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Abstract: Lagomorphs are important consumers and prey in ecosystems worldwide, but have declined due to land use changes and habitat loss, and such losses may be exacerbated for specialist species. We compared survival and habitat use of two closely related lagomorphs, the swamp rabbit (*Sylvilagus aquaticus* (Bachman, 1837)), a bottomland hardwood forest (BLH) specialist, and the eastern cottontail (*S. floridanus* (Allen, 1890)), a habitat generalist. We tested whether survival and habitat use differed between radiocollared swamp rabbits ($n = 129$) and eastern cottontails ($n = 72$) monitored during Dec 2009–Dec 2013 in southern Illinois. We found interactive effects of species and season on survival rates: swamp rabbits had higher annual survival (0.37 ± 0.05 [estimate $\pm$ SE]) than did cottontails (0.20 ± 0.05), but this difference occurred primarily during the growing season. Swamp rabbits were located closer to watercourses in areas characterized by higher basal area and more mature BLH cover compared to eastern cottontails. Our results suggest that BLH may be marginal habitat for cottontails, and indicate predation as the primary cause of mortality for both species. Swamp rabbits use of early-successional BLH suggests that restoration efforts have been successful. However, as specialists, swamp rabbits remain restricted to a narrow band of bottomlands near watercourses and may benefit from improved upland cover that serves as refugia from flooding.

Key words bottomland hardwood forest, eastern cottontail, habitat, predation, survival, swamp rabbit, *Sylvilagus aquaticus*, *Sylvilagus floridanus*, sympatry.

Introduction

Populations at the margins of a species' geographic range are of special conservation concern, in part, because they experience a greater risk of local extinction compared to centrally-located populations (Lesica and Allendorf 1995; Guo et al. 2005). These peripheral populations typically have lower densities and are patchily distributed, as individuals encounter fewer optimal habitats and more hostile environmental conditions (Levin 1970; Brown 1984; Lesica and Allendorf 1995; Wilson et al. 2009). Although poleward and upslope migrations already have been documented for several species, endemic specialists, especially at range boundaries, may be unable to respond to the impacts of climate change, and instead may face range contraction and extinction (Parmesan 2006; Anderson et al. 2009; Clavel et al. 2011). Climate change, coupled with habitat loss and predation can exacerbate extinction risk for populations at range margins, particularly for species with limited dispersal ability and narrow niche breadth (Holt 2003; Parmesan 2006; Anderson et al. 2009; Wilson et al. 2009).

Lagomorphs are keystone consumers and prey in many ecosystems, but are threatened worldwide by habitat loss, human activities, and climate change (Chapman and Flux 2008; Anderson et al. 2009; Tablado and Revilla 2012). Habitat loss and patch isolation increase the risk of local extinction for species that are spatially structured as metapopulations, such as lagomorphs, especially at the edge of geographic range boundaries (Sievert and Keith 1985; Anderson et al. 2009). In addition, specialist lagomorphs may be particularly well suited as indicators when assessing impacts of habitat loss or the effectiveness of management actions (Litvaitis 2001; Chapman and Litvaitis 2003; Hillard et al. 2017). Given their metapopulation structure, lagomorphs can serve as model species when studying population dynamics, habitat

use, and interspecific interactions at range boundaries (Roy Nielsen et al. 2008; Anderson et al. 2009; Berkman et al. 2015).

The swamp rabbit (*Sylvilagus aquaticus* (Bachman, 1837)) is a bottomland hardwood forest (BLH) specialist found throughout the south-central United States (Chapman and Feldhamer 1981; Smith and Boyer 2008). As a specialist, swamp rabbits are strongly associated with permanent water and rely on both early- and late-successional BLH (Terrel 1972; Zollner et al. 2000a; Scharine et al. 2009; 2011). Swamp rabbits occur in patchily distributed metapopulations in southern portions of Illinois, Indiana, and Missouri, the northernmost extent of the species' geographic range (Barbour et al. 2001; Roy Nielsen et al. 2008; Berkman et al. 2015). The species has declined both at its northern range margin and throughout the southeast due to substantial BLH habitat loss (> 80%) in the Lower Mississippi Alluvial Valley (LMAV) during the last century (Dickson 2001; King et al. 2006; Bunch et al. 2012). In Illinois, swamp rabbits have been extirpated from the northern edge of their historic range and are restricted to major rivers in the southernmost counties of the state (Barbour et al. 2001).

The eastern cottontail (*S. floridanus* (Allen, 1890); hereafter "cottontail") is a habitat generalist commonly associated with old fields, grasslands and early-successional woodlands (Chapman and Litvaitis 2003). Consequently, cottontails have the widest geographic distribution of any member of the genus, overlapping in range with several *Sylvilagus* spp. (Chapman and Litvaitis 2003). Although cottontails once thrived in fragmented agricultural landscapes containing abundant early-successional and edge habitats, populations have declined throughout the Midwest since the mid-20th century due to land use changes, particularly "clean" intensive agriculture that provides little cover or edge (Mankin and Warner 1999a, b).

