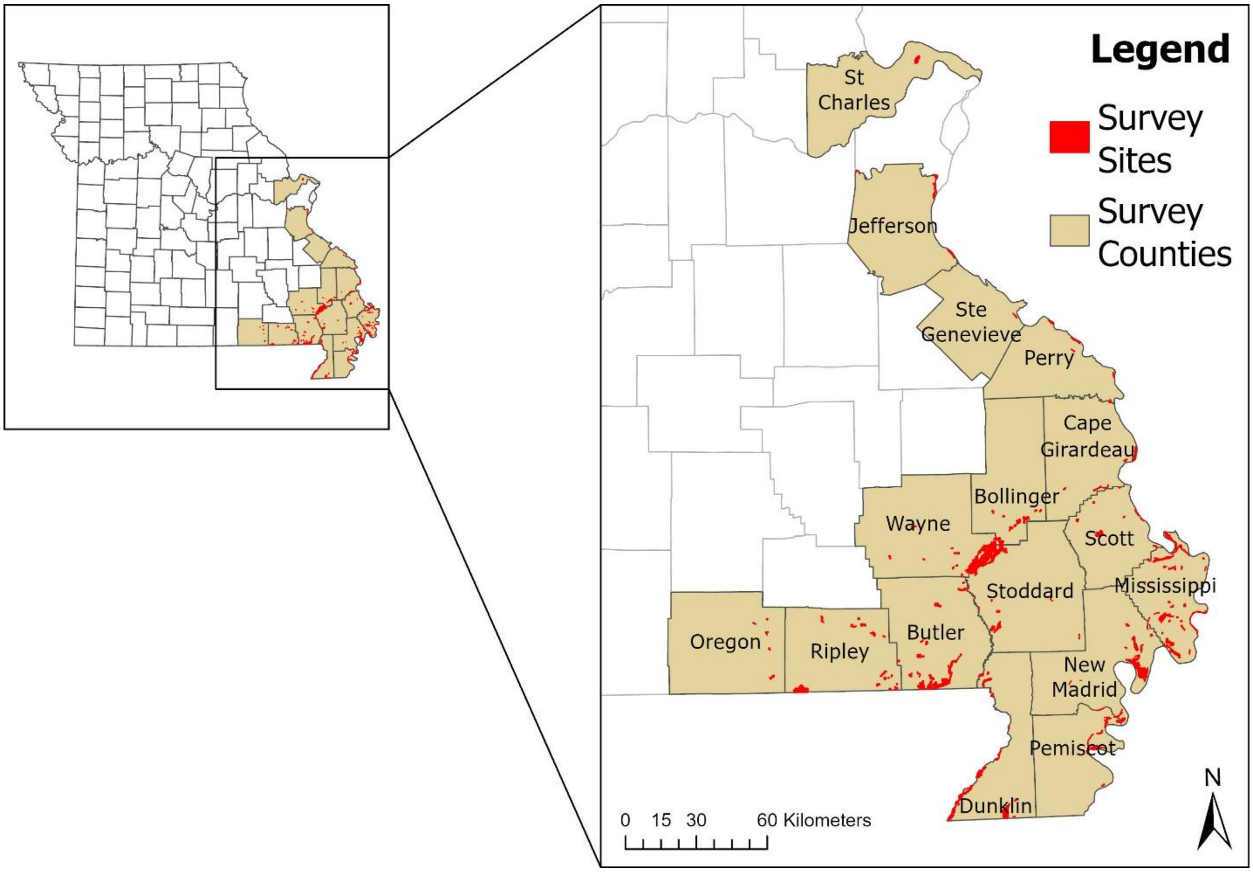

Figure 2. Map of swamp rabbit survey sites (n=176) for 2022-2023 decadal survey in southeast Missouri, USA.

Of the 176 sites surveyed in 2022-2023, 127 were located within the Lower Mississippi Alluvial Valley, characterized by low elevations, flat to gently undulating topography, and sandy low ridges and hills along the Mississippi River (Appendix A(a); Hanberry et al., 2012; Fantz et al., 2017). Elevations at these sites ranged from 72 m to 145 m. Historically, this region was dominated by bottomland hardwood forests of primarily sweetgum (*Liquidambar styraciflua*), elms (*Ulmus* spp.), black oak (*Quercus velutina*), and white oak (*Quercus alba*) (Hanberry et al., 2012). Other abundant species included ashes (*Fraxinus* spp.), maples (*Acer* spp.), cottonwoods (*Populus* spp.), hickories (*Carya* spp.), and baldcypress (*Taxodium distichum*) (Hanberry et al., 2012). Today, the Mississippi Alluvial Valley has been heavily developed for agricultural use, with major crops including cotton, rice, soybeans, and corn. Over 75% of forests have been cleared since European colonists arrived in the 1700s (Oliver & Gardiner, 2004; Hanberry et al., 2012) and extensive channelization and drainage projects have crippled the natural hydrologic and disturbance cycles that once maintained them (Hanberry et al., 2012). The bottomland hardwood forests that remain are often persistently wet or flood-prone, which has protected them from development (Oliver & Gardiner, 2004). Currently, forests on the floodplains are dominated by sweetgums, elms, maples, hickories, overcup oaks (*Quercus lyrata*), willows (*Salix spp.*), hackberry (*Celtis occidentalis*), baldcypress and water tupelo (*Nyssa aquatica*) swamps, and mixed emergent marshes, while higher ridges and hills consist primarily of white oaks, pines (*Pinus spp.*), elms, and hickories (Hanberry et al., 2012; Fantz et al., 2017).

An additional 31 sites were situated along major streams in the Black River Hills Border region of the Ozark Highlands, an area directly north and west of the Mississippi Alluvial Valley (Appendix A(b)). The Black River Hills are predominantly forested with some valley bottoms cleared for pasture and row crops. They have greater relief than the MAV, with thin, rocky soils on slopes and claypan and loess on valley and river flats (Chapman et al., 2002). Forest composition in this region is transitional from the bottomland hardwoods of the Mississippi Alluvial Valley to the predominantly oak forests of the interior Ozark Highlands (Chapman et al., 2002). Bottomland forests in the Ozark Highlands are dominated by slippery elm (*Ulmus rubra*) and American sycamore (*Platanus occidentalis*) along with a mix of typical bottomland species such as willows, silver maple (*Acer saccharinum*), and boxelder (*Acer negundo*), while more upland sites are dominated by oaks, black hickory (*Carya texana*), and shortleaf pine (*Pinus echinata*) (Ware et al., 1992). Elevations at these sites ranged from 100 m to 277 m.

The remaining 18 sites were on the Interior River Valleys and Hills ecoregion directly north of the Mississippi Alluvial Valley and along the Mississippi River (Appendix A(c); Chapman et al., 2002). This region is characterized by rocky, forested slopes and hills with moderately to poorly drained alluvium in river valleys (Chapman et al., 2002). Areas along the Mississippi River are largely dominated by mesic mixed hardwood forest and mixed riverfront forest. Some areas have been cleared for grazing and row cropping, particularly in the northern reaches. Inland areas consist mainly of pasturelands and row crop fields, interspersed with forest remnants (Chapman et al., 2002; Fantz et al., 2017). Major crops include soybeans, corn, and pasturelands (USDA, 2024). Elevations at these sites ranged from 97 m to 181 m.

2.2 Pellet Surveys

For the 2022-2023 decadal survey, observers were trained in identifying swamp rabbit latrines by the Missouri Department of Conservation and U.S. Fish and Wildlife Service staff. Pellet surveys took place between November 30, 2022 and March 2, 2023 when downed logs are easiest to observe because most understory vegetation is dormant and pellets degrade more slowly due to cooler temperatures and reduced insect activity (Flinders & Crawford, 1977). Because snowfall can obscure latrines, sites were not surveyed while snow was on the ground. Pellet surveys were conducted following the protocol developed by Fantz et al. (2017). Surveyors walked a semi-random path of least resistance through the site and identified swamp rabbit latrines on logs or other elevated surfaces. All sites were surveyed by the same team of five observers barring one site that could only be accessed by boat; this site was surveyed by three U.S. Forest Service employees who attended the initial training at the beginning of the field season and who had participated in past swamp rabbit surveys.

Survey duration was a function of site size following Scheibe and Henson (2003). A maximum of one hour was spent surveying sites ≤ 100 acres, a maximum of two hours was spent surveying sites > 100 acres and < 1000 acres, and a maximum of three hours was spent surveying sites ≥ 1000 acres. For two- and three-hour sites, if a latrine was not found within the first hour, the surveyor moved to a new area within the survey site for each additional hour until a latrine was found or the time limit had been met. Each site was surveyed three times by an independent observer within a 10-day period to ensure observers remained unbiased and met closure assumptions of the modeling procedure. Regardless of whether a latrine was documented, surveyors carried out three site visits, with a unique surveyor completing each visit. Repeated surveys allow for an estimation of detection probability (MacKenzie et al., 2003) as well as a direct comparison to the survey data from the 2011-2012 survey completed by Fantz et al. (2017). Eight of the two- and three-hour sites were surveyed for only one hour due to a lack of landowner permissions on portions of the site, leaving < 5 acres accessible in some cases. If a latrine was found, a GPS point was logged, the site was marked as occupied, and the survey was considered complete during that visit.

One adjustment to the previous survey protocol (Fantz et al., 2017) was the inclusion of ground latrines. Swamp rabbits are known for their unique behavior among lagomorphs in which they deposit fecal pellets on logs and other elevated surfaces such as stumps and rocks (Lowe, 1958; Schauber et al., 2008). This characteristic allows surveyors to quickly identify sites where swamp rabbits occur. Generally, swamp rabbit pellets can be distinguished from eastern cottontail (*Sylvilagus floridanus*) pellets by their larger size. Swamp rabbit pellets range from 7-

15 mm in diameter, with an average of 12.47 mm, while cottontail pellets range from 6-10 mm in diameter, with an average of 7.58 mm (Whitaker & Abrell, 1986). Thus, there is some overlap in size of swamp rabbit and cottontail pellets (Scheibe & Henson, 2003; Whitaker & Abrell, 1986), which is why detecting pellets on elevated surfaces (e.g., logs, stumps, rocks) is the easiest way to confirm swamp rabbit presence. However, some swamp rabbit pellets likely roll off logs onto the ground.

There is also evidence from multiple studies that they do not exclusively use elevated latrine sites (McCollum & Holler, 1994; Fowler & Kissell, 2007; Barbour et al., 2001; Terrel, 1972). McCollum & Holler (1994) reported that in some locations more than 60% of pellet groups in Alabama were found on the ground. Anecdotal data suggest that swamp rabbit usage of elevated latrines declines in the spring and summer (Lowe, 1958; Terrel, 1972; Whitaker and Abrell, 1986; Zollner et al., 1996), so it is possible that they do not exclusively use elevated latrines during the fall and winter. By excluding ground latrines from the detection method, surveyors may be dismissing valuable information for a species with declining populations in many states.

Previous decadal surveys did not consider ground latrines in their surveys because of the potential for pellets on the ground to have originated from eastern cottontails, however, ground latrines have been included in other studies (McCollum & Holler, 1994, Fowler & Kissell, 2007; Barbour et al., 2001). During the 2022-2023 decadal survey, ground latrines were included as detections only when surveyors were certain they originated from swamp rabbits, using size (above the threshold for cottontails), location (within the forest interior), and occasionally visual detection of a swamp rabbit near the ground latrine during a survey. The surveyor noted when pellets were detected on the ground versus on an elevated surface.

2.3 Dynamic Occupancy Analysis

I used dynamic occupancy models (MacKenzie et al., 2003) to estimate key ecological parameters (detection (*p*), occupancy (ψ), colonization (γ), and extinction (ε) probabilities) for swamp rabbits in southeast Missouri during 2010 - 2023. Dynamic occupancy models (also known as multi-season occupancy models) offer a valuable framework for assessing changes in species occurrence over time and the ecological drivers of those changes. By identifying the relationships between environmental predictors and parameters, these models allow a comprehensive understanding of species dynamics (MacKenzie et al., 2003). Detection probability (*p*) is the probability a species is detected given it is present at a site, occupancy probability (ψ) is the probability a species occurs at a site, colonization probability (γ) is the probability of an unoccupied site becoming occupied, and extinction probability (ε) is the probability of an occupied site becoming unoccupied (MacKenzie et al., 2003). Detection data are collected across multiple years or seasons termed *primary sampling periods,* in which changes in occupancy may occur (MacKenzie et al., 2003). Within each primary sampling period are *secondary sampling periods,* in which investigators visit sites to collect detection-non-detection data and where the site is assumed closed to changes in occupancy (MacKenzie et al., 2003, MacKenzie et al., 2002). The modeling process produces probability estimates for colonization, extinction, and first-year (or season) detection and occupancy, and detection and occupancy estimates for succeeding years can be derived. Because occupancy modeling accounts for imperfect detection by repeatedly sampling sites within a single season, it is an ideal modeling framework to use for a cryptic species like the swamp rabbit that may not be detected even if they are present at a site (MacKenzie et al., 2002, 2005).

My study used dynamic occupancy models to compare the results of the 2022-2023 decadal survey to the previous decadal survey from 2010-2012. *Encounter histories* were compiled using detection data from 175 sites sampled during both primary survey periods. For example, an encounter history of “001011” indicates that swamp rabbits were detected during the third, fifth, and sixth sampling occasions, but not during the first, second, or fourth. One site surveyed in 2022-2023 had to be excluded from the analysis because of missing data from 2010-2012. I used the package *unmarked* (Kellner et al., 2023; Fiske & Chandler, 2011) in Program R version 4.2.1 (R Core Team 2022) to fit all models. I scaled and centered predictor variables to mitigate the impact of variables with large ranges, encourage convergence, and facilitate model comparison (Marquardt, 1980). I then used model selection to identify the most supported ecological predictors of the ecological and observational parameters (Burnham & Anderson, 2022).

I used a secondary candidate set strategy to compare all occupancy models (Morin et al., 2020, Bromaghin et al., 2013). With this strategy, the modeling process is divided into two stages (two model sets). In the first stage, sub-models are developed to test each parameter (e.g., colonization probability) independently, with sub-models representing a priori hypotheses for the parameter of interest while holding the remaining parameters constant. The sub-models from the first set are then ranked, and the top sub-models for each parameter are retained for testing of all parameters in the second set. I developed five *a priori* sub-models for the detection parameter, eleven sub-models for the occupancy parameter, five for the colonization parameter, and seven for the extinction parameter. Efforts were made to limit model complexity by including no more than two additive effects for a single parameter. I ranked all models using Akaike’s Information Criterion (AIC), where the model with the lowest AIC score was considered the top model

(Burnham & Anderson, 2002). Because the secondary candidate set strategy requires more liberal selection criteria during the first stage (Morin et al., 2020, Bromaghin et al., 2013), sub-models with ΔAIC ≤ 5 (Burnham & Anderson, 2002) were retained for further analysis.

Following the first stage of model selection, a secondary set of all combinations of the top sub-models from the first stage was developed. A total of nineteen models were tested during the second stage of model selection using the "L-BFGS-B" optimization method. Models with ΔAIC ≤ 2 were considered competing hypotheses (Burnham & Anderson, 2002). For the second modeling stage, an ensemble approach was employed using the *MuMIn* package (Bartoń, 2023) in Program R version 4.2.1 (R Core Team, 2022). Because occupancy estimates for succeeding survey years cannot be derived in *unmarked* for model-averaged sets, a non-parametric bootstrap approach with 1000 replications was applied (Kéry & Royle, 2020). This method accounted for model uncertainty and variability in occurrence across time steps (2010-2012 and 2022-2023) and generated 1000 estimates of occupancy probability for both time steps for all top models. The mean of these estimates was computed across all top models with standard errors and 95% confidence intervals to get model-averaged predictions of occurrence for 2010-2012 and 2022-2023.

