Occupancy, detection, and habitat associations of sympatric lagomorphs in early-successional bottomland forests

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The status of early-successional habitats and wildlife species associated with them recently has become a concern in the eastern United States. Although federal farm programs have the potential to create early-successional habitats for wildlife, relatively few studies have assessed wildlife response to these land use changes. During 2006–2007 we studied habitat factors associated with occupancy and detection of 2 species of lagomorphs, swamp rabbit (Sylvilagus aquaticus) and eastern cottontail (Sylvilagus floridanus), in agricultural lands recently afforested via federal farm programs in southern Illinois. Lagomorphs were live captured, and habitat variables were measured at 27 bottomland sites. Detection probabilities of eastern cottontails and swamp rabbits were 0.44 (SE = 0.05) and 0.12 (SE = 0.03), respectively. Canopy closure (w, (i) > 0.94) had the most influence on detection probability for both eastern cottontails and swamp rabbits. Detection probability decreased with increasing canopy closure for eastern cottontails but increased with increasing canopy closure for swamp rabbits. Eastern cottontails and swamp rabbits were estimated to occupy 80% and 71% of sites, respectively. Little support was found for habitat variables influencing site occupancy by eastern cottontails. Distance to a semipermanently flooded or intermittently exposed wetland had the most influence (w, (i) = 0.54) on the probability of site occupancy by swamp rabbits. Our study provides novel information regarding use of early-successional habitats by eastern cottontails and swamp rabbits and unique insight into how habitat structure and landscape configuration affect these 2 lagomorphs.

Key words: detection, early-successional habitat, eastern cottontail, federal farm programs, occupancy, swamp rabbit, Sylvilagus aquaticus, Sylvilagus floridanus

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Because numerous wildlife species depend on early-successional habitats for all or part of their life requirements (Litvaitis 2001; Lorimer 2001), the status of early-successional habitats and wildlife species associated with them recently has become a concern in the eastern United States (Askins et al. 1990; Droege 1998; Trani et al. 2001). Because of habitat loss, many early-successional wildlife species have become extinct, endangered, threatened, or categorized as species of concern (Dessecker and McAuley 2001; Hunter et al. 2001; Litvaitis 2001). Wildfires and other natural disturbances maintained early-successional forests in presettlement times (Lorimer 2001). However, in modern times, fire suppression, selective harvesting, and cessation of agricultural abandonment have contributed to the decline of these habitats (Trani et al. 2001).

Cottontails (Sylvilagus spp.) are likely the most widespread group of early-successional obligate mammals in the eastern United States (Litvaitis 2001). Lagomorphs are important as prey, and changes in their abundance can influence other trophic levels (Boutin et al. 1995; Wagner 1981). For example, declines of New England cottontails (S. transitionalis) in the Northeast have elicited functional and numeric responses in bobcats (Lynx rufus—Litvaitis 1993). Without the dense cover provided by early-successional habitats, cottontails are vulnerable to predation (Brown and Litvaitis 1995). Therefore, management of cottontails has focused on creating early-successional habitats primarily through even-aged timber management (Litvaitis 2001).

Two lagomorph species occur sympatrically in much of the southeastern United States, eastern cottontails (S. floridanus)

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and swamp rabbits (S. aquaticus). Eastern cottontails are among the most studied lagomorphs in North America, and swamp rabbits are the least studied (Allen 1985; Zollner et al. 2000b). Both species require the dense understory vegetation provided by early-successional cover types as an important component of their habitat (Allen 1985; Chapman and Feldhamer 1981; Chapman et al. 1980). However, eastern cottontails are largely habitat generalists, possessing a much wider distribution (Chapman et al. 1980, 1982), whereas swamp rabbits are considered habitat specialists, occurring primarily in forested wetlands and wetland-associated habitats in the southeastern United States (Allen 1985; Chapman and Feldhamer 1981).

As with other early-successional species, many lagomorph species have declined throughout their range. Eastern cottontail numbers decreased ≥70% throughout Illinois between 1956 and 1978, with declines as much as 90% in the most intensively farmed regions of the state (Mankin and Warner 1999a). This precipitous loss in cottontail numbers in Illinois has been attributed to increased intensity of row-crop agriculture after 1945 (Edwards et al. 1981). Swamp rabbits also have declined throughout much of their range due to the loss of forested wetlands (Dickson 2001). In southern Illinois, the northern extent of the range of the species, swamp rabbits are found clustered in patches of suitable habitat along the Cache, Mississippi, and Ohio rivers (Barbour et al. 2001; Kjolhaug et al. 1987; Scharine et al. 2009). The patchy nature of these remaining habitats increases the risk of local extirpations due to habitat loss and stochastic events (Barbour et al. 2001; Woolf and Barbour 2002). In nearby southwestern Indiana Swamp rabbits exhibited a classic metapopulation structure at equilibrium, but management and conservation of remaining patches of bottomland habitat were deemed crucial for continued persistence of the metapopulation (Roy Nielsen et al. 2008).