Since the 1990s, federal and state BLH restoration projects in the LMAV have created a patchwork of early-successional BLH stands that border mid- to late-successional BLH forests along waterways (Kruse and Groninger 2003; King et al. 2006). These recently-afforested stands have been planted in marginal croplands near existing BLH and typically contain higher amounts of herbaceous and woody ground cover than older stands with closed canopies (Kruse and Groninger 2003). Because dense understory vegetation is an important microhabitat feature for both swamp rabbits and cottontails, these changes may provide suitable habitat for both species where they co-occur (Chapman and Feldhamer 1981; Allen 1985; Chapman and Litvaitis 2003). In southern Illinois, cottontails have been found in early-successional BLH stands alongside swamp rabbits (Scharine et al. 2011), thereby providing the opportunity to study joint habitat use at the swamp rabbit's northern range boundary.

To our knowledge, only a few studies have noted joint habitat use between cottontails and swamp rabbits (Taylor and Lay 1949; Toll et al. 1960; Scharine et al. 2011), and none have compared survival rates or habitat use of the two species where they co-occur. Although previous studies have contributed to our understanding of swamp rabbit ecology, much of that knowledge comes from studies conducted in mature BLH stands or in BLH prior to restoration efforts in the 1990s (Toll et al. 1960; Terrel 1972; Zollner et al. 2000*a, b*). Previous radiotelemetry studies of swamp rabbit habitat use relied on small sample sizes (<10 rabbits; Kjolhaug and Woolf 1988; Zollner et al. 2000*b*; Vale and Kissell 2010; Dumyah and Zollner 2010), and none have examined factors that influence survival. Consequently, managers lack detailed information about habitat use, space requirements, and survival of both species in restored BLH.

The goal of our research was to provide information on survival rates of swamp rabbits and cottontails and the extent to which these species were using recently-afforested BLH stands adjacent to older BLH. Our specific research objectives were to 1) document survival rates and mortality causes of both species, 2) compare micro- and macrohabitat use within core areas and home ranges of the two species, and 3) compare where the two species were located relative to important cover types, such as wetlands. Given the larger body size, specialized life history, and predator evasion tactics of swamp rabbits (Chapman and Feldhamer 1981; Swihart 1984), we predicted that swamp rabbits would have higher survival than cottontails in BLH landscapes. In addition, despite past reports of joint occupancy of early-successional BLH (Scharine et al. 2011), we expected differences in habitat use given each species' habitat preferences. Accordingly, we expected cottontails to remain on the periphery of bottomlands, primarily occupying early-successional BLH and adjacent grasslands, whereas swamp rabbits would be found closer to permanent watercourses and in areas with greater forest cover.

Materials and methods

Study area

We studied rabbit survival and space use at 7 BLH sites located along the Cache River and Cypress Creek within the Cypress Creek National Wildlife Refuge in southern Illinois (Fig. 1.). We used multiple sites to increase our trapping success, choosing sites based on previous knowledge of co-occurring swamp rabbits and cottontails (Scharine et al. 2009). Sites ranged from 6 to 32 ha ($\bar{x} \pm SD = 17.6 \pm 9.8$ ha) in size and were composed of early- and late-successional BLH forests adjacent to varying amounts of early-successional uplands and

agriculture. Early-successional BLH patches were afforested within the last 20 years and were dominated by green ash (*Fraxinus pennsylvanica*, Marsh.), box elder (*Acer negundo*, L.), and sweetgum (*Liquidambar straciflua*, L.). Other tree species included various oaks (*Quercus* spp., L.), hickories (*Carya* spp., Nutt), willow (*Salix* spp.), sycamore (*Platanus occidentalis*, L.), and bald cypress (*Taxodium distichum*, (L.) Rich.) (Kruse and Groninger 2003). Common understory species in early-successional bottomlands and adjacent uplands at our sites included late goldenrod (*Solidago gigantea*, Aiton), rushes (*Juncus* spp., L.), poison ivy (*Toxicodendron radicans*, (L.) Kuntze), blackberry (*Rubus allegheniensis*, Porter), honeysuckle (*Lonicera japonica*, Moore), trumpet creeper (*Campsis radicans*, (L.) Seem. ex Bureau), smartweeds (*Pesicaria* spp., Mill.), sedges (*Carex* spp., L.), and broomsedge (*Andropogon virginicus*, L.) (Kruse and Groninger 2003). Bottomland hardwood forests in southern Illinois were characteristically flat and periodically flooded, with the severity and duration of inundation influenced by elevation, soil, drainage, and weather conditions (Hosner and Minckler 1963).

The study area had a continental climate, with hot summers and cool winters, and an average annual temperature of 14°C. The average growing season was 190 days, with the last killing frost around 7 April and the first killing frost around 21 October. Median leaf on and off dates were 31 Mar and 28 Oct, respectively, during the study period (USA-NPN 2016).

Capture and radiotelemetry

We captured rabbits during December–March each year from 2009 to 2013 using collapsible Tomahawk live traps (Model 205) placed in areas with rabbit sign. Traps were covered with burlap and vegetation, baited with a quartered apple, and checked daily during 0700–1100 hr. We placed each captured rabbit in a pillowcase before determining its weight and sex. All

captured rabbits were ear-tagged. Radiocollars (35–42 g; Advanced Telemetry Systems, Isanti, MN) were fitted to all adult rabbits with mass >1.0 kg (cottontails) or >1.9 kg (swamp rabbits). Radiocollars were equipped with 6-hr mortality sensors and had a 1 yr battery life. Animals were released immediately following processing at the site of capture; handling times averaged <10 min. We captured and handled rabbits using methods approved by the Institutional Animal Care and Use Committee at Southern Illinois University Carbondale (SIUC Animal Assurance Number A–3708–01, protocol 09–044).