2.3.1 Selection of Predictor Variables

I investigated several predictors for the detection, occupancy, and local colonization and extinction parameters. For the detection parameter, I considered survey duration, site area, precipitation, and Julian date (Table 1). To assess the influence of search effort, I predicted higher swamp rabbit detections with shorter survey durations, drawing on anecdotal observations from current and previous studies that swamp rabbits are detected quickly where they occur. However, after exploratory analysis, the survey duration predictor seemed more closely related to the occupancy state of the site rather than the observation process, so this predictor was removed from the dynamic occupancy analysis. I predicted that detection probability would increase with site area, aligning with findings from Fantz et al. (2017) and Scheibe and Henson (2003). Additionally, I expected increased detections after rainfall, based on Hunt's (1959) study suggesting heightened swamp rabbit activity after rain events. Lastly, I predicted higher detections earlier in the survey season, reflecting a decline in latrine log usage during spring and summer (Lowe, 1958; Terrel, 1972; Zollner et al., 1996).

Table 1. Descriptions of predictors used for estimations of swamp rabbit occupancy, detection, colonization, and extinction probabilities in southeast Missouri, USA, 2022-2023.

Parameter	Predictor	Description	Source
Occupancy	Proportion of BLH forest	The proportion of a site comprised of bottomland hardwood forest	1-arc-second Digital Elevation Model (USGS, 2023), National Land Cover Dataset (USGS, 2011; USGS, 2021), Web Soil Survey (NRCS, 2023), US Ecoregions Level III Dataset (US EPA 2013)
	Total site area	Total area (ha) of a site	ArcGIS Pro ver. 3.1 (ESRI, 2023)
	Site isolation	Distance (km) from site to nearest patch of distinct bottomland hardwood forest ≥ 16 ha	ArcGIS Pro ver. 3.1 (ESRI, 2023)
	Edge length	The length of edge (km) of each site	ArcGIS Pro ver. 3.1 (ESRI, 2023)
	Patch richness density	Number of distinct land cover type patches (per 100 ha) at a site	landscapemetrics (Hesselbarth et al., 2019); Program R ver. 4.2.1 (R Core Team, 2022)
Colonization & Local Extinction	Number of floods	A factor with two levels: "more" indicated the site had more floods than the average, "less" indicated the site had less floods than the average from May 2012 to October 2021.	Dartmouth Flood Observatory (Brakenridge, 2023)

	Flood severity	A factor with two levels: "more" indicated flood severity at the site was more severe than the average, "less" indicated flood severity at the site was less severe than the average from May 2012 to October 2021.	Dartmouth Flood Observatory (Brakenridge, 2023)
	BLH forest increase	A factor with two levels: "1" indicated the site experienced an increase in the proportion of BLH forest, "0" indicated the site experienced no change in the proportion of BLH forest since the previous decadal survey.	1-arc-second Digital Elevation Model (USGS, 2023), National Land Cover Dataset (USGS, 2011; USGS, 2021), Web Soil Survey (NRCS, 2023), US Ecoregions Level III Dataset (US EPA 2013)
	BLH forest decrease	A factor with two levels: "1" indicated the site experienced a decrease in the proportion of BLH forest, "0" indicated the site experienced no change in the proportion of BLH forest since the previous decadal survey.	1-arc-second Digital Elevation Model (USGS, 2023), National Land Cover Dataset (USGS, 2011; USGS, 2021), Web Soil Survey (NRCS, 2023), US Ecoregions Level III Dataset (US EPA 2013)
	Site isolation change	Change in site isolation (km) since the previous decadal survey.	ArcGIS Pro ver. 3.1 (ESRI, 2023)
Detection	Duration	Length of time (min) spent searching at a site	Survey data
	Precipitation	Amount of precipitation in a 24-hour period on the day of sampling occasion	Daily Observational Data (NCEI, 2023)
	Julian date	Day of year surveyed	Survey data

For occurrence probability, I assessed five predictors describing proportion of bottomland hardwood forest, site area (ha), site isolation, patch richness density, and edge length. I predicted that occupancy probability would increase with site size (Fantz et al., 2017), and decrease as the site became more isolated from other patches of bottomland hardwood forest that were ≥ 16 ha. I selected 16 ha as the BLH forest patch threshold because this was the site size threshold used by the first decadal survey in Missouri (Dailey et al., 1993). To evaluate support for my landscape heterogeneity hypothesis, I predicted that occupancy probability would increase with the proportion of bottomland hardwood forest (Dailey et al., 1993; Scheibe and Henson, 2003) because swamp rabbits are considered BLH forest specialists (Chapman & Feldhamer, 1981). Additionally, I predicted a positive relationship between occupancy probability and the amount of edge, as swamp rabbits use early-successional vegetation conditions, which are often associated with edge, for cover and possibly food (Harper et al., 2005; Scharine et al., 2009; Terrel, 1972; Zollner et al., 2000a). After exploratory analysis, edge length was removed as an occupancy predictor as it was highly correlated (r = 0.93) with site area. I predicted occupancy probability would decrease with higher patch richness density, which describes the number of patch types per 100 ha of a landscape or site (Hesselbarth, et al., 2019), as this may indicate fragmentation.

Four predictors were considered for models of local colonization: number of floods, flood severity, increase in the proportion of bottomland hardwood forest (hereafter, “forest increase”), and decrease in site isolation. For the extinction parameter, the number of floods and flood severity predictors were included, in addition to a decrease in the proportion of bottomland hardwood forest (hereafter, “forest decrease”) and an increase in site isolation. Evaluating the flooding activity hypothesis, I predicted that more floods and higher flood severity would increase extinction probability and decrease colonization probability. Prolonged or extensive floods have been suggested to cause direct mortalities, increase depredation and starvation, decrease reproductive rates, and decrease available cover (Barbour et al., 2001; Conaway et al., 1960; Zollner et al., 2000b). The number of floods predictor was a factor with two levels: “higher” indicated that the site experienced a higher number of floods than the average across all sites, and “lower” indicated that the site experienced a lower number of floods than the average across all sites. The flood severity predictor was also a factor with two levels: “more” indicated that the site experienced more severe floods than the average across all sites, and “less” indicated that the site experienced less severe floods than the average across all sites.

Testing the forest change hypothesis, I anticipated increased extinction probability and therefore decreased colonization probability with the loss of bottomland hardwood forest at a site. Forest change was split into two factors, each with two levels: proportion of BLH forest increase, where 0 = no change and 1 = increase in proportion of BLH forest; and proportion of BLH forest loss, where 0 = no change and 1 = loss of proportion of BLH forest. Similarly, for the isolation change hypothesis, I predicted increased extinction probability and decreased colonization probability with an increase in site isolation, in line with Barbour et al.’s (2001) observation that recolonization of extirpated sites could be hindered in the absence of connectivity. However, after summarizing these values, 95% of sites experienced a change in isolation of ≤ 1 m between decadal surveys, which is not a biologically meaningful change for swamp rabbit dispersal. Therefore, this predictor was removed from the analysis.

While survey duration and date data were collected in the field, all other predictor data were remotely sensed. Employing Geographic Information System software (ESRI, 2023), I extracted information from a 1-arc-second digital elevation model (DEM; USGS, 2023), the National Land Cover Dataset (USGS, 2011; USGS, 2021) the Dartmouth Flood Observatory (Brakenridge, 2023), daily precipitation data (NCEI, 2023), soil surveys (NRCS, 2023), and the U.S. Ecoregions Level III Dataset (U.S. EPA, 2013). These datasets were used to quantify the proportion of bottomland hardwood forest, site area, site isolation, edge length, forest change, isolation change, number of floods, flood severity, and precipitation for each sampling site. The bottomland hardwood forest raster layer was developed by identifying National Land Cover Dataset classes 41, 43, and 90 (deciduous forest, mixed forest, wooded wetlands) in locations with maximum elevations of 154 meters and with hydric soils. The flood severity index was a function of the flood-return period (Brakenridge, 2023). Average flood frequency and average flood severity were the mean of all flood events across all sites from May 2012 to October 2021. I used the *landscapemetrics* package (Hesselbarth et al., 2019) in Program R version 4.2.1 (R Core Team, 2022) to measure patch richness density. I excluded the six largest sites from analyses due to their extreme site area values, which highly skewed the site size distribution. "Trace amounts" of precipitation were recorded as 0.001 inches and missing values were omitted. All continuous predictors were scaled before analysis and checked for multicollinearity using a correlation cutoff of r = 0.7 (Jeng, 2023).

2.4 Influence of Inclusion of Ground Latrines on Occupancy and Detection Probabilities

Previous research has indicated that most swamp rabbit occupancy studies focus primarily on detections from elevated latrines, with few explicitly stating if and how many ground latrines were also detected or included (McCollum & Holler, 1994; Barbour et al., 2001; Heuer & Perry, 1976; Fowler & Kissell, 2007). Therefore, I predicted that expanding my detection methods to include ground latrines would increase detection probability and would also increase occupancy probability if sites had no elevated latrine detections but did have ground latrine detections. To investigate this relationship, I used single-species, single-season occupancy models (MacKenzie et al., 2002). Encounter histories for the 2022-2023 survey season were generated as described above for dynamic occupancy models, and all parameter predictors remained the same. To test this comparison, I fit two single-season occupancy models (MacKenzie et al., 2002) using the R package *unmarked* (Kellner et al., 2023; Fiske & Chandler, 2011): (1) detection histories using the latrines detected only on an elevated surface (hereafter, “elevated-only”) and (2) detection histories generated by all latrine detections – that is, ground latrines and elevated surface latrines (hereafter, “elevated + ground”). These single-season models explored the effects (if any) that the inclusion of ground latrines may have had on detection and occupancy. A secondary candidate set strategy was used for testing models as previously described for the dynamic occupancy analyses.

CHAPTER 3

RESULTS

3.1 Pellet Surveys

Over 59 days spanning from late November 2022 to early March 2023, observers dedicated a total of 359.5 hours to pellet surveys. These surveys covered 176 sites across 16 counties in southeast Missouri and totaled 29,783 ha. 25% of sites were publicly owned, 55% were privately owned, and the remaining 20% consisted of both privately and publicly owned parcels. Swamp rabbit latrines of any type were detected at 148 sites (Table 2). Elevated latrines were identified at 137 sites, while an additional 11 sites had ground latrine detections exclusively. 51 sites had both elevated and ground latrines (Table 2).

Table 2. Detection summary for swamp rabbit survey sites in southeast Missouri, USA, 2022-2023.

	Detection Summary	
	Elevated-only (# of sites)	Elevated + Ground (# of sites)
0 Detections	39	28
1 Detection	34	32
2 Detections	17	19
3 Detections	86	97

3.2 Dynamic Occupancy Models

3.2.1 First Modeling Stage

Five sub-models were tested for the detection parameter while occupancy, colonization, and extinction were held constant. The sub-model containing the year predictor accounted for 97% of the model weight and was the only sub-model within $\Delta AIC < 5$, so it was retained for testing in the second modeling stage (Appendix B). Thus, my hypotheses for the influence of site area, survey date, and precipitation on detection probability were not supported, as these predictors were not included, while my hypotheses that survey year influences detection probability was supported.

Eleven sub-models describing drivers of initial occupancy probability were fit while detection, colonization, and extinction sub-models were held constant. Two of the 11 models met the ΔAIC < 5 selection criterion (Appendix C) and accounted for 91% of the cumulative model weight. Therefore, these two sub-models were retained for testing in the second modeling stage. Three of the four occupancy predictors were included in the top sub-models: site isolation, patch richness density, and site area. This supports my hypotheses that these predictors influence occupancy probability. The proportion of bottomland hardwood forest predictor was not included, suggesting that it did not influence initial occupancy probability.

Five sub-models were tested for the colonization parameter while detection, occupancy, and extinction were held constant. All five sub-models met the ΔAIC < 5 selection criterion (Appendix D), so to further reduce this set, sub-models with an Akaike model weight of ≥ 10% were selected. Thus, three sub-models were retained for the second modeling stage. All three colonization predictors (number of floods, flood severity, and forest increase) were included within these sub-models, indicating support for my hypotheses that these predictors influence colonization probability.

Finally, seven sub-models were tested for the extinction parameter while detection, occupancy, and colonization were held constant. Three sub-models met the ΔAIC < 5 selection criterion (Appendix E) and were thus retained for testing in the second modeling stage. Two of the three extinction predictors (number of floods and forest decrease) were included in these sub-models. These support my hypotheses that these predictors influence extinction probability, while my hypothesis that flood severity influences extinction probability was not supported.

3.2.2 Second Modeling Stage

A total of nineteen models, consisting of all possible combinations of predictors from the sub-models from the first stage of modeling plus an intercept-only model that serves as baseline (hereafter, "null model"), were compared to identify a model best explaining occurrence dynamics (Table 3). All candidate models performed better than the null model. Twelve models were within ΔAIC < 2 and accounted for 85% of the cumulative weight, so model averaging was performed (Table 4; see Appendix F for the subset). Only one model had an Akaike model weight of >10%. All predictors were retained at least once within these twelve models. None of the interactive models were included in the top models.

Table 3. AIC-ranked dynamic occupancy models for swamp rabbits in southeast Missouri, USA, 2022-2023. Psi = occupancy parameter, gam = colonization parameter, eps = extinction parameter, and p = detection parameter. Isol = site isolation from nearest tract of bottomland hardwood forest ≥ 16 ha (km), PRD = patch richness density (number of patches/100 ha), SiteArea = size of the site (ha), AvgNumFl = a factor for the number of floods relative to the average, AvgFlSev = a factor for flood severity relative to the average, propBLH.gain = a factor for an increase in the proportion of bottomland hardwood forest, propBLH.loss = a factor for a decrease in the proportion of bottomland hardwood forest, year = the year the survey occurred. AIC = Akaike's information criterion, ΔAIC = the difference in AIC values between a specific model and the best fit model, w_i = Akaike model weight, and K = the number of parameters estimated.