Approximately 80% of pre-European bottomland hardwood forest (BLH) in the Lower Mississippi Alluvial Valley has been lost within the last century, and many remaining forests exist as smaller and more fragmented patches (Creaseman et al. 1992, Twedt and Loesch 1999). Bottomland restoration efforts in the Lower Mississippi Alluvial Valley have been underway since the early 1990s, with a goal of restoring approximately 800,000 ha of BLH (Haynes 2004). Restorations occur primarily on private lands enrolled in federal farm programs (e.g., Wetlands Reserve Program—Kruse and Groninger 2005; Twedt et al. 2010; United States Department of Agriculture Natural Resources Conservation Service 2004). Afforested lands typically have been in agriculture for the past several decades and can differ considerably in soil conditions, vegetative communities, drainage, and hydrology compared to sites lacking this history (Groninger 2005). Despite these challenges, restoration of BLH has benefited Neotropical migratory songbirds, waterfowl, and other birds in the Lower Mississippi Alluvial Valley (Hoover 2009; King et al. 2006; Twedt et al. 2010). However, composition of vegetative communities and landscape configuration can influence use by certain species (Twedt et al. 2010).

As has been demonstrated for other wildlife species (King et al. 2006), federal farm programs and other management strategies that provide early-successional woody cover could provide suitable habitat for lagomorphs (Litvaitis 2001). However, joint use of these lands by cottontails and swamp rabbits has not been documented. Eastern cottontails commonly use grassland cover types but also use early-successional woody areas as resting sites and for thermal cover during winter (Althoff et al. 1997; Bond et al. 2002; Mankin and Warner 1999b; Medve 1987). Swamp rabbits have been observed using early-successional habitat in the form of canopy gaps within BLH (Zollner et al. 2000b). Relative abundance of swamp rabbits increased with density of tree stumps and stem density, which are variables consistent with early-successional habitats created via stochastic events in mature BLH (Scharine et al. 2009). Given documented habitat associations, patches of young BLH might benefit swamp rabbits by providing canopy gaps on a large scale. However, swamp rabbits are reportedly restricted to patches ≤ 2 km from a permanent water source (Terrel 1972), and consequently, use also might be influenced by landscape configuration.

A quantitative assessment of the relationship between habitat and species occupancy and detection (MacKenzie 2006; MacKenzie et al. 2002, 2006) is important for understanding how early-successional bottomlands might benefit lagomorphs. Occupancy modeling is especially useful when studying rare or cryptic species such as the swamp rabbit, for which detection probabilities are inherently low (MacKenzie et al. 2005; Roy Nielsen et al. 2008). Our goal was to determine the extent to which swamp rabbits and eastern cottontails jointly use early-successional bottomlands and assess the influence of habitat and landscape characteristics on habitat use. We modeled detection and occupancy of eastern cottontails and swamp rabbits in recently afforested bottomlands within the Cache River Watershed in southern Illinois. We predicted that patch use by cottontails would be higher given their ability to use multiple habitat types. Swamp rabbits are more restricted in their habitat use, and we expected patch occupancy for this species to be influenced by both patch and landscape factors such as distance to water, distance to mature BLH, and patch shape. We also examined the influence of several measures of cover on patch occupancy and expected occupancy of both species to be influenced positively by cover. Early-successional bottomlands have the potential to provide habitat otherwise lost throughout much of southern Illinois. An understanding of the structure of habitats used by swamp rabbits and eastern cottontails is necessary to understand how these species coexist in Illinois and elsewhere.

**Materials and Methods**

**Study area.—** We assessed occupancy and detection of swamp rabbits and eastern cottontails in early-successional habitats at 27 bottomland sites in southern Illinois. All sites were located within a conservative dispersal distance for...
swamp rabbits (<2 km—Terrel 1972) from BLH patches that were occupied historically by swamp rabbits (circa 1890–1982—Porath 1997). BLH sites were identified from research conducted over the past 20 years occurring primarily along the Cache, Big Muddy, Ohio, and Mississippi rivers in southern Illinois (Barbour et al. 2001; Kjolhaug et al. 1987; Scharine et al. 2009; Woolf and Barbour 2002). All early-successional study sites were retired agricultural lands that recently (i.e., within 15 years) were afforested as part of federal farm programs or otherwise planted <15 years ago along the Cache River (e.g., afforestations by the United States Fish and Wildlife Service). Sites ranged from 1.6 to 74.6 ha in size. Dominant overstory species were swamp white oak (Quercus bicolor), pin oak (Q. palustris), red oak (Q. rubra), bald cypress (Taxodium distichum), sweetgum (Liquidambar styr-aciflua), and American sycamore (Platanus occidentalis). Understory species present included Allegheny blackberry (Rubus allegheniensis), poison ivy (Toxicodendron radicans), broom sedge (Andropogon virginicus), goldenrod (Solidago spp.), and various sedges (Carex spp. and Cyperus spp.).