We monitored radiocollared rabbits for survival every 24–48 hr until the signal was lost or 1 year passed. We estimated rabbit locations by triangulation at least twice weekly during morning (0500–0900 hr), daytime (0900–1700 hr) and evening (1700–2400 hr) periods on a rotating schedule. Locations were estimated primarily during late winter through early fall after the trapping period and before the collar battery died; rabbits were censored beginning 1 November. Dead animals were retrieved ≤ 3 days of receiving a mortality signal, and most often retrieved within 24 hours. Flooding, weather, and access to land sometimes prevented us from reaching a deceased animal for up to 3 days. We categorized cause of death as predation, harvest, weather, vehicle, or unknown. Deaths classified as weather-related included rabbits that were found intact under snow as well as animals that drowned in flooded gullies or wetlands. If only a collar was found without any other signs of death, data were right-censored for analysis.

Habitat variables

We recorded microhabitat variables that characterized small-scale vegetation structure and composition, and had been identified as potentially important to swamp rabbits (Zollner et al. 2000b; Fowler and Kissell 2007; Scharine et al. 2009, 2011). We characterized vegetation at

each study site during 15 May – 15 Aug 2012, focusing on the portion of each site occupied by radiocollared individuals of each rabbit species. In ArcGIS v.10.2.1 (ESRI 2011), we generated a random spatial distribution of circular (8-m radius, 0.02 ha) plots for microhabitat sampling at each site, at a density of 3.5 plots/ha. Within each plot, we estimated percentage canopy closure using a densiometer and visually estimated percentages of ground covered by herbaceous plants (i.e., forbs and grasses) and non-arborescent woody ground cover (i.e., shrubs/vines). We also recorded basal area (m^2/ha) of standing live trees within the entire plot. Finally, we estimated visual obstruction at the center of each plot using a 1.5 m Robel pole (Robel et al. 1970) placed 4 m from the observer at the plot center, at compass bearings of 30, 150, and 270 degrees.

We quantified macrohabitat characteristics (i.e., those that involve aspects of land cover types) previously identified as potentially important to swamp rabbits (Zollner et al. 2000a; Fowler and Kissell 2007; Scharine et al. 2009; 2011). We characterized macrohabitat within 1-km and 2-km radii around the center of each study site because previous studies suggested swamp rabbits were restricted to sites located ≤ 2 km of a water source (Terrel 1972; Scharine et al. 2009). All radiolocations and resulting home ranges were well within the boundaries of the 1-km radius at each site. These measurement scales represented land cover patterns experienced by all rabbits at each site, and thus, were the same for swamp rabbits and cottontails at each site. We digitized land cover in ArcGIS 10.2.1 from digital color orthophoto quarter quadrangle images (DOQQs) accessed through the National Agriculture Imagery Program (USDA 2010), classifying patches into 1 of 4 cover types (agriculture, early-successional BLH [EBLH], mature BLH [MBLH], and upland). We calculated landscape metrics that characterized patch shape (area-weighted mean shape index; AMWSI), variation in patch size (percent coefficient of

variation in patch size; PCOV), and edge density (ED) in Fragstats v. 4.2 (McGarigal et al. 2012).

Survival

To estimate survival of radiocollared rabbits, we fit parametric survival models representing the influence of intrinsic characteristics (species, sex, season, site, and year) and macrohabitat covariates (proportions of each cover type and AWMSI, PCOV, ED). Models were fitted assuming an exponential event-time distribution using the ‘survreg’ function in the ‘survival’ package (version 2.37.7) in the R statistical programming language (version 3.1.1; R Development Core Team 2011). Survival was coded weekly for 47 weeks each year, and animals alive at the end of that period were right-censored. All animals still alive at the end of October were censored.

In the first model set, we evaluated a series of models that included intrinsic characteristics as covariates. We compared survival between the growing season (GS; 31 Mar –31 Oct) and non-growing season (NG; 11 Dec – 30 Mar) in southern Illinois, as delimited by median dates of leaf-on and leaf-off for deciduous woody plants and forbs in southern Illinois (USA-NPN 2016). All combinations of variables were modeled (up to 2-way interactions); however, we did not include interactions between year and site terms due to the prohibitively small sample sizes that would have resulted from such models. Given that sample The second and third model sets evaluated the influence of landscape covariates at the 1-km and 2-km scales on survival, respectively, after accounting for intrinsic factors found to be important in the first model set. At each scale, models included the proportions of each cover type and the AWMSI, PSCOV, and ED metrics calculated for each study site. Macrohabitat-based models included season and a

season $\times$ species interaction as fixed effects, while study site was specified as a random effect using the ‘frailty’ option within the ‘survival’ package in R. We used Akaike’s Information Criterion corrected for small sample size (AIC_c) to evaluate support for models in each set. We considered models competitive if they were ≤ 4 AIC_c units of the top model (Burnham and Anderson 2002). We ranked models and estimated model-averaged parameters in the R package “MuMIn” (version 1.7.2).

Habitat use

We estimated the boundaries of annual (*i.e.*, year-long) core areas and home ranges for each rabbit with ≥ 30 locations from the 50% and 95% isopleths, respectively, of fixed-kernel density estimators using the reference smoothing parameter (Worton 1989). Home range estimation was carried out using the “adehabitatHR” (version 0.4.7) package in the R statistical programming language (R Development Core Team 2011). We used Wilcoxon rank sum tests to evaluate differences in core area and home range size between sexes within each species prior to pooling data for habitat analyses. We also used Wilcoxon rank sum tests to test for differences in home range and core area size between species.