Model	AIC	ΔAIC	w_i	K
psi (Isol+PRD), gam (AvgNumFl-1), eps (AvgNumFl-1), p (year-1)	978.11	0	0.11	9
psi (Isol+PRD), gam (AvgNumFl-1), eps (AvgNumFl + propBLH.loss), p (year-1)	978.53	0.43	0.09	10
psi (Isol+PRD), gam (AvgFlSev-1), eps (AvgNumFl-1), p (year-1)	978.56	0.46	0.09	9
psi (Isol+PRD), gam (propBLH.gain-1), eps (AvgNumFl-1), p (year-1)	978.83	0.72	0.08	9
psi (Isol+SiteArea), gam (AvgNumFl-1), eps (AvgNumFl-1), p (year-1)	978.89	0.79	0.08	9
psi (Isol+PRD), gam (AvgFlSev-1), eps (AvgNumFl+propBLH.loss), p (year-1)	978.98	0.88	0.07	10
psi (Isol+PRD), gam (propBLH.gain), eps (AvgNumFl+propBLH.loss), p (year-1)	979.26	1.15	0.06	10

psi (Isol+SiteArea), gam (AvgNumFl-1), eps (AvgNumFl+propBLH.loss), p (year-1)	979.35	1.24	0.06	10
psi (Isol+SiteArea), gam (AvgFlSev-1), eps (AvgNumFl-1), p (year-1)	979.35	1.25	0.06	9
psi (Isol+SiteArea), gam (propBLH.gain-1), eps (AvgNumFl-1), p (year-1)	979.62	1.52	0.05	9
psi (Isol+SiteArea), gam (AvgFlSev-1), eps (AvgNumFl+propBLH.loss), p (year-1)	979.81	1.7	0.05	10
psi (Isol+SiteArea), gam (propBLH.gain-1), eps (AvgNumFll+propBLH.loss), p (year-1)	980.08	1.98	0.04	10
psi (Isol+PRD), gam (AvgNumFl-1), eps (AvgNumFl*propBLH.loss), p (year-1)	980.38	2.27	0.04	11
psi (Isol+PRD), gam (AvgFlSev-1), eps (AvgNumFl*propBLH.loss), p (year-1)	980.83	2.72	0.03	11
psi (Isol+PRD), gam (propBLH.gain-1), eps (AvgNumFl*propBLH.loss), p (year-1)	981.1	2.99	0.03	11
psi (Isol+SiteArea), gam (AvgNumFl-1), eps (AvgNumFl*propBLH.loss), p (year-1)	981.18	3.08	0.02	11
psi (Isol+SiteArea), gam (AvgFlSev-1), eps (AvgNumFl*propBLH.loss), p (year-1)	981.64	3.53	0.02	11
psi (Isol+SiteArea), gam (propBLH.gain-1), eps (AvgNumFl*propBLH.loss-1), p (year-1)	981.91	3.8	0.02	11
psi (.), gam (.), eps (.), p (.)	1028.05	49.95	0.02	4

Table 4. Full set model-averaged parameter estimates (Est), standard errors (SE), and 95% confidence intervals (CI) for the AIC best-ranked dynamic occupancy models for swamp rabbits in southeast Missouri, USA. Psi = occupancy parameter, gam = colonization parameter, eps = extinction parameter, and p = detection parameter. Isol = site isolation from nearest tract of bottomland hardwood forest ≥ 16 ha (km), PRD = patch richness density (number of patches/100 ha), SiteArea = size of the site (ha), AvgNumFl = a factor for the number of floods relative to the average, AvgFlSev = a factor for flood severity relative to the average, propBLH.gain = a factor for an increase in the proportion of bottomland hardwood forest, propBLH.loss = a factor for a decrease in the proportion of bottomland hardwood forest, year = the year the survey occurred.

Coefficient	Estimate	SE	Lower CI	Upper CI
psi intercept	0.68	0.19	0.30	1.06
psi Isol	-1.01	0.30	-1.60	-0.42
psi PRD	-0.30	0.28	-0.85	0.26
psi SiteArea	0.26	0.37	-0.46	0.97
col AvgNumFl more	0.29	0.40	-0.50	1.08
col AvgNumFl less	0.01	0.41	-0.79	0.81
col AvgFlSev less	0.22	0.37	-0.50	0.94
col AvgFlSev more	0.06	0.36	-0.64	0.77
col propBLH.gain 0	0.15	0.29	-0.42	0.72
col propBLH.gain 1	0.27	0.62	-0.96	1.49
ext intercept	-1.31	1.62	-4.48	1.86
ext AvgNumFl more	-1.72	1.52	-4.70	1.26

ext AvgNumFl less	0.19	1.53	-2.81	3.19
ext propBLH.loss 1	0.34	0.58	-0.79	1.47
p year 2010-2012	2.18	0.19	1.81	2.54
p year 2022-2023	1.28	0.13	1.03	1.53

3.2.2.1 Occupancy

The model-averaged swamp rabbit occupancy probability was 0.66 (SE = 0.01) for the 2010-2012 decadal survey and 0.79 (SE = 0.01) for the 2022-2023 decadal survey (Table 4; Fig. 3). Of the three predictors retained for the occupancy parameter, only the site isolation model-averaged estimate was statistically significant; this predictor appeared in every top model and had a model-averaged estimate of -1.01 (SE = 0.30; Table 4). As expected, occupancy probability decreased as a site became more isolated from patches of bottomland hardwood forest ≥ 16 ha (Fig. 4).

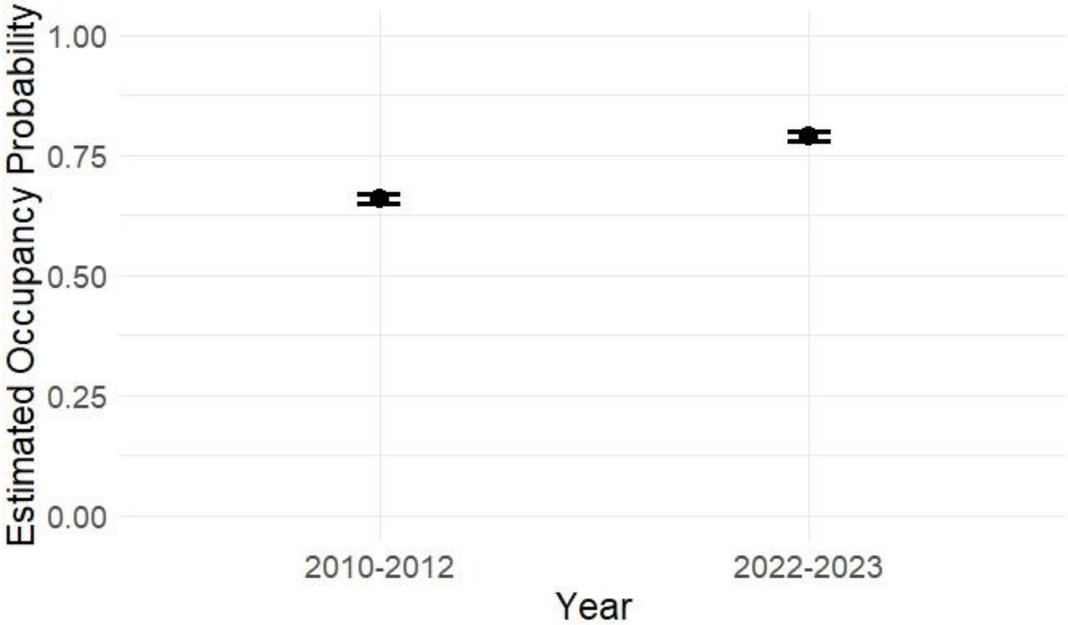

Figure 3. Model-averaged swamp rabbit occupancy probability estimates with standard error bars for survey sites in southeast Missouri, USA during the 2010-2012 and 2022-2023 decadal surveys.

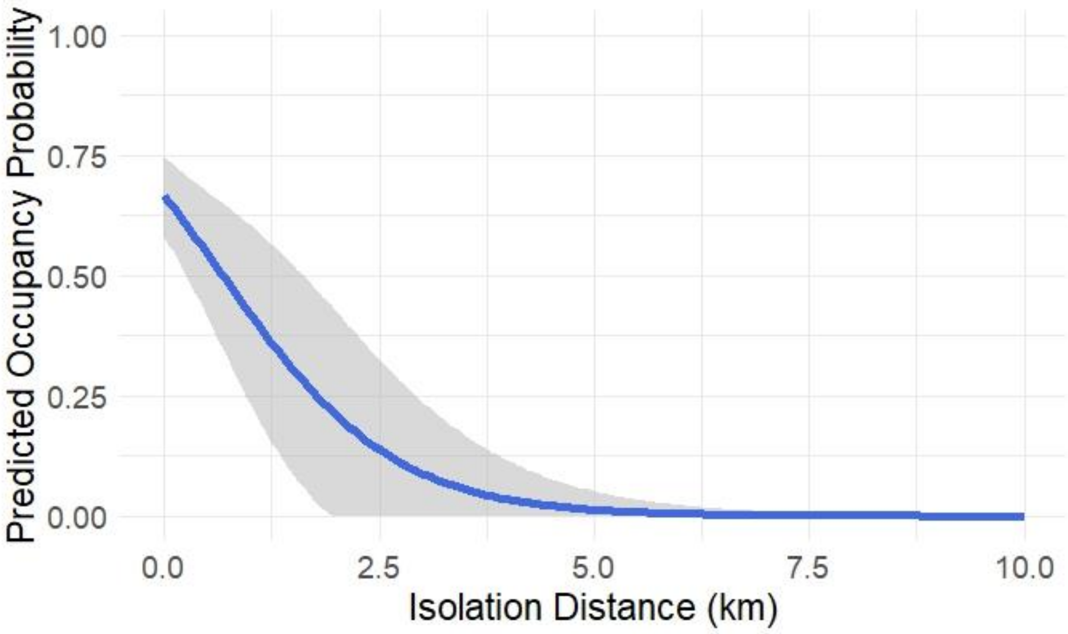

Figure 4. Model-averaged estimate of swamp rabbit occupancy probability with standard errors as a function of site isolation (km) for survey sites in southeast Missouri, USA during the 2010-2012 decadal survey.

While the patch richness density predictor was statistically significant in all individual models, it was not statistically significant in the model-averaged set (Table 4). The model-averaged estimate for patch richness density was -0.30 (SE = 0.28), indicating a negative relationship between occupancy probability and this predictor, as expected (Fig. 5). The site area predictor was also statistically significant in all individual models but not significant in the model-averaged set (Table 4). Thus, in individual models, site area may affect occupancy probability, but when the variability across all models is accounted for, this effect weakens. As expected, site area had a positive relationship with occupancy probability (0.26 ± 0.37), indicating that occupancy probability increased with site area (Fig. 6). Patch richness density performed slightly better in most models than site area, with patch richness density appearing higher in the model selection summary in almost all top models than site area.

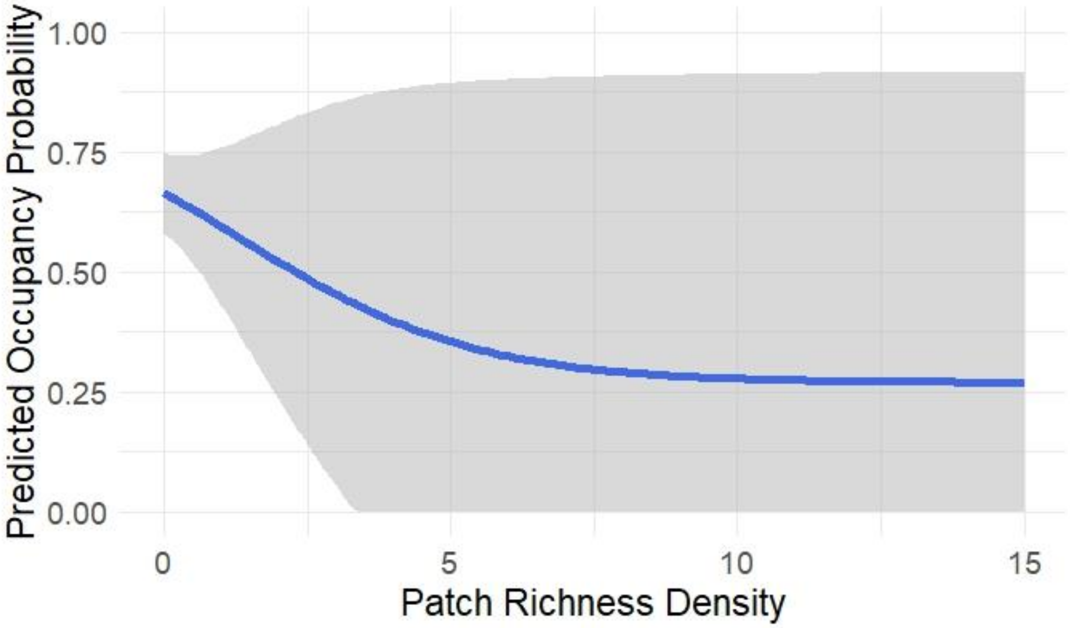

Figure 5. Model-averaged estimate of swamp rabbit occupancy probability with standard errors as a function of patch richness density for survey sites in southeast Missouri, USA during the 2010-2012 decadal survey.

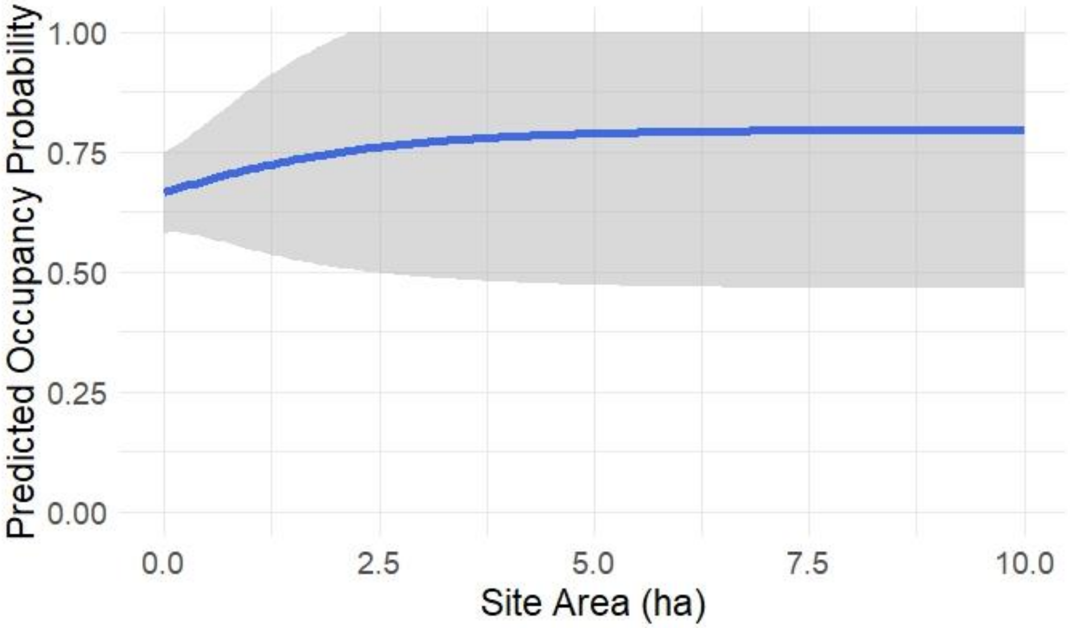

Figure 6. Model-averaged estimate of swamp rabbit occupancy probability with standard errors as a function of site area (ha) for survey sites in southeast Missouri, USA during the 2010-2012 decadal survey.

3.2.2.2 Colonization

None of the three predictors retained in the top models of colonization probability exhibited statistical significance in the model-averaged set (Table 4). Specifically, the colonization probability estimates for both the more and less floods than average levels were 0.29 (SE = 0.40) and 0.01 (SE = 0.41), respectively. While the individual models showed varying significance levels for the number of floods, with more floods significantly increasing colonization probability and fewer floods exhibiting a positive but nonsignificant effect (Fig. 7), the lack of significance for both levels in the model-averaged set suggests weakened effects when accounting for variability across all models. These estimates were not consistent with my prediction that colonization probability would decrease as the number of floods increased.