The climate in southern Illinois was characteristic of the continental climate type with extreme heat in summer and cool winters (Voigt and Mohlenbrock 1964). The average annual temperature in the region was 14°C, and annual precipitation was 112 cm. The length of the growing season ranged from 185 to 200 days, with the last killing frost occurring around 10 April and the first killing frost around 24 October (Voigt and Mohlenbrock 1964).

Capture and handling.—Between 15 December 2006 and 31 March 2007 we used Tomahawk collapsible live traps (model 205, 23 × 23 × 66 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin—Kjolhaug and Woolf 1988; Watland et al. 2007) to capture swamp rabbits and eastern cottontails at the 27 sites. Depending on site area, we placed 10–20 traps at each site (trap density = 0.3–6 traps/ha) and checked them daily for 14 days. Traps were not moved during each 14-day interval. We covered traps with burlap and brush to provide greater security for captured rabbits, and traps were baited with a quartered apple (Kjolhaug and Woolf 1988; Watland et al. 2007). Animals were captured and handled in accordance with guidelines of the American Society of Mammalogists (Gannon et al. 2007), and methods were approved by the Institutional Animal Care and Use Committee at Southern Illinois University Carbondale (protocol 06-035).

Microhabitat variables.—During May–August 2006 and 2007 we measured 8 microhabitat variables at each site (Porath 1997). We measured percent canopy closure, percent shrub cover, percent ground coverage, visual obstruction, stem density, number of trees ≥ 2 m in height and ≥ 10 cm diameter at breast height (DBH), number of trees ≥ 2 m in height and < 10 cm DBH, and the presence–absence of beaver activity. Microhabitat data were collected in 0.02-ha (7.98-m-radius) circular plots arranged in a uniform grid on the site. The number of plots (10–40 plots/site) and distance between them were a function of the size and the shape of the patch; plot density was 0.5–6.0 plots/ha. The mean value of each measurement was calculated for each site and used in the analysis. We also estimated the age of the stand based on management history provided by the Natural Resource Conservation Service, the United States Fish and Wildlife Service, or private landowners.

Macrohabitat variables.—We used FRAGSTATS 3.3 (McGarigal et al. 2002) to quantify landscape-level metrics (i.e., those that involve aspects of all land-cover types at each site) for the 27 early-successional sites using digitized boundaries (polygons) of each site as a base layer. Metrics calculated included those that provide a measure of spatial configuration and composition of the landscape. These included the total area of the landscape, patch density, landscape shape index, mean patch area distribution, mean perimeter-to-area ratio, percentage of like adjacencies, mean patch shape index, mean related circumscribing circle distribution, mean fractal dimension index distribution, mean contiguity index, mean core area distribution, the disjunct core area density, the aggregation index, and the effective mesh size. Because each site was considered the same cover type, we did not calculate class-level metrics for early-successional cover, as in other studies considering multiple cover types (Kolowski and Nielsen 2008; McDonald et al. 2008; Nielsen and Woolf 2002). We used a geographic information system to calculate the edge-to-edge distance from each study site to the closest BLH patch within size categories of ≥100 ha and 20–100 ha. We also used digitized maps of wetlands in southern Illinois obtained from the United States Fish and Wildlife Service National Wetland Inventory (Cowardin et al. 1979) to measure the distance from each site to the closest wetland that was permanently flooded; at minimum, semipermanently flooded; or at minimum, intermittently exposed. According to the classification of nontidal water regime modifiers by Cowardin et al. (1979), an intermittently exposed wetland is one where surface water is present yearlong except in years of extreme drought, and a semipermanently flooded wetland is one where surface water is present throughout the growing season during most years. When surface water is absent, the water table is usually at or very close to the surface. All geographic information system operations were conducted using ArcGIS version 9.2 (Environmental Systems Research Institute 2004).