We calculated the mean and coefficient of variation (%) of each microhabitat variable from plots that fell within each animal’s core area and home range during each seasonal period. Means of several variables were highly correlated with one another (Table 1). We omitted the number of saplings/plot because < 1 sapling was recorded in $> 70\%$ of plots. Accordingly, we only included mean basal area, and the coefficients of variation in herbaceous cover and woody ground cover (among plots) in statistical analyses. We used Wilcoxon rank sum tests for differences in microhabitat variables between species because habitat variables remained non-normally

distributed after log-transformation. Significance was assessed after a Bonferroni correction for multiple tests was applied ($\alpha < 0.05/m$ tests; $\alpha_{\text{adjusted}} < 0.01$ for all microhabitat tests; Holm 1979).

We used a modified compositional analysis to compare land cover composition of core areas and home ranges between species and sites ("Problem 3" of Aebischer et al. 1993). Proportions of cover types within core areas and home ranges were calculated in ArcGIS as the log ratio of each cover type proportion relative to agriculture within core areas and home ranges (e.g., $\log(\text{MBLH}/\text{Ag})$). We also evaluated differences between species in their locations relative to cover types and permanent water. For each rabbit, we used ArcGIS to measure the Euclidean distance (m) from each radiolocation to the nearest patch of each cover type and to the nearest permanent watercourse. Then, we applied a natural log transformation to distances [$\ln(\text{distance} + 1)$] and calculated each rabbit's average transformed distance to each cover type and watercourse. We used these average transformed distances as dependent variables in a MANOVA to test for differences between species (independent variable). We did not include the distance to early-successional BLH patches as a dependent variable because it was highly correlated with distance to upland cover ($r = -0.71$, $P < 0.001$, $d.f. = 79$). For both land cover proportions and distance data, we assessed departures from normality using Shapiro-Wilk multivariate normality tests and graphical examination of residuals. Multivariate significance was assessed using Hotelling-Lawley T^2 approximation of F ; significance of each variable in the model was evaluated by separate F -tests (ANOVAs). We performed MANOVAs and tested model assumptions in the R statistical programming environment, using the "stats" package (version 3.1.1) for MANOVAs and the "mvnrmtest" package for Shapiro-Wilk multivariate tests (version 0.1.9).

Results

We monitored 129 swamp rabbits (69 M, 60 F) and 72 cottontails (35 M, 37 F) during 2009–2013 (Table 2). We recorded 95 (74%) mortalities for swamp rabbits and 53 (72%) for cottontails. Seven swamp rabbits and 14 cottontails were censored because mortality could not be confirmed, because carcasses were inaccessible or rabbits may have slipped their collars. An additional 27 swamp rabbits (21%) and nine cottontails (11%) were confirmed to have survived the entire year. Predation (71%) was the primary mortality cause for both species, followed by weather (9%) and hunter harvest (6%). We identified 10 predations most likely by bobcats (*Lynx rufus* (Schreber, 1777)), one by domestic cat (*Felis catus* (L. 1758)), and four by coyote (*Canis latrans* (Say, 1983)) or domestic dog (*C. lupus familiaris*, (L. 1758)) based on tracks, scat, and the condition of the carcass. Three predations most likely were by avian predators based on feathers at the scene and carcass condition. Specific predators could not be identified for the remaining predations. Carcasses were too severely scavenged to assign cause of death for 12 swamp rabbits (9%) and seven cottontails (9%).

Survival

The top four survival models in the intrinsic model set ($n = 40$) had $\Delta AIC_c \leq 4$ and cumulatively accounted for 82% of model weight; together, they indicated consistent support for differences between seasons and species (Table 3). The model-averaged coefficient for season indicated that survival was higher during the growing season than during the non-growing season [$\beta_{GS} = 1.76 \pm 0.33$ (SE throughout), cumulative Akaike model weight (ΣW_{GS}) = 1.0]. A season-

by-species interaction was included in 3 models in the competitive model set (model averaged $\beta_{SR \times GS} = 0.85 \pm 0.36$, $\Sigma W_{SR \times GS} = 0.80$; Fig. 2), indicating that swamp rabbits had higher survival during the growing season, but experienced survival rates similar to cottontails during the non-growing season. Consequently, models including species also were competitive, but species alone was not an important predictor of survival (model averaged $\beta_{SR} = -0.06 \pm 0.28$, $\Sigma W_{SR} = 0.90$). Sex was included in one competitive model but was a poor predictor of survival ($\beta_{Male} = -0.05 \pm 0.18$, $\Sigma W_{Male} = 0.21$). Year and study site were not included in any competitive models. Using model-averaged coefficients, swamp rabbits and cottontails had similar survival rates during the non-growing season ($SR = 0.47 \pm 0.04$; $CT = 0.41 \pm 0.07$), but swamp rabbits experienced a higher survival rate than cottontails during the growing season ($SR = 0.61 \pm 0.03$; $CT = 0.25 \pm 0.07$). The model-averaged estimate of survival over the entire study period was 0.37 ± 0.05 for swamp rabbits and 0.20 ± 0.05 for cottontails. None of the macrohabitat covariates at either the 1-km or 2-km scales were individually important ($\Sigma W_i \leq 0.22$) and all such covariates had model-averaged confidence intervals that overlapped zero. The null model was the second ranked model and within 1 AIC_c unit of the top-ranked model in both landscape model sets.