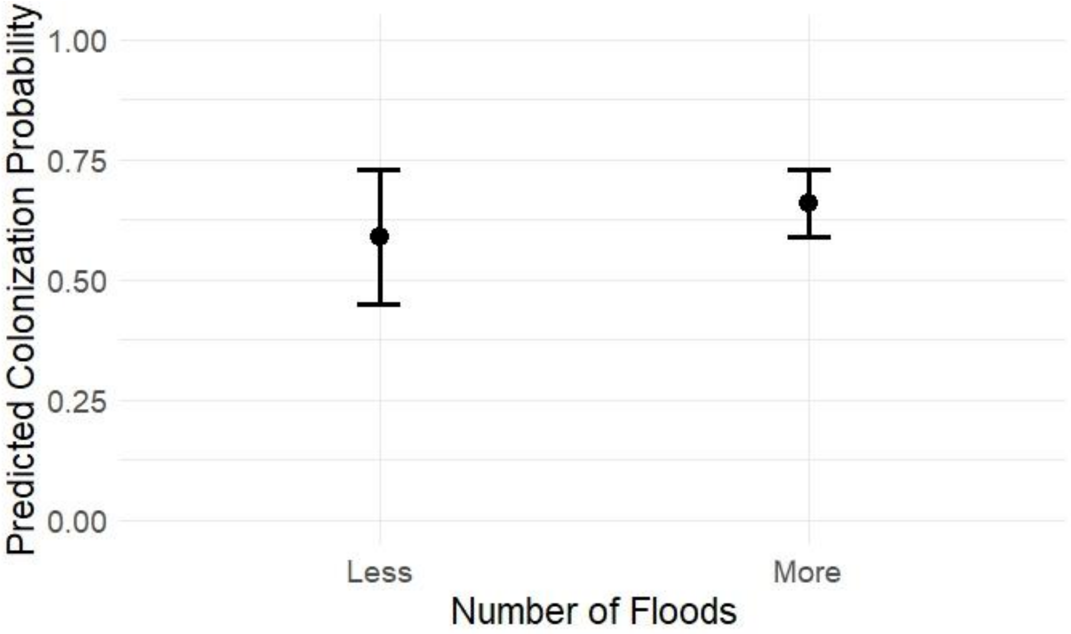

Figure 7. Model-averaged estimate of swamp rabbit colonization probability with standard errors as a function of the number of floods for survey sites in southeast Missouri, USA. “Less” indicates the site experienced fewer floods than the average, and “more” indicates the site experienced more floods than the average.

The model-averaged estimates for the levels for more and less severe floods than average were 0.06 (SE = 0.36) and 0.22 (SE = 0.37), respectively. Although the less severe floods level was not significant in the model-averaged set, it demonstrated significance in all individual models, indicating a positive relationship with colonization probability (Fig. 8). Conversely, the more severe floods level lacked significance in any individual model. The number of floods and flood severity at a site were highly negatively correlated (Appendix G), so these results align with those for the number of floods effect on colonization. Despite these varying degrees of significance in individual models, the lack of significance for both levels in the model-averaged set suggests a weakened influence when considering variability across all models.

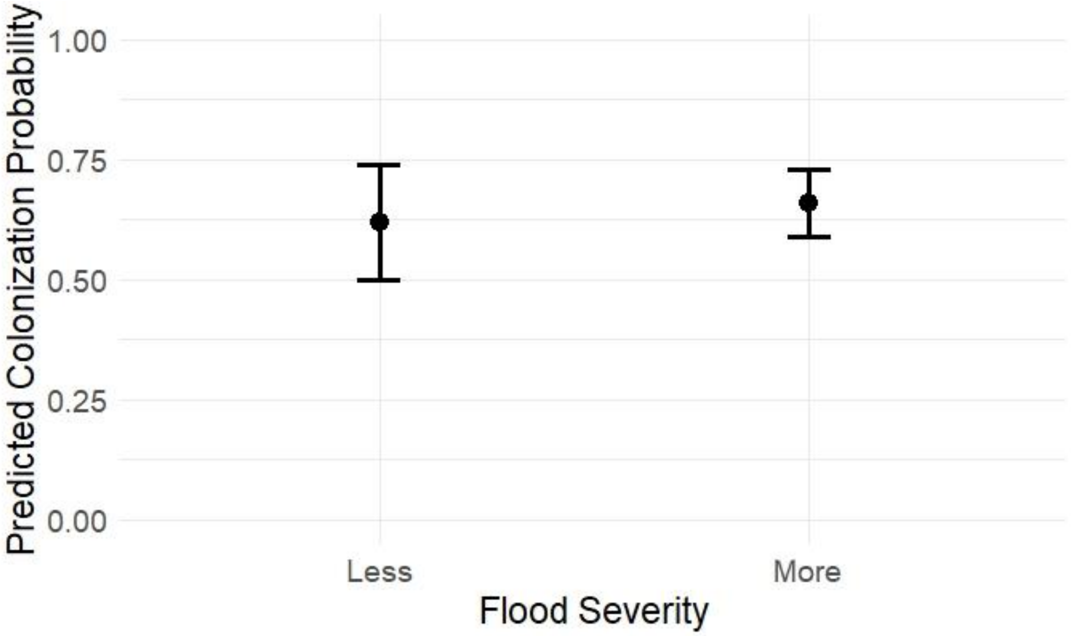

Figure 8. Model-averaged estimate of swamp rabbit colonization probability with standard errors as a function of flood severity for survey sites in southeast Missouri, USA. “Less” indicates the

site experienced less severe floods than the average, and “more” indicates the site experienced more severe floods than the average.

Interestingly, the predictor for bottomland hardwood forest cover increase was not significant in any individual model at either level. The model-averaged estimates for an increase in bottomland hardwood forest were 0.27 (SE = 0.62) and 0.15 (SE = 0.29) for no change. This lack of significance in all models precludes making any conclusions about the relationship between forest increase and colonization probability.

Lastly, the number of floods predictor generally outperformed both the flood severity and forest increase predictors, often ranking higher in the model selection summary. The flood severity predictor demonstrated slightly better performance than the forest increase predictor.

3.2.2.3 Extinction

Neither the number of floods nor forest decrease predictors exhibited statistical significance in the model-averaged set when testing extinction probability (Table 4). However, both levels of the number of floods predictor were significant in all individual models, suggesting there is uncertainty in the relationship between the number of floods and extinction probability. The estimate for more floods than average was -1.72 (SE = 1.52), and the estimate for fewer floods than average was 0.19 (SE = 1.53; Table 4). These results suggest that extinction probability is lower at sites with more floods than average and higher at sites with fewer floods than average (Fig. 9). This aligns with the results obtained for the colonization parameter, but contradicts my prediction that extinction probability would increase with the number of floods.

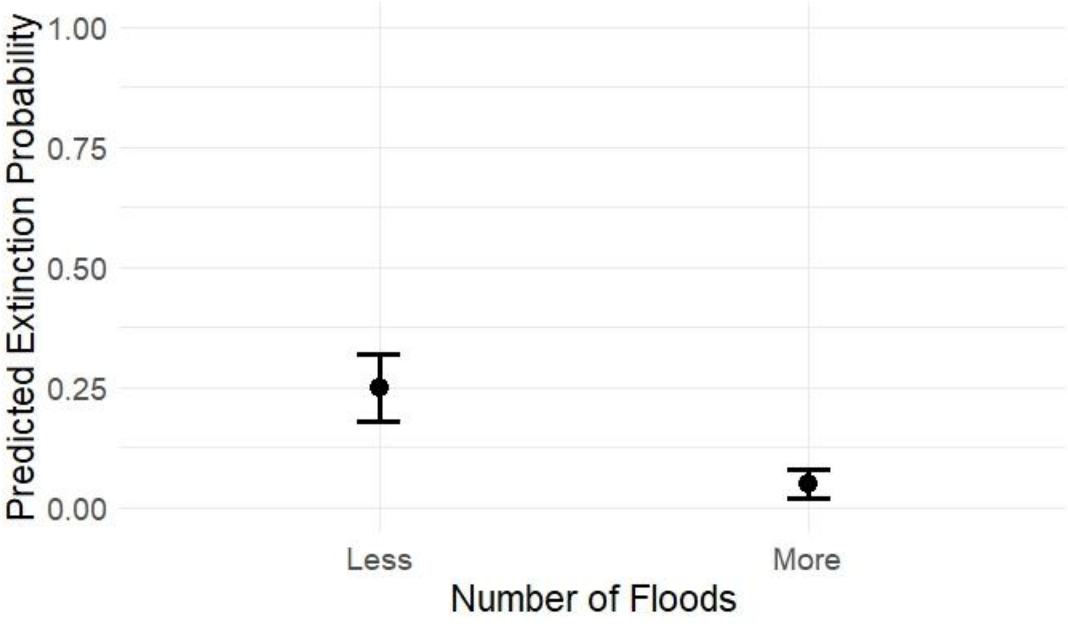

Figure 9. Model-averaged estimate of swamp rabbit extinction probability with standard errors as a function of the number of floods for survey sites in southeast Missouri, USA. “Less” indicates the site experienced fewer floods than the average, and “more” indicates the site experienced more floods than the average.

Although a positive relationship was observed between forest decrease and extinction probability, indicating that extinction probability increases with a decrease in bottomland hardwood forest, this relationship was not significant in any individual model. Therefore, there is too much uncertainty to draw any conclusions from this result. The number of floods predictor was retained in every model for the extinction parameter and performed better as an individual effect than it did in models with forest decrease as an additive effect.

3.2.2.4 Detection

As expected, survey year influenced detection probability of swamp rabbits, with the real-scale model-averaged estimate for 2010-2012 at 2.18 (95% CI = 1.81-2.54) and 1.28 in 2022-2023 (95% CI = 1.03-1.53; Table 4). Both estimates were statistically significant. The model-averaged detection probability decreased from 0.90 (SE = 0.19) in the 2010-2012 decadal survey to 0.78 (SE = 0.13) in the 2022-2023 decadal survey (Fig. 10).

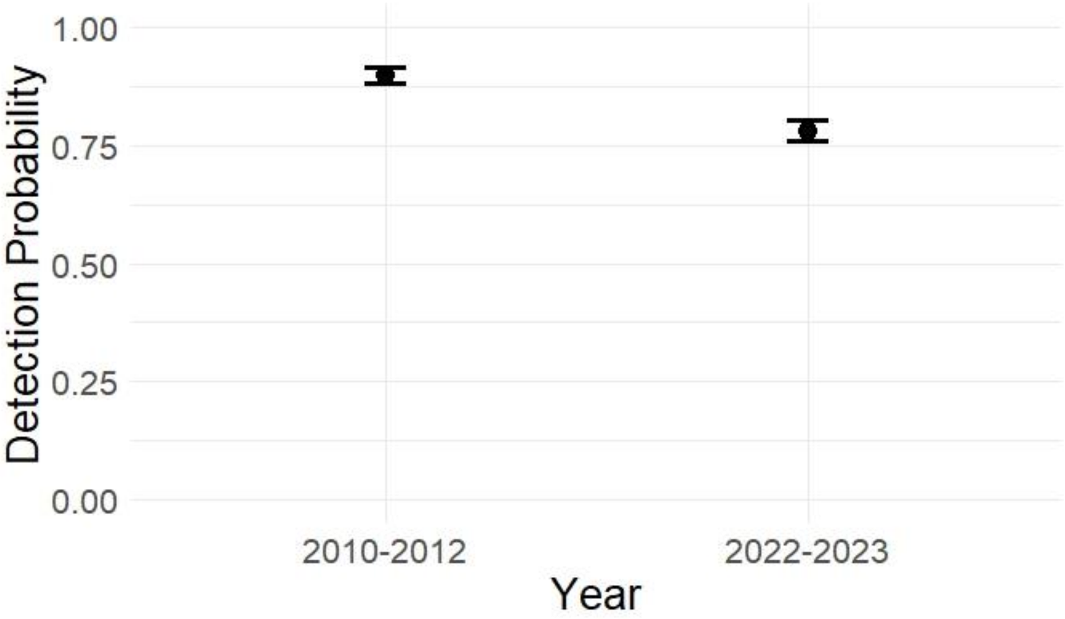

Figure 10. Model-averaged swamp rabbit detection probability estimates with standard error bars for survey sites in southeast Missouri, USA during the 2010-2012 and 2022-2023 decadal surveys.

3.3 Influence of Inclusion of Ground Latrines on Occupancy and Detection Probabilities

Thirteen sub-models were tested for the occupancy parameter while the detection parameter was held constant, for both the elevated-only and elevated + ground analyses. In both cases, 9 of 13 sub-models met the ΔAIC < 5 selection criterion (Appendix H, Appendix I). To further reduce these model sets, sub-models with an Akaike model weight of ≥ 5% and that were within approximately 90% of the cumulative model weight were selected. Thus, seven sub-models for the elevated-only analysis and eight sub-models for the elevated + ground analysis were retained for the second stage of modeling. All five occupancy predictors (site isolation, site area, proportion of BLH forest, edge length, and patch richness density) were retained in at least one of the sub-models for each analysis. Of seven sub-models testing the detection parameter, with occupancy held constant in the first stage, the top sub-model contained survey duration as a predictor (Appendix J, Appendix K) for both elevated-only and elevated + ground analyses. In both cases, this sub-model had 100% of the Akaike model weight. Thus, this predictor was retained for testing in the second stage.

In the second stage of testing for the elevated-only analysis (Table 5), four top models emerged (ΔAIC < 2), while the elevated + ground analysis (Table 6) identified three top models (ΔAIC < 2). The occupancy probability in the leading model was 0.95 (95% CI = 0.84-0.99) for the elevated-only analysis and 1.00 (95% CI = 0.93-1.00) for the elevated + ground analysis, although swamp rabbits were not identified at every site (Fig. 11). The detection probability in the leading model was 0.68 (95% CI = 0.60-0.75) for the elevated-only analysis and 0.84 (95% CI = 0.78-0.89) for the elevated + ground analysis (Fig. 12). In both analyses, site area and the proportion of bottomland hardwood forest repeatedly emerged in top models as predictors of occupancy probability, while site isolation also appeared in the elevated-only analysis (Table 7, Table 8). Survey duration was the only predictor that influenced detection probability.

Table 5. AIC-ranked occupancy models for elevated-only analyses of occupancy (psi) and detection probability (p) of swamp rabbits in southeast Missouri, USA, 2022-2023. dur = survey duration (min), prop.BLH = the proportion of a site comprised of bottomland hardwood forest, site.area = size of the site (ha), Isol = site isolation from nearest tract of bottomland hardwood forest ≥ 16 ha (km), edge = length of edge at a site (km), PRD = patch richness density (number of patches/100 ha), AIC = Akaike's information criterion, ΔAIC = the difference in AIC values between a specific model and the best fit model, w_i = Akaike model weight, and K = the number of parameters estimated.

Model	AIC	ΔAIC	w_i	K
p (dur), psi (prop.BLH)	357.16	0.00	0.31	4
p (dur), psi (site.area)	357.74	0.59	0.23	4
p (dur), psi (prop.BLH+Isol)	358.28	1.12	0.18	5
p (dur), psi (site.area+Isol)	358.62	1.46	0.15	5

p (dur), psi (edge)	359.31	2.15	0.11	4
p (dur), psi (PRD)	362.07	4.91	0.03	4
p (dur), psi (Isol)	364.91	7.76	0.01	4

Table 6. AIC-ranked occupancy models for elevated + ground analyses of occupancy (psi) and detection probability (p) of swamp rabbits in southeast Missouri, USA, 2022-2023. dur = survey duration (min), prop.BLH = the proportion of a site comprised of bottomland hardwood forest, site.area = size of the site (ha), Isol = site isolation from nearest tract of bottomland hardwood forest ≥ 16 ha (km), edge = length of edge at a site (km), PRD = patch richness density (number of patches/100 ha), AIC = Akaike’s information criterion, ΔAIC = the difference in AIC values between a specific model and the best fit model, w_i = Akaike model weight, and K = the number of parameters estimated.