Habitat variable reduction.—We combined the macrohabitat data with the microhabitat data and used standard variable reduction techniques (Hosmer and Lemeshow 2000; Nielsen et al. 2003; Rohm et al. 2007; Scharine et al. 2009) to reduce the initial set of variables for further analyses. We did this by deleting variables not well represented at each site, transforming nonnormally distributed variables and removing variables that were unable to be transformed, deleting all scale-dependent variables, and grouping all correlated variables in a cluster analysis. First, we removed variables represented in <40% of habitat patches. We then tested all variables for normality and log-transformed nonnormal variables to improve normality (Shapiro–Wilk > 0.05—Shapiro and Wilk 1965). Variables unable to be transformed were deleted. To remove variables
dependent on the area (i.e., scale) of the site (McGarigal et al. 2002), we regressed each variable against site area using linear regression. Variables with \( r^2 \geq 0.12 \) were considered scale-dependent and removed from the data set; this represented a natural break in the distribution of the \( r^2 \) values among variables. Remaining variables were entered into a cluster analysis (VARCLUS, SAS; SAS Institute Inc., Cary, North Carolina) with an eigenvalue cutoff of 0.7 for cluster separation. The most representative variable from each cluster was retained for further analyses (Table 1).

**Modeling occupancy and detection probabilities.**—Encounter histories from study sites were used to estimate detection probabilities (\( \rho = \) probability of detecting a species during a visit given that the species is present) and occupancy probabilities (\( \psi = \) the probability that a species occupies a site) for both eastern cottontails and swamp rabbits separately using program PRESENCE 2.0 (Proteus Wildlife Research Consultants, Dunedin, New Zealand—MacKenzie et al. 2002). We used trapping data from each site to build a history of encounter occasions (i.e., repeated surveys) based on overall detection or nondetection (1 or 0, respectively) of each species for each site visit.

We examined the influence of habitat covariates for both species separately by modeling detection and occupancy probabilities as logit functions of habitat measurements. We 1st tested the global model from each candidate set of models for lack of fit using the goodness-of-fit test of MacKenzie and Bailey (2004) in PRESENCE 2.0. After confirming that the global model adequately fit the data, we constructed 15 a priori models holding occupancy constant (\( \psi(.) \)), and allowing detection to be a function of covariates, to determine the effect of habitat variables on detection for each species (Gooch et al. 2006; Jackson et al. 2006; MacKenzie 2006). Combinations of variables for a priori models were determined based on considerations regarding lagomorph biology relative to landscape conditions. All models in each species-specific candidate set then were ranked according to Akaike’s information criterion corrected for small sample size (AICc). Those habitat variables appearing in the most-parsimonious detection model then were preserved to model occupancy. To accomplish this, we ran 15 a priori models maintaining detection as a function of the variables occurring in the most-parsimonious detection model and varied occupancy by different combinations of habitat covariates (MacKenzie 2006). This approach specifically accounts for factors that affect detection when modeling occupancy as a function of covariates (MacKenzie 2006). Models were ranked by AICc, and model weights were calculated (Burnham and Anderson 2002). Models were considered competitive if \( \Delta \text{AICc} \) was \( \leq 2 \). To better understand the relative influence of a given covariate, model weights were summed for all models in the candidate model set with the given covariate \( (w_\psi(.)—\text{Burnham and Anderson 2002}). \)

### RESULTS

We captured swamp rabbits 34 times and eastern cottontails 209 times during 4,741 trap nights. Capture success was 0.7 individuals/100 trap nights for swamp rabbits and 4.4 individuals/100 trap nights for eastern cottontails. We detected presence of swamp rabbits at 11 (40.7\%) of 27 sites and eastern cottontails at 21 (77.8\%) of 27 sites. Swamp rabbits rarely were detected in \( >1 \) or \( 2 \) of the 14 trapping nights, clearly demonstrating that detection probabilities were \( <1 \). Eastern cottontails were detected in more repeated surveys than were swamp rabbits; however, eastern cottontails never were detected on every repeated survey at an occupied site, demonstrating that detection probabilities also were \( <1 \) for this species.

When we adjusted naïve occupancy estimates for observed detection probabilities, the estimated total percentage of sites occupied (100 \( \times \) \( \bar{\psi}/27 \)) was 80% for eastern cottontails and 71% for swamp rabbits. This corresponds to a 2.5% increase over the naïve occupancy estimate for eastern cottontails and a 73.7% increase over the naïve occupancy estimate for swamp rabbits.

**Detection probability models.**—The average detection probability for eastern cottontails across all sites was 0.44 (SE = 0.05). Detection of eastern cottontails was affected by habitat covariates; 6 models with detection as a function of habitat covariates outperformed the model in which detection was held constant (Table 2). Of the variables considered in the analysis, canopy closure had the most influence on detection \( (w_\psi(.) > 0.99) \), followed by site area \( (w_\psi(i) = 0.37) \), and distance to a permanently flooded wetland \( (w_\psi(i) = 0.19; \text{Table 3}) \). All variables negatively influenced detection for eastern cottontails (Fig. 1). The top detection model in the candidate model set for eastern cottontails \( (\psi(.)\cdot p(\text{Canopy} \text{ + Area})) \) was retained for modeling occupancy.