Habitat use

We quantified core area and home range boundaries and habitat use for 60 swamp rabbits (34 M, 26 F) and 21 cottontails (10 M, 11 F). Mean home range and core area sizes for swamp rabbits were 2.52 ha (± 2.51) and 12.00 ha (± 11.94), respectively, and did not differ by sex (both $W \geq 467$, $P \geq 0.436$). Cottontails had average core area and home range sizes of 1.91 ha (± 1.20) and 10.69 ha (± 6.65), respectively, and sizes did not differ by sex (both $W \geq 41$, $P \geq 0.349$). We

pooled sexes within each species for all subsequent analyses. Swamp rabbits had larger core areas than cottontails ($W = 806$, $P = 0.029$), but did not differ significantly in home range size ($W = 717$, $P = 0.176$). Microhabitat use differed by species; typically, swamp rabbits occupied more heavily-forested areas with lower levels of herbaceous and shrub cover than cottontails (Table 4). Swamp rabbits had core areas and home ranges in areas with higher basal area compared to cottontails (both $W \geq 965$, $P < 0.001$), but also greater coefficients of variation in basal area and herbaceous cover throughout their home ranges and core areas (all $W \geq 266$, $P \leq 0.005$). Because basal area was strongly negatively correlated with visual obstruction (give correlation or point to table of microhabitat variable correlation matrix), this pattern indicated that cottontails occupied space with denser ground cover.

Swamp rabbits and cottontails also differed in macrohabitat use within both core areas and home ranges (Table 5; core area: $T^2 = 0.80$, $F_{3,74} = 19.80$, $P < 0.001$; home range: $T^2 = 0.36$, $F_{3,74} = 8.86$, $P < 0.001$). Swamp rabbits had core areas and home ranges composed of significantly higher proportions of early-successional BLH (core area: $F_{1,74} = 17.94$, $P < 0.001$; home range: $F_{1,74} = 11.96$, $P = 0.001$) and mature BLH (core area: $F_{1,74} = 6.58$, $P < 0.001$; home range: $F_{1,74} = 3.42$, $P = 0.004$) than cottontails. Use of upland land cover within core areas or home ranges was similar between species (core area: $F_{1,74} = 2.69$, $P = 0.20$; home range: $F_{1,74} = 0.018$, $P = 0.89$).

Swamp rabbits and cottontails differed in their locations within the landscape ($T^2 = 1.32$, $F_{1,70} = 23.2$, $P < 0.001$). Swamp rabbits were located significantly closer to a permanent watercourse than were eastern cottontails ($F_{1,70} = 33.81$, $P < 0.001$; Fig. 3). Indeed, 95% of all swamp rabbit radiolocations were ≤ 332.0 m away from a permanent watercourse (mean = 169.0 $\pm$ 100.0 m; range = 1.0 – 571.0 m), whereas 95% of cottontail radiolocations were ≤ 536.0 m

away from a permanent watercourse (mean = 289.0 ± 142.0 m; range = 1.7 – 670.0 m). Swamp rabbits also were significantly closer to mature BLH patches ($F_{1,70} = 12.53$, $P < 0.001$) and farther from agriculture ($F_{1,73} = 23.92$, $P < 0.001$) than cottontails.

Discussion

Our study is the first to provide survival estimates for swamp rabbits, and is one of only a few studies to present evidence of differences in survival and habitat use between eastern cottontails and sympatric leporids (also see Keith and Bloomer 1993). As expected, cottontails used more open grasslands and shrublands that bordered the bottomlands, whereas swamp rabbits primarily inhabited EBLH and MBLH stands and used adjacent early-successional uplands to a lesser extent. We also found that predation was the most important cause of mortality, particularly during the non-growing season, and that swamp rabbits survived better than cottontails during the growing season. These findings are consistent with species-specific traits, namely life history and habitat fit, being more important factors affecting survival rates than habitat features per se.

Predation accounted for at least half of all identifiable mortalities for both rabbit species in our study. Sources of mortality for swamp rabbits have not been well documented, but Terrel (1972) reported that hunting was the most important source of mortality in Indiana, and Watland et al. (2007) found that predators killed most swamp rabbits translocated to a novel site. Domestic dogs also kill swamp rabbits (Lowe 1958). Although in most cases we were unable to confirm the predatory species, predators of both swamp rabbits and cottontails in southern Illinois include bobcats, coyotes, domestic cats and dogs, and avian predators (Watland et al. 2007). Snow accumulation could be involved in the lower survival rates of rabbits we observed

during the non-growing season. Predation of cottontails is higher during periods of snow accumulation due to their conspicuous brown pelage, difficulty moving through snow, and increased energy needs (Keith and Bloomer 1993; Boland and Litvaitis 2008).

Both species in our study had similarly low survival rates outside of the growing season, although swamp rabbits had somewhat higher survival than cottontails during the growing season. This pattern has at least 3 plausible explanations, and are not mutually exclusive: 1) cottontails occupied areas poorer in quality for both species during the growing season, 2) BLH provided seasonally better habitat for swamp rabbits than cottontails, or 3) higher seasonal survival for swamp rabbits stemmed from their behavior or life history.