Model	AIC	ΔAIC	w_i	K
p (dur), psi (prop.BLH + site.area)	309.32	0.00	0.35	5
p (dur), psi (site.area)	309.79	0.47	0.28	4
p (dur), psi (prop.BLH * site.area)	309.86	0.54	0.27	6
p (dur), psi (Isol + site.area)	311.72	2.40	0.11	5
p (dur), psi (prop.BLH)	327.16	17.84	0.00	4
p (dur), psi (edge)	330.77	21.45	0.00	4
p (dur), psi (PRD)	330.77	21.45	0.00	4
p (dur), psi (prop.BLH+edge)	330.77	23.45	0.00	5

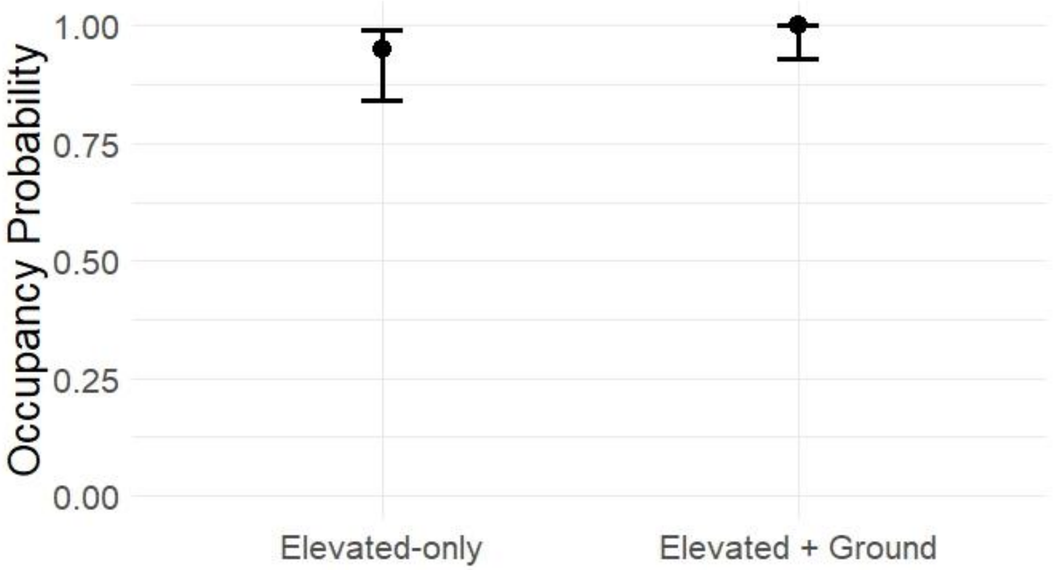

Figure 11. Occupancy probability and 95% confidence intervals at averaged predictor values for the top model for elevated-only and elevated + ground analyses for swamp rabbits in southeast Missouri, USA, 2022-2023. The top model for the elevated-only analysis included proportion of bottomland hardwood forest as a predictor of occupancy, whose average was 0.57. The top model for the elevated + ground analysis included proportion of bottomland hardwood forest and site area as predictors of occupancy, whose averaged values were 0.57 and 100 ha, respectively. While the occupancy probability for the elevated + ground analysis is estimated at 1.00, swamp rabbits were *not* detected at every site.

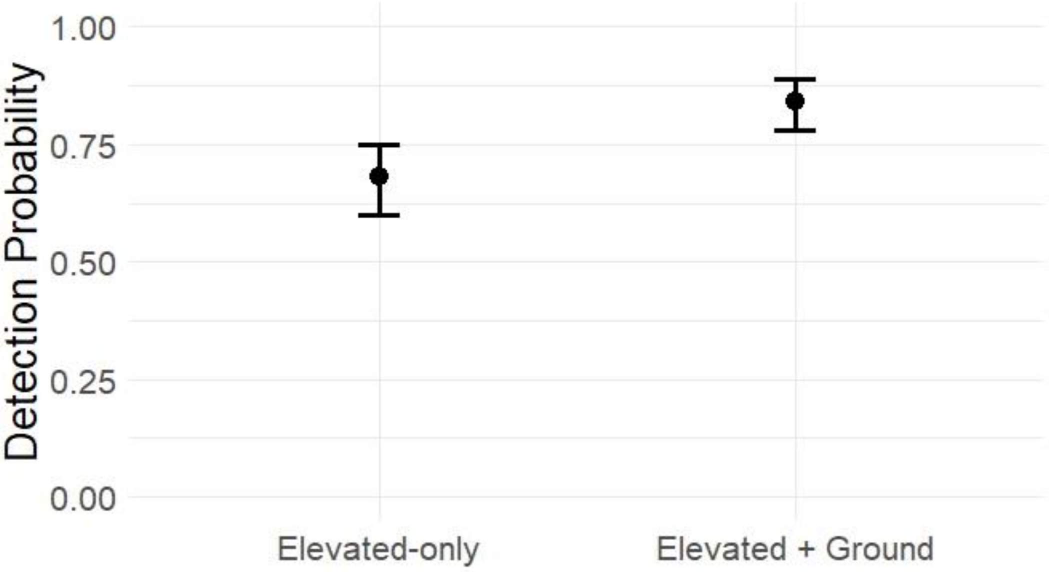

Figure 12. Detection probability and 95% confidence intervals at averaged predictor values for the top model for elevated-only and elevated + ground analyses for swamp rabbits in southeast Missouri, USA, 2022-2023. Both top models included survey duration as a predictor of detection probability. Averaged survey durations for both elevated-only and elevated + ground analyses were 39 min.

Table 7. Parameter estimates (Est) and 95% confidence intervals (CI) for the AIC best-ranked models of the elevated-only analysis of swamp rabbit occupancy (psi) and detection probability (p) in southeast Missouri, USA, 2022-2023. Occupancy and detection probability are modeled as a function of survey duration (dur), site area (site.area), the proportion of a site comprised of bottomland hardwood forest (prop.BLH), and patch isolation (Isol).

Models	Est	Lower CI	Upper CI
p (dur) psi (prop.BLH)			
psi intercept	3.40	0.53	6.26
psi prop.BLH	-0.68	-4.08	2.73

p intercept	3.30	2.71	3.91
p dur	-0.07	-0.08	-0.05
p (dur) psi (site.area)			
psi intercept	1.48	-0.23	3.19
psi site.area	0.02	-0.01	0.06
p intercept	3.23	2.66	3.80
p dur	-0.06	-0.07	-0.05
p (dur) psi (prop.BLH + Isol)			
psi intercept	4.09	-0.01	8.20
psi prop.BLH	-1.49	-6.16	3.17
psi Isol	-0.02	-0.06	0.02
p intercept	3.32	2.72	3.93
p dur	-0.07	-0.08	-0.05
p (dur) psi (Isol + site.area)			
psi intercept	1.61	-0.01	3.23
psi Isol	-0.02	-0.04	0.01
psi site.area	0.02	-0.01	0.06
p intercept	3.25	2.68	3.83
p dur	-0.06	-0.07	-0.05

Table 8. Parameter estimates (Est) and 95% confidence intervals (CI) for the AIC best-ranked models of the elevated + ground analysis of swamp rabbit occupancy (psi) and detection probability (p) in southeast Missouri, USA, 2022-2023. Occupancy and detection probability are modeled as a function of survey duration (dur), site area (site.area), the proportion of a site comprised of bottomland hardwood forest (prop.BLH), and patch isolation (Isol).

Models	Est	Lower CI	Upper CI
p (dur) psi (prop.BLH + site.area)			
psi intercept	0.35	-1.73	2.44
psi prop.BLH	-1.64	-3.96	0.69
psi site.area	0.09	0.02	0.16
p intercept	4.00	3.31	4.68
p dur	-0.06	-0.07	-0.05
p (dur) psi (site.area)			
psi intercept	-0.42	-2.12	1.29
psi site.area	0.08	0.01	0.14

p intercept	3.98	3.29	4.66
p dur	-0.06	-0.07	-0.05
p (dur) psi (prop.BLH * site.area)			
psi intercept	-2.65	-8.1	2.81
psi prop.BLH	2.12	-4.25	8.48
psi site.area	0.29	-0.10	0.67
psi prop.BLH:site.area	-0.23	-0.65	0.18
p intercept	3.97	3.29	4.64
p dur	-0.06	-0.71	-0.05

CHAPTER 4

DISCUSSION

4.1 Dynamic Occupancy Models

Dynamic occupancy models are a useful modeling framework for studying distribution dynamics, such as changes in nesting areas of golden eagles in Alaska (Martin et al., 2009), the spread of chronic wasting disease in white-tailed deer (*Odocoileus virginianus*) in Wisconsin (Cook et al., 2022), and the recolonization of France by grey wolves (*Canis lupus*) (Louvrier et al., 2018). The results of such studies allow wildlife and natural resource managers to understand current and past changes in state variables (e.g., occupancy, colonization, extinction, and detection), and to predict future changes in state variables based on changes in their predictors. While several studies have identified drivers of swamp rabbit distribution at the northern extent of their range, they have not, to date, analytically linked decadal studies to estimate drivers of change over time as my study has done. Overall, swamp rabbits were more likely to occur at sites that were large and well-connected with a limited number of land cover types, and they exhibited some degree of resiliency to both flood frequency and severity.

Although swamp rabbits are designated as imperiled in Missouri (MDC, 2015), I documented swamp rabbits at 148 of 176 sites (84%) compared to 144 of 211 in 2012 (68%; Fantz et al., 2017). Additionally, occupancy probability increased from 0.66 (SE = 0.01) in 2010-2012 to 0.79 (SE = 0.01) in 2022-2023. This is consistent with results from Pajda-de La O et al. (2013) who concluded that Missouri's swamp rabbit populations are expected to persist given no change in patch size and dispersion. Additionally, for all levels of predictors, colonization probabilities for swamp rabbits in Missouri were high (≥ 0.50), and extinction probabilities were low (≤ 0.25). I offer a few explanations that might explain the increase in occupancy, high colonization, and low extinction rates.

First, the suitability of conditions in bottomland hardwood forests changes over time (Scharine et al., 2009), which would influence swamp rabbit occupancy, colonization, and extinction probabilities. Crawford et al. (2018) reported that swamp rabbits in Illinois occupied more heavily forested sites with high basal areas. In Missouri, basal areas (m^2/ha) of common bottomland canopy species such as American sycamore and sweetgum have been increasing for many decades (Knapp & Pallardy, 2018). Further, canopy gaps are a key component of swamp rabbit habitat because they release the understory and stimulate early-successional growth (Allen, 1985; Zollner et al., 2000a; Scharine et al., 2009; Crawford et al., 2018). An increase in canopy gaps in Missouri may have been facilitated by the extreme drought in 2012 that preceded elevated canopy tree mortalities in 2013 (Knapp & Pallardy, 2018). Thus, Missouri's bottomland hardwood forests and other forested riparian areas have become more desirable for swamp rabbits, exhibiting higher basal areas and more canopy gaps.

However, without active forest management practices, swamp rabbit occupancy within these sites may follow a cyclical pattern. Occupancy probability could peak during successional stages when canopy gaps and understory vegetation are prevalent. Yet, as the canopy closes completely, reducing the sunlight reaching the forest floor necessary for sustaining understory vegetation, swamp rabbits may phase out of these sites. This pattern of colonizations and extinctions could persist for decades unless there are changes in, or the adoption of, management practices such as select-cut logging and uneven-aged forest management.

Second, climate change could be facilitating swamp rabbit occupancy. The increasing frequency of extreme stochastic events such as flooding, drought, tornadoes, and storms

(Swanston et al., 2018; Bouwer, 2011; Ummenhofer & Meehl, 2017) could contribute to the opening of forest canopies by causing tree mortality and creating canopy gaps in formerly dense canopy systems (Broadfoot & Williston, 1973; Cosgriff et al., 2007). Additionally, as the number of freezing days in southeast Missouri has trended downward over time (Appendix L(a); NWS, 2024), the number of days bodies of water in northern sites are frozen over would also have trended downward. Because swamp rabbits use bodies of water to escape predators (Lowe, 1958; Terrel, 1972), sites where water regularly freezes would impede this predator-avoidance behavior. These colder waters also increase the risk of hypothermia and physiological stress. Further, as winter temperatures have increased, winter snowfall in southeast Missouri has decreased (Appendix L(b); Ford et al., 2021; Demaria et al., 2016; NWS, 2024). Snow cover has been reported to increase swamp rabbit mortality risk indirectly due to increased risk of predation and, to a lesser degree, directly due to hypothermia (Hillard et al., 2018), and may also reduce food availability. Therefore, the observed trends in warmer winters and less snowfall would reduce these risks and allow swamp rabbits to expand their range northward, provided suitable forest conditions exist (Hillard et al., 2018). In 2010-2012, all thirteen sites in the three northernmost counties were unoccupied. However, 8 of these sites were colonized between 2012 and 2022, which supports these assertions.

Third, changes in land management may have contributed to this high colonization. For example, the number of acres enrolled in Wetland Practices of the U.S. Department of Agriculture’s Conservation Reserve Program doubled for floodplains and bottomland hardwood forests between September 2012 and December 2023 (USDA, 2012; USDA, 2023). This uptake in conservation practices by Missouri’s private landowners, who primarily own smaller, more isolated sites, may have improved conditions at formerly unoccupied sites, making them more attractive to swamp rabbits. Further, as our understanding of historic conditions in bottomland hardwood forests has evolved, management practices to maintain and restore these forests may have adapted accordingly (Stanturf et al., 2000; Hanberry et al., 2012).

While acknowledging that direct comparisons across studies are difficult due to differences in methodology, swamp rabbit populations in Missouri do fall on the higher end of reported occupancy probabilities, with estimates ≥ 0.66 over the past decade. Other states along the northern edge of the swamp rabbits’ range have reported occupancy probabilities of 0.71 in Illinois (Scharine et al., 2011) and 0.35 in Indiana (Roy Nielsen et al., 2008). Studies in other neighboring states have reported naïve occupancies of > 0.75 in Arkansas where swamp rabbit populations are considered secure (Fowler & Kissell, 2007; NatureServe, 2023), and 0.49 in Kentucky (Sole, 1994). While Roy Nielsen et al. (2008) accounted for detection probability in Indiana, there were only 7 contiguous habitat patches > 50 ha in their entire 7-county study area. This lack of large, contiguous sites may contribute to swamp rabbits' low occupancy in this state. In Kentucky (Sole, 1994), two factors may have contributed to their lower naïve occupancy estimate: 1) since sites were surveyed only once, a detection probability could not be estimated, potentially leading to an underrepresentation of true occupancy, and 2) surveys were conducted in June and focused primarily on identifying elevated latrines. However, a seasonal pattern in elevated latrine usage has been noted in many studies, with usage dropping during the summer (Lowe, 1958; Terrel, 1972; Whitaker and Abrell, 1986; Zollner et al., 1996). Therefore, it’s possible swamp rabbits were more likely to go undetected during the survey period due to this seasonal variation.