Detection probabilities for swamp rabbits \( (\rho = 0.12, \text{SE} = 0.03) \) also were influenced by habitat covariates. Eight models with detection as a function of habitat covariates

### TABLE 1. Description of habitat variables retained from cluster analysis and used in analysis of eastern cottontail and swamp rabbit occupancy and detection in recently afforested bottomlands of southern Illinois, 2006–2007.

| Variable          | Description                                        |
|-------------------|----------------------------------------------------|
| Area              | Area of habitat patch (ha)                         |
| VOR               | Visual obstruction (%)                             |
| Canopy            | Canopy closure (%)                                 |
| Dist20            | Distance index to nearest habitat patch > 20 ha and < 100 ha |
| Dist100           | Distance index to nearest habitat patch > 100 ha   |
| Circle            | Mean related circumscribing circle distribution of the landscape |
| Frac              | Mean fractal dimension index of the landscape      |
| Wetland_H         | Distance (m) to permanently flooded wetland, pond, lake, or river |
| Wetland_FG        | Distance (m) to semipermanently flooded or intermittently exposed wetland |
| Wetland_FGH       | Distance (m) to wetland that is at minimum semipermanently flooded |

* A measure of patch elongation.  
* A measure of patch shape complexity.
outperformed the model with detection held constant (Table 2). Of the variables considered in the analysis, both canopy closure ($w_c(i) = 0.94$) and site area ($w_c(i) = 0.92$) had the most influence on detection of swamp rabbits (Table 3). Canopy closure positively influenced detection (Fig. 2A), but site area negatively affected detection (Fig. 2B). The top detection model in the candidate model set for swamp rabbits ($\psi(.) p(\text{Canopy + Area})$) was retained for modeling occupancy.

### Table 2.—Model selection results for competing models of detection ($\rho$) with associated occupancy ($\psi$) estimates and SE for eastern cottontails and swamp rabbits captured during 2006–2007 in recently afforested bottomlands of southern Illinois. Variables are defined in Table 1.

| Model | $\Delta$AIC$_c$ | $w^c$ | $K_d$ | $\psi$ | $\psi$ SE |
|-------|----------------|-------|------|-------|---------|
| Eastern cottontails | | | | | |
| $\psi(.) p(\text{Canopy + Area})$ | 0.00 | 0.370 | 4 | 0.7925 | 0.0819 |
| $\psi(.) p(\text{Canopy})$ | 0.20 | 0.335 | 3 | 0.7904 | 0.0819 |
| $\psi(.) p(\text{Canopy + Wetland_H})$ | 1.38 | 0.186 | 4 | 0.8102 | 0.0869 |
| $\psi(.) p(\text{Canopy + VOR})$ | 2.53 | 0.105 | 4 | 0.7916 | 0.0822 |
| $\psi(.) p(VOR)$ | 10.70 | 0.002 | 3 | 0.7826 | 0.0806 |
| $\psi(.) p(VOR + Area)$ | 10.76 | 0.002 | 4 | 0.7818 | 0.0805 |
| $\psi(.) p(\text{Canopy + Area})$ | 15.48 | 0.000 | 2 | 0.7787 | 0.0801 |
| Swamp rabbits | | | | | |
| $\psi(.) p(\text{Area + Canopy})$ | 0.00 | 0.871 | 4 | 0.694 | 0.156 |
| $\psi(.) p(\text{Canopy})$ | 5.94 | 0.045 | 3 | 0.600 | 0.160 |
| $\psi(.) p(\text{Area + VOR})$ | 7.03 | 0.026 | 4 | 0.525 | 0.121 |
| $\psi(.) p(\text{Canopy + Wetland_FGH})$ | 8.28 | 0.014 | 4 | 0.610 | 0.161 |
| $\psi(.) p(\text{Area})$ | 7.64 | 0.019 | 3 | 0.514 | 0.118 |
| $\psi(.) p(\text{Canopy + VOR})$ | 8.67 | 0.011 | 4 | 0.599 | 0.161 |
| $\psi(.) p(VOR)$ | 10.59 | 0.004 | 3 | 0.448 | 0.107 |
| $\psi(.) p(\text{Dist100})$ | 12.72 | 0.002 | 4 | 0.482 | 0.118 |
| $\psi(.) p(\text{Frac})$ | 11.75 | 0.002 | 2 | 0.432 | 0.101 |
| $\psi(.) p(\text{Circle})$ | 12.63 | 0.002 | 3 | 0.430 | 0.101 |
| $\psi(.) p(\text{Wetland_FG})$ | 14.21 | 0.001 | 3 | 0.432 | 0.101 |
| $\psi(.) p(\text{Wetland_FGH})$ | 14.24 | 0.001 | 3 | 0.433 | 0.102 |
| $\psi(.) p(\text{Wetland_H})$ | 14.27 | 0.001 | 3 | 0.432 | 0.101 |