The first explanation – cottontails inhabited locations that would be poorer for both species – is plausible given the somewhat different habitat associations of each species. Cottontails are known to inhabit edges, residential greenspaces, and the upland agricultural matrix (Chapman and Litvaitis 2003), whereas swamp rabbits are closely tied to BLH cover (Chapman and Feldhamer 1981; Zollner et al. 2000a; Dickson 2001). In our study, both microhabitat and macrohabitat analyses confirmed that swamp rabbits were more closely associated with BLH than cottontails, whereas cottontails had home ranges on the periphery of bottomlands in closer proximity to field edges and roads. Other studies have identified small- and large-scale habitat influences on lagomorph survival. Trent and Rongstad (1974) suggested survival of cottontails in Wisconsin was most related to the availability of suitable resting and escape cover, especially during winter. Dense ground cover is important for both species for thermoregulation and concealment from predators in both winter and summer (Allen 1985; Althoff et al. 1997; Bond et al. 2002). Given that cottontails are diet generalists, habitat use may be more related to available cover than to food resources (Bond et al. 2002; Chapman and Litvaitis 2003). Cottontails in our

study typically had home ranges on the edges of bottomlands in areas with fewer trees (*i.e.*, low basal area) and greater herbaceous and woody ground cover (Table 4). Thus, it seems unlikely that the lower survival of cottontails was due to a lack of suitable vegetative cover necessary for escape, concealment, and thermoregulation.

The second explanation for the higher survival rate we observed for swamp rabbits relies on the two species experiencing different suitability in similar habitat. In our study, the annual survival rate for adult cottontails is among the lowest reported in the literature (typically 0.20 – 0.40 annual survival rate; Trent and Rongstad 1974; Bond et al. 2001; Boland and Litvaitis 2008). Only Boland and Litvaitis (2008) reported a lower survival rate (0.05) during a particularly severe winter. As habitat generalists, cottontails have proliferated where introduced in North America and Europe, and may be less sensitive to habitat fragmentation than native lagomorphs (Probert and Litvaitis 1996; Smith and Litvaitis 2000; Bertolino et al. 2013). Yet the relatively open understory of BLH forests in southern Illinois may be less suitable for cottontails than early-successional grasslands and shrublands with dense ground cover (Smith and Litvaitis 2000; Bertolino et al. 2013).

A third reason for higher survival among swamp rabbits during the growing season may be related to differences in life history and behavior. Lagomorphs have “fast” life histories compared to other mammals of similar size, with shorter lifespan, earlier onset of sexual maturity, and larger litter sizes than predicted based on body size (Swihart 1984; Promislow and Harvey 1990). Within the lagomorph order, larger body size is associated with later onset of maturity, smaller litter size, and longer lifespan (Swihart 1984). Swamp rabbits are approximately twice the body mass of cottontails, reach sexual maturity at 152 days of age, and have a gestation period of 39 days. Females produce 2.8 kits/litter over 2–5 litters/season. In

contrast, cottontails are prolific breeders, capable of producing ≤ 40 offspring/season and 5 kits/litter (Swihart 1984; Chapman and Litvaitis 2003). Cottontails also begin reproduction earlier (100 d) and have shorter gestation periods (29 d) than swamp rabbits. Consequently, lower survival of cottontails may be expected given the different life history strategies between swamp rabbits and cottontails in which lower adult survival among cottontails should be balanced by higher reproduction early in life (Swihart 1984).

Along with differences in fecundity, differences in predator evasion tactics between species also contributed to survival differences between swamp rabbits and cottontails on our study area. For example, permanent water courses are presumed to be critical escape routes from predators for swamp rabbits (Terrel 1972; Chapman and Feldhamer 1981), and the probability of swamp rabbit occupancy in BLH declines below 0.50 when patches are > 400 m from a water source (Scharine et al. 2011). We generally found swamp rabbits closer to water sources than cottontails, even at sites where early-successional BLH extended up to 1 km from the river. Swamp rabbits can evade predators by swimming away from threats, whereas cottontails respond by hiding or running in a zig-zag pattern toward cover (Lowe 1958; Marsden and Holler 1964; Terrel 1972). Swimming as a mode of predator evasion would likely only be available during warmer months, when water is ice-free and swamp rabbits would not risk hypothermia. Yet, the ability to use water as an escape route, at least seasonally, as well as the use of hollow logs and trees as form sites (Lowe 1958; Terrel 1972; Dumyahn and Zollner 2010), may be advantageous in BLH forests and explain the higher survival we observed for swamp rabbits during the growing season.

Flood severity and duration of flooding was highly variable among sites in our study due to differences in topography and landscape position. Although the proportion of upland cover

within 2 km was not included in top survival models, flooding was an important weather-related mortality cause for swamp rabbits at some sites. During periods of inundation, cottontails moved quickly to higher ground, including to farm fields and residential areas, whereas swamp rabbits escaped to higher ground only at sites that were adjacent to upland grasslands and shrublands. We never observed radiocollared swamp rabbits to cross open areas such as agricultural fields, roads, and residential areas. At sites where swamp rabbits were required to do so to escape flooding, rabbits either remained on the edges of flooded bottomlands or died in the flooded interior within 1 week of inundation. For example, flooding killed 4 of 6 swamp rabbits inhabiting a site bordered by residences and agricultural fields. Zollner et al. (2000b) and Vale and Kissell (2010) also reported that adjacent uplands were important habitat for swamp rabbits during periods of inundation in Arkansas. These results highlight the importance of creating and maintaining upland habitat that is connected to flood-prone BLH through natural corridors.