Although colonization and extinction probabilities for swamp rabbit populations in other states are currently unavailable, Roy Nielsen et al. (2008) reported that the colonization parameter for the top 3 occupancy models for swamp rabbits in Indiana was constant, with no predictor influencing colonization. However, they did not report the parameter estimate or probability. The colonization probabilities reported here are higher than published colonization probabilities for other *Sylvilagus* species, while extinction probabilities are similar. Like swamp rabbits, New England cottontails (*Sylvilagus transitionalis)* are habitat specialists, exist as metapopulations, and are also experiencing population declines and habitat loss (Bischoff et al., 2023; Litvaitis et al., 2003). Colonization and extinction probabilities for New England cottontails were 0.129 and 0.143, respectively (Bischoff et al., 2023). The same study reported that colonization and extinction probabilities for eastern cottontails, a habitat generalist, were 0.346 and 0.076, respectively. An endangered species endemic to the Lower Keys of Florida, the Lower Keys marsh rabbit (*Sylvilagus palustris hefneri*) also exists in metapopulations threatened by habitat loss and fragmentation, as well as sea-level rise, habitat succession, and exotic predators (Forys & Humphrey, 1996; Cove et al., 2018). The colonization and extinction probabilities for the Lower Keys marsh rabbit are 0.012 and 0.110, respectively (Cove et al., 2018). While differences in survey methodology and life history for each of these species likely affect these probabilities, the colonization rate for swamp rabbits is notably high.

One possible caveat of my occupancy estimate for southeast Missouri could be attributed to the selection criteria for survey sites. These sites were chosen based on local knowledge that they were known or suspected to be occupied by swamp rabbits. Sites with unknown occupancy history or with habitats not considered suitable were not selected and have not been surveyed in any of Missouri's decadal surveys (Fantz et al., 2017). This focused approach, while allowing for the investigation of population stability over time in specific sites, might contribute to the comparatively high occupancy estimate. It is important to recognize that if less suitable sites or sites with unknown occupancy history were included, the overall estimate might decrease. While surveying sites where swamp rabbit occurrence is expected is valuable for understanding population dynamics in those specific locations, a more comprehensive approach that includes a wide suitability gradient would enhance our understanding of swamp rabbit occupancy in Missouri. Many of the models tested in my study struggled to identify significant predictors of occupancy, which may be an artifact of the consistently high occurrence. Including environmental data from more sites where swamp rabbits were *not* detected or that were considered unsuitable would likely facilitate a more meaningful estimation of these relationships (MacKenzie & Royle, 2005). Future research endeavors should strive to fill this knowledge gap by conducting surveys across various suitability gradients, providing a more complete insight into swamp rabbit distribution in the state.

Research on the impact of flooding on swamp rabbit population persistence is limited, yet vital for understanding potential threats and developing conservation strategies. Rabbits are an important prey item for bobcats (*Lynx rufus*) and raptors, so a decline in swamp rabbit populations could have detrimental impacts on these predators (Fritts & Sealander, 1978; Steenhof & Kochert, 1988). Swamp rabbit declines may also disrupt essential ecological processes like nutrient cycling and seed dispersal in bottomland hardwood forest ecosystems (Parsons et al., 2016; Coggan et al., 2018). Additionally, as a valued game species, their loss could result in diminished recreational opportunities for hunters. Robinson et al. (2016) reported that quasi-extinction risks for populations in Illinois increased to as high as 40% with increases in catastrophic flooding. Reported effects of flooding on swamp rabbits include increases in predation, starvation, hunter-take, drowning, and decreased fecundity (Conaway et al., 1960; Bunch et al., 2005; Zollner et al., 2000b; Crawford et al., 2018). However, Barbour et al. (2001)

suggested that flood events improved swamp rabbit habitat in part of their study area by killing trees and opening up the canopy, allowing an increase in early-successional growth in the understory.

Contrary to my predictions, swamp rabbits in my study area were generally equally as likely to colonize sites with more floods than fewer, and generally equally as likely to colonize sites with more severe floods than less severe ones. Interestingly, the results revealed a strong negative correlation between the number of floods and flood severity predictors. Sites experiencing higher flood frequencies tended to have milder flood events, while those with fewer occurrences faced more extreme inundation. This correlation aligns with the geographical distribution of sites on or off a batture, which are lands between a levee and a major river or body of water. In general, sites with fewer floods were on the Mississippi and St. Francis River battures. These are two major rivers in the Missouri Bootheel with greater water-holding capacity than smaller waterways further inland or further upstream (USGS NWIS, 2024). Thus, it would take more extreme rainfall or snowmelt events for these rivers to overflow their banks and flood the batture (Decker & Guinan, 2011). By contrast, the smaller waterways have less water-holding capacity and flood more frequently from less severe rainfall or snowmelt events (Brakenridge, 2023; Decker & Guinan, 2011). An exception to this relationship is observed at sites farther north in the greater St. Louis area where waterways are more heavily impacted by snowmelt, leading to a positive correlation between flood frequency and severity.

Overall, this relationship sheds light on the slightly higher colonization probabilities observed at sites experiencing more frequent floods. The rare yet intense flood events along major rivers may inflict more substantial damage to bottomland hardwood forests and understory growth compared to the cumulative impact of multiple mild floods. However, because colonization probabilities were very similar for all levels of flood predictors (0.50-0.57), the difference in effects may not be biologically meaningful to swamp rabbits, which may explain the low extinction probabilities for both flood frequency levels. These findings are consistent with a prior study conducted on a subset of my sites following a significant flood event, which reported higher occupancy rates along the flood-prone batture on the Mississippi River compared to areas at lower risk of flooding, such as those protected by ditches or levees (Timm et al., 2022).

The uncertainty associated with flooding effects on colonization and extinction probabilities could stem from underlying site characteristics such as soil type and vegetation. For example, in Alabama, McCollum & Holler (1994) reported that sites impacted by flooding from beaver dams had twice as many pellet groups as lower floodplains and up to 17 times as many pellet groups as headwater floodplains. These beaver-impacted sites had higher herbaceous canopy cover, lower basal area, and reduced tree canopy cover than both the lower and headwater floodplains. Therefore, sites with a more productive, well-drained soil profile and seed bank may benefit from increased flooding that creates stochastic disturbances by killing trees and opening the canopy, enhancing early-successional growth. Increased flooding may, in fact, transport seeds and more productive soils to sites. However, this relationship might evolve over time, with repeated, severe floods potentially altering the forest structure and composition beyond the threshold for swamp rabbits, precluding swamp rabbit occupancy and colonization and encouraging extinction. Changes in forest and soil compositions can subsequently affect flood patterns by altering the forest's infiltration and water storage capacity, particularly on afforested and reforested sites (Humann et al., 2011).

Regardless, these results suggest swamp rabbits exhibit some level of resiliency towards flood effects, despite Robinson et al.'s (2016) suggestion that catastrophic flooding increases quasi-extinction risks. This is an encouraging finding because climate models have predicted that flood occurrence and severity are expected to increase in Missouri in the future (Swanston et al., 2018; Andersen & Shepherd, 2013; Winkler et al., 2014). However, these results should be interpreted with caution, as Timm et al. (2022) suggested that larger patches and better connectivity at batture sites may have facilitated higher populations at these sites than the smaller and more isolated lower flood risk sites outside of the batture. In line with this, Barbour et al. (2001) suggested that major flooding events at sites that were very isolated and fragmented in Illinois contributed to the extirpation of these populations. Therefore, future research on flooding effects on swamp rabbit occupancy should investigate site size, connectivity, and microhabitat variables such as understory growth and canopy cover that might explain the uncertainties in these estimates.

Swamp rabbit occupancy in Missouri exhibited a negative association with patch richness density, indicating that sites with more land cover types were less likely to be occupied, which is consistent with my prediction. This trend aligns with the species' status as a habitat specialist (Chapman & Feldhamer, 1981), requiring higher proportions of bottomland hardwood forest and, consequently, fewer land cover types. However, there was some uncertainty around this estimate, suggesting that underlying site characteristics may influence the relationship between swamp rabbit occupancy and patch richness density. One possible explanation is that certain types of land cover (e.g., wooded wetland, emergent herbaceous wetland, deciduous forest) are more likely to be occupied than other types (e.g., agriculture, urban). For example, Crawford et al. (2018) reported that swamp rabbits selected sites closer to early-successional and mature bottomland hardwood forest patches and avoided agricultural fields and residential areas, even during periods of flooding when they had no other upland refugia, subsequently dying in the inundated forest. Thus, sites with higher patch richness density of the former types likely affect occupancy differently than sites with higher patch richness density of the latter types. Preferred land cover types would positively impact occupancy by providing needed forage and refugia throughout the year as understory growth and flood or standing waters shift. My study did not investigate the specific composition of land cover types at sites, so I could not resolve these potential differences. Further research exploring this relationship would help improve our understanding of how different land cover types at different densities affect swamp rabbit occupancy.

Swamp rabbits in Missouri were more likely to occupy larger sites, which is consistent with my prediction and with results from other studies (Pajda-De La O et al., 2013; Roy Nielsen et al., 2008). However, predicted occupancy plateaued when site size reached approximately 4 ha, indicating that sites ≥ 4 ha have a similar probability of being occupied (Figure 6). Korte (1975) suggested that swamp rabbits in Missouri needed ≥ 100 ha of suitable habitat to maintain populations, but several studies have since documented swamp rabbits occurring at sites much smaller than 100 ha (Sole, 1994; Scheibe & Henson, 2003; Scharine et al., 2011; Roy Nielsen et al., 2008; McCollum & Holler, 1994). Additionally, swamp rabbit home ranges have been reported as less than 4 ha in many locations (Dumyahn & Zollner, 2010; Zollner et al., 2000b; Terrel, 1972; Allen, 1985). Most recently, Crawford et al. (2018) reported mean home ranges of 2.52 ha (± 2.51) in Illinois. This result indicates that in many cases, sites as large or slightly larger than a single swamp rabbit's home range size could be occupied.

While some might interpret this result as an indication that swamp rabbits do not necessarily require large sites, it's crucial to consider that occupancy at smaller sites may depend on connectivity with other suitable sites to sustain viable populations over time. Smaller sites may also serve as stopover points for dispersing rabbits, resulting in fluctuating occupancy throughout the year. This pattern aligns with the metapopulation dynamics of swamp rabbits in Missouri (Pajda-de La O et al., 2013), where dispersal is limited, but movement occurs among patches, and colonizations counteract local extinctions (Roy Nielsen et al., 2008; Levins, 1969). The uncertainty surrounding the effects of site area as a predictor of occupancy may be linked to underlying site characteristics, such as vegetation structure and composition. A small but highly suitable site may be more likely to be occupied than a small, less suitable site or a larger, unsuitable site (Whitaker & Abrell, 1986; Fowler & Kissell, 2007). Additionally, this uncertainty may be associated with connectivity – sites with better connectivity may be more likely to be occupied than more isolated sites, regardless of size (Fowler & Kissell, 2007).

As predicted, swamp rabbit occupancy probability decreased as the isolation from bottomland hardwood forest patches increased. This finding aligns with the results reported by Pajda-de La O et al. (2013), where isolation from one source population was identified as a significant predictor of swamp rabbit occupancy in both the 1991-1992 and 2001-2002 decadal surveys. Although swamp rabbits were detected at forested sites over 150 kilometers from the bottomland hardwood forests of the Mississippi Alluvial Valley that constitute the majority of their range in Missouri, these populations were apparently less abundant, with fewer overall detections and pellet groups. Changes in isolation between 2010-2012 and 2022-2023 were minimal, so the relationship between isolation and colonization or extinction rates was unable to be determined. Had more substantial changes in isolation been observed, it might have been possible to estimate these relationships, and changes in occupancy, colonization, or extinction parameters may have resulted.

Given the observed negative relationship between isolation distance and swamp rabbit occupancy, a reasonable expectation would be a decrease in colonization rates and an increase in extinction rates as sites become more isolated. However, Roy Nielsen et al. (2008) found no support for the effects of isolation on colonization rates for swamp rabbits in Indiana. They suggested that this lack of support might be attributed to small sample sizes or a difference in importance between straight-line distance and dispersal corridor distance, yet there is virtually no data on swamp rabbit dispersal distances. Some studies have assumed dispersal distances > 1 km (Woolf & Barbour, 2002; Roy Nielsen et al., 2008; Scharine et al., 2011), although this is much higher than the dispersal distances of other *Sylvilagus* species. Robinson et al. (2016) used a dispersal distance of 200 m, reasoning that swamp rabbits likely don’t disperse as far as marsh rabbits (*Sylvilagus palustris*), who evolved in patchy habitats along the Gulf and Southeast coasts and had an average dispersal distance of 300 m. My results indicate that swamp rabbit occupancy probability decreases very quickly as sites become more isolated, with the likelihood dropping to 0.40 when a site is 1 km from other bottomland hardwood forest patches and to 0.20 when a site is 2 km from other BLH forest patches. The average distance from other BLH forest patches ≥ 16 ha in my study area was over 11 km, and much of the intervening land cover was an agricultural matrix. This indicates that many populations likely have little opportunity to disperse beyond the boundaries of their forest patch as swamp rabbits have not been observed to cross agricultural fields (Crawford et al., 2018). These discrepancies emphasize the necessity of ongoing monitoring to understand the effects of isolation on swamp rabbit populations and to address lingering questions regarding swamp rabbit dispersal distance.

Interestingly, while swamp rabbits are bottomland hardwood forest specialists (Chapman & Feldhamer, 1981), the predictor for the proportion of BLH forest at a site was not included in top models. This is not consistent with my prediction. Further, while the predictors for an increase or decrease in the proportion of BLH forest were included in top models for both the colonization and extinction parameters, none of the estimates were significant in either individual models or the model-averaged set. This may be because values for change in the proportion of bottomland hardwood forest were uniformly low; 96% of sites experienced a less than 3% change in either direction. Additionally, the variation in the proportion of BLH forest ranged from 0-100% with a mean of 58% and a median of 81%, and swamp rabbits occupied sites across this entire gradient. Occupied sites with 0% bottomland hardwood forest were largely dominated by deciduous forest. This suggests that underlying site features may influence the relationship between occupancy, colonization, and extinction, such as microhabitat characteristics that are not as easily measured by GIS remote sensing techniques. Previous occupancy studies have included predictors such as patch area and site area, without explicitly considering the proportion of bottomland hardwood forest within a site (Pajda-De La O et al., 2013; Dailey et al., 1993; Scheibe & Henson, 2003; Fantz et al., 2017; Roy Nielsen et al., 2008; Scharine et al., 2011). However, these predictors are often vaguely defined and sometimes encompass multiple land cover types. Although these predictors may share similarities, they are not identical, posing challenges for making direct comparisons between studies.

One possible explanation for the lack of significance for this predictor is that our understanding of swamp rabbit habitat needs at the edge of their range is incomplete, as these peripheral environments often differ from core environments (Hardie & Hutchings, 2010; Dumyahn et al., 2015). Indeed, Terrel (1972) noted that while swamp rabbits in Indiana did not occur beyond the southern bottomland hardwood forest type they were quite flexible in site selection within this type. Populations in Missouri appear to exhibit this same flexibility as they occur at many sites not dominated by southern BLH forests and with a wide range of patch richness densities.