### Table 3.—Summed Akaike information criterion weights ($w_c(i)$) for all models in the candidate set where each variable occurred when modeling detection for eastern cottontails and swamp rabbits captured during 2006–2007 in recently afforested bottomlands of southern Illinois. Variables are defined in Table 1.

| Variable | Eastern cottontail $w_c(i)$ | Swamp rabbit $w_c(i)$ |
|----------|-----------------------------|-----------------------|
| Canopy   | 0.996                       | 0.941                 |
| Area     | 0.372                       | 0.916                 |
| Wetland_H | 0.186                       | 0.001                 |
| VOR      | 0.108                       | 0.042                 |
| Dist100  | 0.000                       | 0.002                 |
| Constant () | 0.000                      | 0.002                 |
| Circle   | 0.000                       | 0.001                 |
| Frac     | 0.000                       | 0.002                 |
| Wetland_FGH | 0.000                     | 0.015                 |
| Wetland_FG | 0.000                      | 0.001                 |
| Dist20   | 0.000                       | —                     |

### Occupancy models.—As expected, cottontails were present across a larger number of habitat patches, and occupancy was not strongly related to habitat variables. Of the 15 candidate models in which occupancy of eastern cottontails varied as a function of habitat covariates, only 1 model outperformed the constant occupancy model (Table 4). Five models were $< 2 \Delta$AIC$_c$ of the top model, including the constant occupancy model, indicating relatively high model uncertainty and providing a lack of strong support against the constant model. Both measures of patch shape, mean related circumscribing circle distribution ($w_c(i) = 0.276$), and mean fractal dimension index ($w_c(i) = 0.260$) had limited positive influence on occupancy, and distance to a permanently flooded wetland ($w_c(i) = 0.232$) had even less influence on occupancy (Table 5).

As expected, occupancy of patches by swamp rabbits appeared to be influenced by proximity to wetlands, but we could not detect the influence of other landscape characteristics. Because of a low detection probability for swamp rabbits and relatively small number of study sites, we were unable to examine models with occupancy a function of >1 habitat covariate while maintaining the most-parsimonious detection model. Therefore, each model in the candidate model set for occupancy of swamp rabbits contained 1 covariate. The model containing distance to a semipermanently flooded or intermittently exposed wetland was the only model to outperform the constant occupancy model (Table 4). However, the difference between the constant model and the top model was $2.77 \Delta$AIC$_c$. 
units, and the associated $w_i = 0.54$ indicated that of the variables considered, distance to a semipermanently flooded or intermittently exposed wetland had the most influence on occupancy by swamp rabbits (Table 4; Fig. 3).

**DISCUSSION**

Our goal was to determine the extent to which swamp rabbits and eastern cottontails occupy early-successional bottomlands and assess the influence of habitat and landscape characteristics on habitat use. We expected differences in habitat factors influencing occupancy of eastern cottontails versus swamp rabbits in recently afforested bottomlands. Eastern cottontails, the most widely distributed cottontail in North America, are considered habitat generalists that occupy a variety of habitats throughout their range (Chapman et al. 1980, 1982). Swamp rabbits are largely habitat specialists, occurring primarily in BLH in the southeastern United States (Chapman et al. 1982; Zollner et al. 2000b). Both species require dense understory vegetation for cover (Chapman et al. 1980; Terrel 1972; Zollner et al. 2000a), but other habitat attributes that affect occupancy of eastern cottontails and swamp rabbits in young BLH are unknown.

Eastern cottontails appeared to be habitat generalists within recently afforested agricultural lands in southern Illinois. Although 1 model outperformed the constant occupancy model, due to high model uncertainty we found little support for model variables significantly affecting occupancy. We expected some measurement of cover to be included in the top model due to eastern cottontail’s preference for early-successional habitats; however, the variable measuring cover (visual obstruction) was not included in the top model and had little relative influence (based on $w_i(i)$). This is likely because visual obstruction is inherently high within recently afforested sites relative to the surrounding bottomland landscape (i.e., mature forest in BLH and row-crop agriculture surrounding BLH). In this study the mean value of visual obstruction in recently afforested agricultural lands was 24.07 ($SE = 1.18$). However, the mean value of visual obstruction was 14.55 ($SE = 0.86$) in a separate study conducted in potential swamp
rabbit habitat within BLH using the same methodology (Scharine 2008). This is considerably lower than what was measured within the recently afforested sites, so we cannot rule out cover as an important factor influencing occupancy of eastern cottontails.