Cottontails and swamp rabbits, though somewhat segregated in their habitat use, still had home ranges that included much of the same cover types due to the proximity of those cover types to one another. However, swamp rabbits were less likely to have home ranges that included agriculture cover. Rather, the inclusion of small amounts of agriculture in some swamp rabbit home ranges attests to how little BLH forest remains in this landscape, as well as its narrow distribution along rivers (King et al. 2009). These findings support those of Taylor and Lay (1949) and Toll et al. (1960) who described a transition from cottontail to swamp rabbit occupancy as land cover changed from upland cover to bottomland forest.

Our comparisons between swamp rabbits and cottontails should be interpreted with caution for several reasons. First, given the objectives and study design, we were more likely to trap swamp rabbits than cottontails in EBLH and adjacent grasslands. Consequently, we monitored at

least twice as many swamp rabbits as cottontails in years 2 and 3 of the study due to low cottontail capture success. Our unbalanced sample size, especially later in the growing season after many cottontails had died, limits our ability to draw conclusions about survival differences between species. Similarly, we were able to estimate home range size and habitat use for only 21 cottontails compared to 60 swamp rabbits. Accordingly, our home range and habitat data were skewed strongly towards swamp rabbits. However, we are confident in the accuracy of our habitat use data, despite the small sample size. Our low cottontail capture rate, coupled with high overwinter mortality and consistent patterns of habitat use among monitored animals, suggest that cottontails were not using BLH habitats, including EBLH, as extensively as swamp rabbits.

We documented extensive use by swamp rabbits of EBLH stands planted within the last 3 decades. Our results demonstrate that swamp rabbits were using restored BLH stands, but they do not provide evidence that swamp rabbits actively avoided MBLH. We tried repeatedly to trap rabbits in MBLH stands, but had few captures. Our low success may indicate lower occupancy in older stands during the winter trapping period, or simply a lower capture success due to the lack of ground cover useful when trapping rabbits (Smythe et al. 2007). Some authors have suggested that MBLH stands are maturing into closed canopy forests lacking ground cover sufficient for swamp rabbits (Baccus and Wallace 1997), and Scharine et al. (2009) documented lower occupancy in stands with higher canopy closure. Our findings support the suggestion that older stands are becoming less optimal for swamp rabbits. Our study sites varied somewhat in the amount of MBLH present, but MBLH stands, where present, usually bordered a watercourse and may not have been available to swamp rabbits during periods of high water in late winter and spring.

Conclusions

Our large sample size of swamp rabbits monitored across several recently-afforested EBLH sites extends the applicability of our findings to conservation and management of BLH in other regions. Previous reports from sign and habitat suitability studies indicated that swamp rabbits declined or disappeared from counties at their northern-most range in Illinois (Barbour et al. 2001). However, after two decades of BLH restoration, swamp rabbit populations appear to be stable in the southern part of the state (Robinson et al. 2016). As specialists, swamp rabbits may have few options in the face of environmental fluctuations and habitat change because they are restricted to a relatively narrow band of bottomlands closely associated with permanent water. Such restricted habitat availability coupled with the requirement for components of both early- and late-successional BLH may make swamp rabbits an ideal indicator species in BLH restoration management (Hillard et al. 2017).

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Table 1. Pearson correlation matrix of mean microhabitat variables averaged across sample plots (0.02 ha; 3.5 plots/ha) randomly sampled within 50% core areas and 95% home ranges of swamp rabbits (*Sylvilagus aquaticus*; $n = 60$) and cottontails (*S. floridanus*; $n = 21$) in bottomland hardwood forests in the Cypress Creek National Wildlife Refuge, southern Illinois, 15 May – 15 Aug 2012. Within each plot, we measured percent canopy closure (CC), percentages of grasses and forbs (Herbs) and shrubs, the number of saplings present, basal area (m^2/ha), and visual obstruction (VO). We also calculated the coefficient of variation for herbaceous COVER (HerbCV) and basal area (BACV). Significant correlations are indicated by an asterisk ($P < 0.001$).

	CC	Herbs	HerbCV	Shrubs	Saplings	BA	BACV	VO
CC	-	-0.79*	0.12	-0.49	0.48	0.85*	-0.41	-0.77*
Herbs	-0.79	-	-0.09	-0.73*	-0.42	-0.70*	0.40	0.83*
HerbCV	0.12	-0.09	-	-0.07	0.01	0.17	-0.01	-0.07
Shrubs	-0.49	-0.73	-0.07	-	-0.21	-0.59	0.16	0.65
Saplings	0.48	-0.42	0.01	-0.21	-	0.30	-0.16	-0.33
BA	0.85	-0.70	0.17	-0.59	0.30	-	-0.33	-0.76*
BACV	-0.41	0.40	-0.01	0.16	-0.16	-0.33	-	0.39
VO	-0.77	0.83	-0.07	0.65	-0.33	-0.76	0.39	-

Table 2. Sample sizes by species, season, and year of radiocollared swamp rabbits (*Sylvilagus aquaticus*; SR) and eastern cottontails (*S. floridanus*; CT) monitored in BLH forests in southern Illinois, USA, 2009–2013. Growing season sample sizes reflect the loss of rabbits that died or were censored during the non-growing season.