Another possible explanation is the targeted surveys of sites that were historically known or suspected to be occupied by swamp rabbits, as previously described. Including more sites that were unoccupied could enable modeling software to better establish the relationship between forest types and occupancy.

Among the predictors considered for detection, only the year predictor was retained in the top models. Though the detection probability changed between decadal surveys, dropping from 0.89 to 0.78, these probabilities are still very high, and higher than others reported in neighboring states. Roy Nielsen et al. (2008) reported a detection probability of 0.70 in Indiana, where, like Missouri, sites are isolated by agriculture and consist of remnant bottomland hardwood forests. Scharine et al. (2011) reported a detection probability as low as 0.12 in southern Illinois. However, this value was based on detections from trapping data, not pellet surveys, and their survey sites had a maximum area of 74.6 ha. By contrast, the average site size in Missouri after removing the six largest sites was 101 ha. Conversely, Barbour et al. (2001) conducted pellet surveys in southern Illinois at sites ranging from 25 ha to > 4400 ha and detected swamp rabbits 48% of the time. These differences in study areas and methodologies likely contributed to Scharine et al.'s (2011) low detection probability.

Although site area has appeared as a significant predictor for swamp rabbit detection in other studies, it was not important in my study. Scharine et al. (2011) reported site area had a negative relationship with detection in Illinois, while Fantz et al. (2017) reported that it had a positive relationship with detection in Missouri in the 2010-2012 decadal survey. This suggests that site area may have a nuanced and context-dependent influence on swamp rabbit detectability. Possible factors contributing to this complexity could include variations in vegetation structure, land cover types, or the overall landscape configuration.

Additionally, weather conditions have been suggested to influence swamp rabbit detection, with Fantz et al. (2017) reporting a negative impact of daily temperature on detection. However, daily precipitation was not retained in top models for detection in my study, despite Hunt's (1959) suggestion that swamp rabbit activity heightened after rain events. Given the consistently high detection probability for both decadal surveys in southeast Missouri, precipitation may have had a negligible impact on detection probability. This may also be attributed to the binary nature of pellet surveys that focus on the presence or absence of, rather than the abundance of, pellets. In areas with both high detection and occupancy probabilities, differences in the abundance of pellets during or after rainfall events may be more obvious than changes in the presence or absence of pellets and may provide more meaningful information regarding swamp rabbit responses to precipitation.

Overall, the observed decrease in detection probability between decades is not concerning. This variability could be attributed to different observers conducting the surveys between decades, variations in the surveyed areas within sites, or differences in visual obstruction of latrines between decades. If a sustained decrease in detection probability was observed over several decadal surveys, with or without an associated decrease in occupancy, or if the decrease between these two surveys was larger, this would be more alarming.

4.2 Influence of Inclusion of Ground Latrines on Detection and Occupancy Probabilities

The presence of latrines on logs, stumps, rocks, and other elevated surfaces is a reliable indicator of swamp rabbit presence, but swamp rabbits do not exclusively defecate on elevated surfaces. Ground latrines have been included in other swamp rabbit occupancy surveys, albeit to a limited degree in some cases. For instance, only one site in Illinois was reported to have a ground latrine (Barbour et al., 2001). While Heuer and Perry (1976) rarely found ground latrines in Louisiana, McCollum and Holler (1994) identified abundant ground latrines in Alabama, constituting up to 90% of all latrines at one site. In Arkansas, swamp rabbits used ground latrines 33.5% and 9.6% of the time in two consecutive years (Fowler & Kissell, 2007).

However, no study has explored how including these ground latrines in the detection methods affected occupancy and detection probabilities. In Missouri, 9.7% of latrines identified during the 2022-2023 decadal survey were on the ground.

As expected, the inclusion of ground latrines did increase occupancy and detection probabilities; however, these changes held limited biological significance. The detection probability rose from 0.68 (95% CI = 0.60-0.75) in the leading model for the elevated-only analysis to 0.84 (95% CI = 0.78-0.89) in the top model for the elevated + ground analysis (Fig. 11). Both values indicate consistently high swamp rabbit detection, even without incorporating an additional detection method. The difference between occupancy probability values was even more negligible: 0.95 (95% CI = 0.84-0.99) in the leading model for the elevated-only analysis and 1.00 (95% CI = 0.93-1.00) in the leading model for the elevated + ground analysis (Fig. 10). This indicates that the sites in my study area have an extremely high likelihood of being occupied by swamp rabbits whether or not ground latrines are considered, though it should be noted swamp rabbits were *not* detected at every site, as the elevated + ground value might suggest.

The increase in detection probability may, however, have practical significance. Field observations suggest that many sites may harbor undetected or inconclusively identified ground latrines, with the possibility that the eleven sites exclusively featuring ground latrines may also contain undetected elevated latrines due to accessibility constraints or time limitations. Despite this, the results suggest that including ground latrines in swamp rabbit occupancy studies might be unnecessary. The risk of misidentifying ground latrines as swamp rabbit in origin rather than cottontail may lead to false positives, potentially outweighing the increases in detection and occupancy probabilities. Yet the season during which surveys are conducted may be an important factor when weighing the risks and benefits. Field observations from March 2023 site visits to collect swamp rabbit pellets for a separate, ongoing project revealed difficulties in locating elevated latrines previously identified during the 2022-2023 decadal survey. In some instances, swamp rabbits appeared to have relocated to areas with better feeding opportunities as spring green-up began or moved to other regions as spring drawdowns affected managed sites and standing waters shifted. Several studies have reported an apparent seasonal pattern in elevated latrine usage by swamp rabbits in line with this trend (Lowe, 1958; Terrel, 1972; Whitaker and Abrell, 1986; Zollner et al., 1996). Thus, the inclusion of ground latrines may exhibit a more significant role in occupancy surveys conducted during the spring and summer when the use of elevated latrines drops. Further research on the seasonality of elevated and ground latrine usage would help clarify this situation.

It's important to acknowledge that, although all observers were trained in swamp rabbit pellet identification, some ground latrines may have been misattributed to swamp rabbits when they actually originated from eastern cottontails, potentially resulting in false-positive errors. Efforts were made to reduce this uncertainty by dismissing inconclusive ground latrines in the field, and by comparing detections against field notes from all three visits to a site and removing suspicious detections of ground latrines. Previous studies reported limited overlap in space use of eastern cottontails and swamp rabbits, with cottontails preferring more open fields and shrubby forest with dense herbaceous understory and swamp rabbits replacing them as stand development moved towards mature forests and swamps (Crawford et al., 2018; Toll et al., 1960; Taylor and Lay, 1949). However, swamp rabbits use early-successional upland habitat as refugia during periods of flooding and have been captured along field and road edges (Lowe 1958; Toll et al., 1960; Terrel 1972; Zollner et al., 2000b; Vale & Kissell, 2010), and eastern cottontails have been captured in bottomland hardwood forests with dense herbaceous understory (Scharine et al., 2011; Crawford et al., 2018). Despite this documented overlap, there has been no research on shared latrine use between these sympatric species, or if the presence of a latrine from one species precludes the presence of a latrine from the other. My study combined our best efforts and identification knowledge to correctly distinguish swamp rabbit pellets for use in occupancy analyses.

4.3 Conclusions

The primary objectives of my study were to enhance management strategies for swamp rabbits in southeast Missouri by (1) estimating probabilities of occupancy, colonization, extinction, and detection, and (2) identifying the environmental factors driving changes in their distribution. Swamp rabbit occupancy has increased over the past decade and colonization rates are promising, suggesting high site suitability within southeast Missouri. Given their proposed role as bioindicators of bottomland hardwood forests (Hillard et al., 2017), these results would imply potential benefits for other BLH forest obligates, including small mammals, invertebrates, amphibians, and forest interior songbirds, among others. In summary, sites should be large and well-connected with a limited number of land cover types. Swamp rabbits appear to exhibit some level of resiliency to the effects of flooding given current site conditions, with floods likely facilitating colonization.

The secondary objective of my study was to investigate the influence of the inclusion of ground latrines on swamp rabbit detection and occupancy probabilities for the 2022-2023 decadal survey. My results indicate that the inclusion of ground latrines in analyses has little effect on these parameters. While both occupancy and detection probabilities slightly increased when ground latrines were included, this step is likely not necessary for fall-winter occupancy surveys but may be prudent for spring-summer surveys when elevated latrine use declines.

My study provides valuable insight into swamp rabbit occupancy dynamics in southeast Missouri and the environmental forces shaping this distribution. However, our understanding of the exact relationship between some of these environmental predictors and occupancy remains limited. Future research should incorporate sites with unknown occupancy history and those considered unsuitable to improve model performance, reduce uncertainty in estimates, and provide a more complete understanding of swamp rabbit habitat needs and environmental thresholds. Attention should also be given to determining swamp rabbit dispersal distances and success, examining the interplay of specific land cover types at a site with site isolation and site size on occupancy, and investigating how soil and forest structure and composition characteristics influence flood effects on bottomland hardwood ecosystems over time, particularly in light of predicted increases in extreme precipitation and flood events.

CHAPTER 5

MANAGEMENT RECOMMENDATIONS

The Swamp Rabbit Working Group at the Missouri Department of Conservation has established an occupancy threshold of 0.80 at which managers should consider changing the swamp rabbit’s state rank in Missouri from an S2 imperiled species to an S3 vulnerable species, provided no other risks to the populations are identified. Occupancy for the 2022-2023 survey season was estimated at 0.79, which is very close to the assigned threshold. If ground latrines had been included in the dynamic occupancy analysis, the estimate could potentially meet or slightly exceed 0.80, as the inclusion of ground latrines was shown to increase the occupancy estimate for the single-season analysis. Additionally, the colonization and extinction probabilities were promising, indicating that swamp rabbits were more likely to colonize sites than to be extirpated from sites. Therefore, it would be reasonable for managers to consider changing the swamp rabbit’s state rank to S3.

It is important to acknowledge that dynamic occupancy models, while informative in assessing current and historical occupancy patterns, do not account for the potential impacts of future climate changes. Given the forecasted risk of increased flooding and associated physiological stress on bottomland hardwood forests, managers should maintain vigilance in monitoring forest conditions, particularly at sites in the Bootheel along the St. Francis and Mississippi Rivers, and at sites in the greater St. Louis region. These areas are prone to more severe floods that could substantially alter soil conditions, and forest composition and vertical structure, with greater potential to negatively influence swamp rabbit occupancy.

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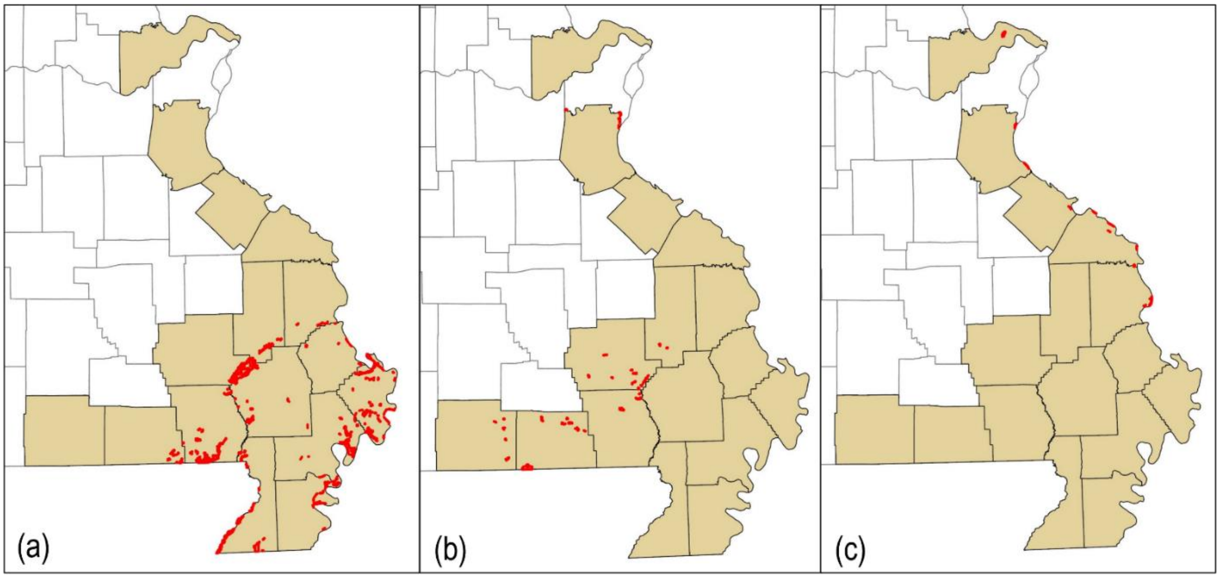
APPENDIX A

STUDY SITES BY ECOREGION. (a) MISSISSIPPI ALLUVIAL VALLEY (N = 127); (b) BLACK RIVER HILLS BORDER REGION OF THE OZARK HIGHLANDS (N = 31); (c) INTERIOR RIVER VALLEYS AND HILLS (N = 18).



APPENDIX B

AIC-RANKED DYNAMIC OCCUPANCY MODELS FOR THE DETECTION PARAMETER DURING THE FIRST STAGE OF MODELING FOR SWAMP RABBITS IN SOUTHEAST MISSOURI, USA.

Model	AIC	ΔAIC	w_i	K
psi (.), gam (.), eps (.), p (year-1)	1012.83	0.00	0.97	5
psi (.), gam (.), eps (.), p (SiteArea)	1019.81	6.99	0.03	5
psi (.), gam (.), eps (.), p (.)	1028.05	15.23	0.00	4
psi (.), gam (.), eps (.), p (prec)	1029.84	17.01	0.00	5
psi (.), gam (.), eps (.), p (Date)	1249.76	236.93	0.00	5
psi (.), gam (.), eps (.), p (prec+Date)	1251.76	238.93	0.00	6

APPENDIX C

AIC-RANKED DYNAMIC OCCUPANCY MODELS FOR THE OCCUPANCY PARAMETER DURING THE FIRST STAGE OF MODELING FOR SWAMP RABBITS IN SOUTHEAST MISSOURI, USA.

Model	AIC	ΔAIC	w_i	K
psi (Isol+PRD), gam (.), eps (.), p (.)	999.68	0.00	0.55	6
psi (Isol+SiteArea), gam (.), eps (.), p (.)	1000.57	0.89	0.35	6
psi (propBLH+Isol), gam (.), eps (.), p (.)	1004.74	5.06	0.04	6
psi (Isol), gam (.), eps (.), p (.)	1005.44	5.76	0.03	5
psi (SiteArea+propBLH), gam (.), eps (.), p (.)	1007.57	7.89	0.01	6
psi (propBLH+PRD), gam (.), eps (.), p (.)	1008.97	9.29	0.01	6
psi (propBLH), gam (.), eps (.), p (.)	1012.03	12.35	0.00	5
psi (PRD), gam (.), eps (.), p (.)	1019.09	19.41	0.00	5
psi (PRD+PRD^2), gam (.), eps (.), p (.)	1019.17	19.49	0.00	6
psi (SiteArea+PRD), gam (.), eps (.), p (.)	1019.67	19.99	0.00	6
psi (SiteArea), gam (.), eps (.), p (.)	1021.78	22.10	0.00	5
psi (.), gam (.), eps (.), p (.)	1028.05	28.37	0.00	4

APPENDIX D

AIC-RANKED DYNAMIC OCCUPANCY MODELS FOR THE COLONIZATION PARAMETER DURING THE FIRST STAGE OF MODELING FOR SWAMP RABBITS IN SOUTHEAST MISSOURI, USA.