We also expected cover to be important in swamp rabbit patch occupancy. Canopy gaps within BLH have been identified as an important component of swamp rabbit habitat (Fredrickson 1980; Scharine et al. 2009; Terrel 1972; Zollner et al. 2000b). Gaps in the canopy provide increased cover and food due to increased herbaceous vegetation at ground level (Baccus and Wallace 1997; Fredrickson 1980). Early-successional BLH patches are similar in form and function to large canopy gaps, providing large areas of dense cover and herbaceous vegetation. Contrary to our expectations, little

TABLE 4.—Model selection results for competing models of occupancy (ψ) while maintaining the most-parsimonious detection model (Canopy + Area) for eastern cottontails and swamp rabbits captured during 2006–2007 in recently afforested bottomlands of southern Illinois. Variables are defined in Table 1.

| Model                                      | ΔAICc  | wi   | K   |
|--------------------------------------------|--------|------|-----|
| Eastern cottontails                         |        |      |     |
| ψ(Circle) p(Canopy + Area)                 | 0.00   | 0.149| 5   |
| ψ(.) p(Canopy + Area)                      | 0.01   | 0.149| 4   |
| ψ(Frac) p(Canopy + Area)                   | 0.15   | 0.139| 5   |
| ψ(Wetland_H) p(Canopy + Area)              | 0.70   | 0.105| 5   |
| ψ(Canopy) p(Canopy + Area)                 | 1.69   | 0.064| 5   |
| ψ(Wetland_FGH) p(Canopy + Area)            | 1.87   | 0.059| 5   |
| ψ(Wetland_H + Frac) p(Canopy + Area)       | 2.09   | 0.052| 6   |
| ψ(VOR) p(Canopy + Area)                    | 2.20   | 0.050| 5   |
| ψ(Circle + Wetland_H) p(Canopy + Area)     | 2.31   | 0.047| 6   |
| ψ(Circle + Canopy) p(Canopy + Area)        | 2.34   | 0.046| 6   |
| ψ(Frac + VOR) p(Canopy + Area)             | 2.87   | 0.036| 6   |
| ψ(Wetland_FG) p(Canopy + Area)             | 2.99   | 0.034| 5   |
| ψ(Circle + Frac) p(Canopy + Area)          | 2.99   | 0.033| 6   |
| ψ(Wetland_H + VOR) p(Canopy + Area)        | 3.37   | 0.028| 6   |
| ψ(Dist100) p(Canopy + Area)                | 5.53   | 0.009| 6   |
| Swamp rabbits                               |        |      |     |
| ψ(Wetland_FG) p(Canopy + Area)             | 0.00   | 0.539| 5   |
| ψ(.) p(Canopy + Area)                      | 2.77   | 0.135| 4   |
| ψ(Frac) p(Canopy + Area)                   | 3.99   | 0.073| 5   |
| ψ(Wetland_FGH) p(Canopy + Area)            | 4.07   | 0.070| 5   |
| ψ(VOR) p(Canopy + Area)                    | 4.58   | 0.055| 5   |
| ψ(Canopy) p(Canopy + Area)                 | 5.54   | 0.034| 5   |
| ψ(Area) p(Canopy + Area)                   | 5.59   | 0.033| 5   |
| ψ(Circle) p(Canopy + Area)                 | 5.73   | 0.031| 5   |
| ψ(Wetland_H) p(Canopy + Area)              | 5.75   | 0.030| 5   |

a (.) indicates the parameter was constant.

b Akaike’s information criterion corrected for small sample size.
c Akaike weight ratio.
d Number of parameters estimated.

TABLE 5.—Summed Akaike information criterion weights (wi(i)) for all models in the confidence set where each variable occurred when modeling occupancy for eastern cottontails captured during 2006–2007 in recently afforested agricultural lands of southern Illinois. Variables are defined in Table 1.

| Variable   | wi(i) |
|------------|-------|
| Circle     | 0.276 |
| Frac       | 0.260 |
| Wetland_H  | 0.232 |
| Constant   | 0.149 |
| VOR        | 0.113 |
| Canopy     | 0.111 |
| Wetland_FGH| 0.059 |
| Wetland_FG | 0.034 |
| Dist100    | 0.090 |

FIG. 3.—Probability of occupancy (± SE) as a function of distance to a semipermanently flooded or intermittently exposed wetland for swamp rabbits captured during 2006–2007 in recently afforested agricultural lands of southern Illinois.
evidence was found for canopy closure or visual obstruction influencing the probability of occupancy for swamp rabbits. Similar to the analysis for eastern cottontails, this is likely due to uniformly high values of visual obstruction and low values of canopy closure among these sites relative to the surrounding landscape.