	Non-growing season		Growing season	
	SR	CT	SR	CT
Year 1	37	25	25	13
Year 2	38	8	20	3
Year 3	27	11	22	7
Year 4	27	28	19	17
Total	129	72	86	40

Table 3. Top-ranked survival models of the effects of intrinsic covariates on survival of radiocollared swamp rabbits (*Sylvilagus aquaticus*; $n = 129$) and eastern cottontails (*S. floridanus*; $n = 72$) monitored in BLH forests in southern Illinois, USA, 2009–2013. For brevity, only the top model and models ≤ 4 AIC_c units of the top model are shown. All models that include interaction terms also include main effects.

Model	ΔAIC_c^*	$w_i^\dagger$	$K^\ddagger$
$S_{\text{season} \times \text{species}}$	0.00	0.48	4
$S_{\text{season} \times \text{species} + \text{sex}}$	2.04	0.17	5
$S_{\text{season} + \text{species}}$	3.36	0.09	3
S_{season}	3.62	0.08	2

* Difference in Akaike’s Information Criteria relative to minimum AIC_c corrected for small sample size (Burnham and Anderson 2002).

† Akaike weight (Burnham and Anderson 2002).

‡ Number of parameters.

Table 4. Mean $\pm$ SD of microhabitat variables averaged across sample plots (0.02 ha; 3.5 plots/ha) randomly sampled within 50% core areas (CA) and 95% home ranges (HR) of swamp rabbits (*Sylvilagus aquaticus*, SR; $n = 60$) and cottontails (*S. floridanus*, CT; $n = 21$) in bottomland hardwood forests in the Cypress Creek National Wildlife Refuge, southern Illinois, 15 May – 15 Aug 2012.

	Canopy	Herbaceous			Basal Area	Visual
	Closure (%)	Cover (%)	Shrubs (%)	Saplings (no.)	(m ² /ha)	Obstruction
CA						
SR	74.0 $\pm$ 22.0	30.0 $\pm$ 17.0	7.0 $\pm$ 9.0	2.69 $\pm$ 2.78	14.43 $\pm$ 5.81	14.48 $\pm$ 17.48
CT	46.0 $\pm$ 33.0	47.0 $\pm$ 22.0	11.0 $\pm$ 11.0	2.32 $\pm$ 2.66	8.33 $\pm$ 4.94	20.57 $\pm$ 15.36
HR						
SR	72.0 $\pm$ 21.0	31.0 $\pm$ 15.0	5.0 $\pm$ 5.0	2.47 $\pm$ 1.52	14.17 $\pm$ 4.97	11.87 $\pm$ 12.84
CT	46.0 $\pm$ 25.0	47.0 $\pm$ 22.0	8.0 $\pm$ 7.0	2.38 $\pm$ 2.36	9.18 $\pm$ 4.90	11.64 $\pm$ 3.12

Table 5. Mean $\pm$ SD of log-ratios of relative macrohabitat use within 50% core areas and 95% home ranges for swamp rabbits (*Sylvilagus aquaticus*, SR; $n = 60$) and cottontails (*S. floridanus*, CT; $n = 21$) monitored in bottomland hardwood forests in the Cypress Creek National Wildlife Refuge, southern Illinois, 2009–2013. Log-ratios were calculated as the proportion of land cover relative to the proportion of agricultural cover within areas of use.

	<i>Log</i> (EBLH/Ag)	<i>Log</i> (MBLH/Ag)	<i>Log</i> (Upland/Ag)
Core Area			
SR	3.48 $\pm$ 2.28	1.94 $\pm$ 2.27	1.29 $\pm$ 2.75
CT	0.78 $\pm$ 4.42	-1.22 $\pm$ 3.44	2.06 $\pm$ 3.93
Home Range			
SR	2.85 $\pm$ 2.59	1.89 $\pm$ 2.76	0.58 $\pm$ 4.48
CT	0.64 $\pm$ 3.87	-0.35 $\pm$ 4.23	0.48 $\pm$ 4.06

Fig. 1. Land cover and locations of 7 study sites along the Cache River and Cypress Creek within the Cypress Creek National Wildlife Refuge in southern Illinois, USA. Sites were monitored for swamp rabbit (*Sylvilagus aquaticus*) and eastern cottontail (*S. floridanus*) survival, 2009–2013.

Fig. 2. Seasonal Kaplan-Meier survival curves and standard errors for radiocollared swamp rabbits (*Sylvilagus aquaticus*, SR; $n = 129$) and eastern cottontails (*S. floridanus*, CT; $n = 72$) monitored in bottomland hardwood forests in southern Illinois, USA, 2009–2013. Survival curves spanning the non-growing season (left) and growing season (right) are shown.

Fig. 3. Boxplots for distance to nearest permanent water course (River), agricultural field (Ag), and mature bottomland hardwood stand (MBLH) for swamp rabbits (*Sylvilagus aquaticus*, SR; $n = 60$) and cottontails (*S. floridanus*, CT; $n = 21$) monitored in bottomland hardwood forests in southern Illinois, USA, 2009–2013. Boxplots display the minimum, first quartile, median (solid line), third quartile, and maximum values of distance from the center of 50% core areas to the nearest patch of each cover type.

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368x476mm (300 x 300 DPI)

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82x58mm (300 x 300 DPI)

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