Model	AIC	ΔAIC	w_i	K
psi (.), gam (.), eps (.), p (.)	1028.05	0.00	0.34	4
psi (.), gam (AvgNumFl-1), eps (.), p (.)	1029.10	1.05	0.20	5
psi (.), gam (AvgFlSev-1), eps (.), p (.)	1029.56	1.51	0.16	5
psi (.), gam (propBLH.gain-1), eps (.), p (.)	1029.85	1.79	0.14	5
psi (.), gam (AvgNumFl+propBLH.gain), eps (.), p (.)	1030.77	2.72	0.09	6
psi (.), gam (AvgFlSev+propBLH.gain), eps (.), p (.)	1031.29	3.24	0.07	6

APPENDIX E

AIC-RANKED DYNAMIC OCCUPANCY MODELS FOR THE EXTINCTION PARAMETER DURING THE FIRST STAGE OF MODELING FOR SWAMP RABBITS IN SOUTHEAST MISSOURI, USA.

Model	AIC	ΔAIC	w_i	K
psi (.), gam (.), eps (AvgNumFl-1), p (.)	1020.41	0.00	0.44	5
psi (.), gam (.), eps (AvgNumFl+propBLH.loss), p (.)	1020.88	0.47	0.35	6
psi (.), gam (.), eps (AvgNumFl*propBLH.loss), p (.)	1022.67	2.25	0.14	7
psi (.), gam (.), eps (AvgFlSev-1), p (.)	1025.96	5.55	0.03	5
psi (.), gam (.), eps (AvgFlSev+propBLH.loss), p (.)	1026.40	5.99	0.02	6
psi (.), gam (.), eps (.), p (.)	1028.05	7.64	0.01	4
psi (.), gam (.), eps (propBLH.loss-1), p (.)	1028.07	7.66	0.01	5
psi (.), gam (.), eps (AvgFlSev*propBLH.loss), p (.)	1028.27	7.66	0.01	7

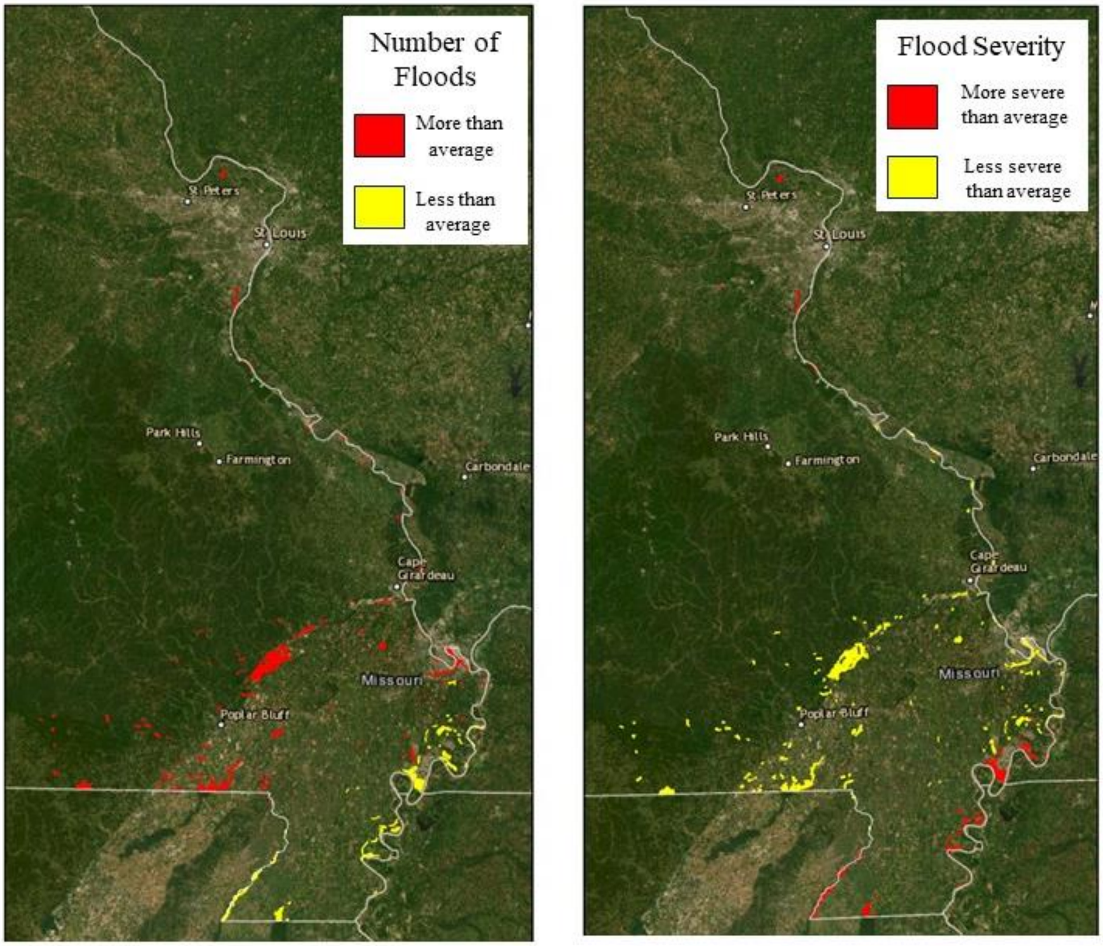
APPENDIX F

SUBSET MODEL-AVERAGED PARAMETER ESTIMATES AND 95% CONFIDENCE INTERVALS FOR THE AIC BEST-RANKED DYNAMIC OCCUPANCY MODELS FOR SWAMP RABBITS IN SOUTHEAST MISSOURI, USA.

Coefficient	Estimate	SE	Lower CI	Upper CI
psi intercept	0.68	0.19	0.30	1.06
psi Isol	-1.01	0.30	-1.60	-0.42
psi PRD	-0.49	0.19	-0.85	0.26
psi SiteArea	0.64	0.30	-0.46	0.97
col AvgNumFl more	0.72	0.32	-0.50	1.08
col AvgNumFl less	0.02	0.64	-0.79	0.81
col AvgFlSev less	0.69	0.32	-0.50	0.94
col AvgFlSev more	0.20	0.61	-0.64	0.77
col propBLH.gain 0	0.54	0.30	-0.42	0.72
col propBLH.gain 1	0.95	0.86	-0.96	1.49
ext intercept	-3.17	0.68	-4.48	1.86
ext AvgNumFl more	-2.93	0.62	-4.70	1.26
ext AvgNumFl less	0.19	1.53	-2.81	3.19
ext propBLH.loss 1	0.82	0.64	-0.79	1.47
p year 2010-2012	2.18	0.19	1.81	2.54
p year 2022-2023	1.28	0.13	1.03	1.53

APPENDIX G

THE NUMBER OF FLOODS AND FLOOD SEVERITY AT SWAMP RABBIT SURVEY SITES IN SOUTHEAST MISSOURI, USA BETWEEN LATE APRIL 2013 AND MID JUNE 2019. VALUES FOR THESE PREDICTORS WERE HIGHLY NEGATIVELY CORRELATED.



APPENDIX H

AIC-RANKED OCCUPANCY MODELS FOR THE OCCUPANCY PARAMETER DURING THE FIRST STAGE OF MODELING THE ELEVATED-ONLY ANALYSIS OF SWAMP RABBITS IN SOUTHEAST MISSOURI, USA, 2022-2023.

Model	AIC	ΔAIC	w_i	K
p (.), psi (Isol)	587.22	0.00	3.00E-01	3
p (.), psi (Isol + site.area)	588.27	1.06	1.80E-01	4
p (.), psi (prop.BLH + Isol)	588.87	1.66	1.30E-01	4
p (.), psi (edge)	589.89	2.68	8.00E-01	3
p (.), psi (site.area)	589.97	2.76	7.70E-02	3
p (.), psi (PRD)	590.42	3.20	6.20E-02	3
p (.), psi (prop.BLH)	590.46	3.24	6.00E-02	3
p (.), psi (prop.BLH + edge)	591.74	4.53	3.20E-02	4
p (.), psi (prop.BLH + site.area)	591.80	4.59	3.10E-02	4
p (.), psi (PRD + prop.BLH)	592.28	5.06	2.40E-02	4
p (.), psi (prop.BLH *site.area)	593.03	5.81	1.70E-02	5
p (.), psi (PRD + edge)	688.39	101.18	3.30E-23	4
p (.), psi (PRD + PRD2)	688.39	101.18	3.30E-23	4

APPENDIX I

AIC-RANKED OCCUPANCY MODELS FOR THE OCCUPANCY PARAMETER DURING THE FIRST STAGE OF MODELING THE ELEVATED + GROUND ANALYSIS OF SWAMP RABBITS IN SOUTHEAST MISSOURI, USA, 2022-2023.

Model	AIC	ΔAIC	w_i	K
p (.), psi (edge)	567.48	0.00	3.00E-01	3
p (.), psi (prop.BLH + edge)	568.99	1.51	1.40E-01	4
p (.), psi (site.area)	569.23	1.74	1.20E-01	3
p (.), psi (prop.BLH * site.area)	569.55	2.07	1.10E-01	5
p (.), psi (PRD)	569.71	2.23	9.80E-02	3
p (.), psi (prop.BLH + site.area)	570.81	3.33	5.60E-02	4
p (.), psi (prop.BLH)	571.08	3.59	5.00E-02	3
p (.), psi (Isol + site.area)	571.09	3.60	4.90E-02	4
p (.), psi (Isol)	571.20	3.72	4.70E-02	3
p (.), psi (prop.BLH + Isol)	572.57	5.08	2.30E-02	4
p (.), psi (PRD + PRD2)	574.93	7.44	7.20E-03	4
p (.), psi (PRD + edge)	647.10	79.62	1.50E-18	4
p (.), psi (PRD + prop.BLH)	647.11	79.62	1.50E-18	4

APPENDIX J

AIC-RANKED OCCUPANCY MODELS FOR THE DETECTION PARAMETER DURING THE FIRST STAGE OF MODELING THE ELEVATED-ONLY ANALYSIS OF SWAMP RABBITS IN SOUTHEAST MISSOURI, USA, 2022-2023.

Model	AIC	ΔAIC	w_i	K
p (dur), psi (.)	355.35	0.00	1.00E+00	3
p (dur + dur2), psi (.)	412.78	57.44	3.40E-13	4
p (site.area), psi (.)	588.06	232.72	2.90E-51	3
p (.), psi (.)	588.70	233.36	2.10E-51	2
p (prec), psi (.)	590.66	235.32	8.00E-52	3
p (date), psi (.)	781.69	426.35	2.60E-93	3
p (date * prec), psi (.)	785.69	430.35	3.60E-94	5

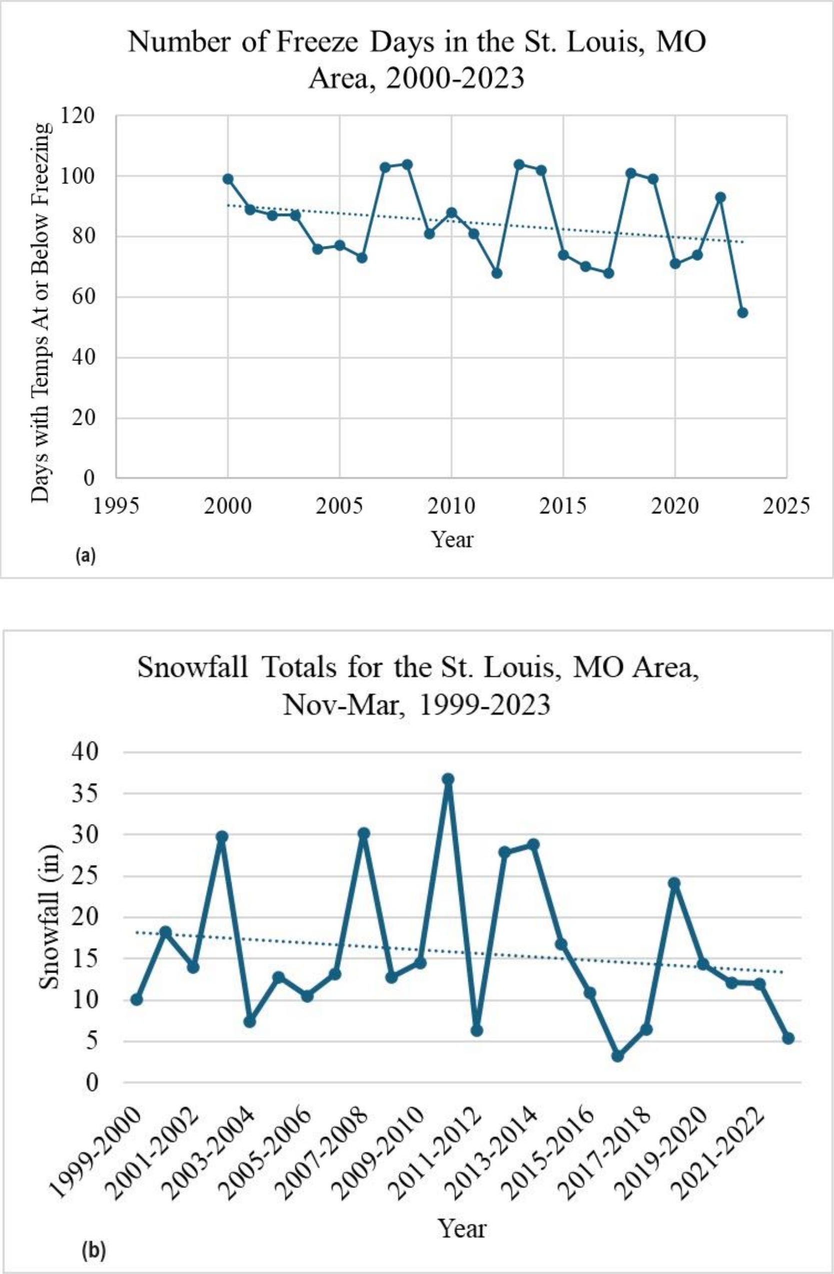
APPENDIX K

AIC-RANKED OCCUPANCY MODELS FOR THE DETECTION PARAMETER DURING THE FIRST STAGE OF MODELING THE ELEVATED + GROUND ANALYSIS OF SWAMP RABBITS IN SOUTHEAST MISSOURI, USA, 2022-2023.

Model	AIC	ΔAIC	w_i	K
p (dur), psi (.)	325.34	0.00	1.00E+00	3
p (site.area), psi (.)	567.37	242.03	2.80E-53	3
p (.), psi (.)	569.32	243.98	1.00E-53	2
p (prec), psi (.)	570.02	244.68	7.40E-54	3
p (dur + dur2), psi (.)	824.84	499.50	3.40E-109	4
p (date), psi (.)	830.03	504.69	2.60E-110	3
p (date * prec), psi (.)	834.03	508.69	3.50E-111	5

APPENDIX L

CLIMATE TRENDS FOR THE ST. LOUIS, MO AREA 1999-2023. (a) NUMBER OF DAYS PER YEAR WITH TEMPERATURES AT OR BELOW FREEZING WITH TRENDLINE. (b) SNOWFALL TOTALS FOR NOVEMBER THROUGH MARCH WITH TRENDLINE.



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Major Professor: Dr. Brent S. Pease