Habitats occupied by swamp rabbits are characterized by frequent flooding (Harris and Gosselink 1990) and are thought to be limited to ≤2 km of a permanent water source (Terrel 1972). We expected distance to water to be an important influence on swamp rabbit patch occupancy, particularly because of their ability to use water when escaping predators (Conaway et al. 1960; Hill 1967; Hunt 1959; Lowe 1958). Of the 3 different measures of distance to water (distance to permanently flooded wetland [Wetland_FG], distance to semipermanently flooded or intermittently exposed wetland [Wetland_FG], and distance to a wetland that is, at minimum, semipermanently flooded [Wetland_FGH]) used to model swamp rabbit occupancy, the model containing Wetland_FG was the most influential in the candidate set.

Although water was present for most of the year in areas of the Wetland_FG classification, it was not permanent. Predicted occupancy rates of swamp rabbits decreased rapidly for sites located >200 m from a wetland with the Wetland_FG classification, declining to 50% occupancy at a distance of approximately 400 m (Fig. 3). Therefore, the farther a recently afforested site is from a wetland with this classification, the lower the probability that swamp rabbits would use it as part of their established range within BLH. This indicates that swamp rabbits might be using these areas as extensions of their established habitats within BLH, rather than as core habitat, or that these wetlands might be located within BLH that already supports swamp rabbit populations. When pursued by a predator, swamp rabbits often will flee to water, using it as escape cover (Conaway et al. 1960; Hill 1967; Hunt 1959; Lowe 1958). Because many of the study sites lacked standing water for most of the growing season, adjacent wetlands with standing water also might be important to swamp rabbits as escape cover. These findings indicate that use of recently afforested agricultural lands by swamp rabbits depends on those sites occurring much closer to open water than the suggestion by Terrel (1972) of ≤2 km for swamp rabbits in BLH.

Detection probabilities of swamp rabbits and eastern cottontails were <1, which underscores the importance of accounting for imperfect detection when modeling factors associated with occupancy. A disparity in regards to detection probabilities would be expected between eastern cottontails and swamp rabbits because low capture success is typical in studies of swamp rabbits (Kjolhaug and Woolf 1988; Terrel 1972; Watland et al. 2007), even when trapping in areas of relatively high density (Woolf and Barbour 2002). For both species, as the size of the patch increased, the detection probability decreased. This result is most likely a consequence of our trapping scheme. Because of the large range in area of our sites (1.6–74.6 ha) and limited resources, we were unable to use a constant trap density among sites. This resulted in higher trap densities at smaller sites, and, thus, higher detection probabilities.

Canopy closure was the most important variable affecting detection of both swamp rabbits and eastern cottontails. The effect was negative for eastern cottontails, but positive for swamp rabbits. However, Smyth et al. (2007) found that capture success for swamp rabbits was higher in areas with lower canopy cover. The reason why canopy closure affected detection probability by livetrapping in our study is unclear, and we interpret these results with caution. Decreased canopy closure results in increased understory vegetation, which could affect detection by hindering the ability of a rabbit to locate a baited trap either by sight or smell. Additionally, rabbits might be more susceptible to aerial predators in areas with less canopy closure, and the 2 species might employ differing strategies to avoid predation (finding cover versus fleeing) that could influence detection. Also, density of a species is often the largest source of heterogeneity in detection probabilities (Bailey et al. 2004; Royle and Nichols 2003). Therefore, it is possible that abundances of the 2 species varied according to canopy closure, which in turn, influenced detection. However, why abundances of eastern cottontails and swamp rabbits appear to be affected differently by canopy closure is unknown because both species likely would prefer areas with more open canopies (Zollner et al. 2000b).

Detection probabilities also could have been influenced by behavioral differences in habitat use. Cottontails use habitat differentially according to sex, season, and reproductive status (Althoff et al. 1997; Bond et al. 2002; Medve 1987). Similarly, swamp rabbits have been reported to select areas with decaying logs as latrine sites and areas of dense ground cover as resting sites, but habitat associations were not detected during foraging (Zollner et al. 2000a). Forage and ground cover are more available in early-successional sites during winter, when our trapping was conducted. It is possible that detection probabilities could have been biased if rabbits were not foraging and, therefore, less likely to be captured. Although it is not within the scope of this paper to draw conclusions as to specific habitat use within early-successional BLH, it is expected that these areas represent only a portion of a rabbit’s home range and that differential habitat use could influence detection probabilities.

Although many studies have documented use of early-successional habitats by eastern cottontails (Chapman et al. 1982; Edwards 1987; Fredrickson 1980; Litvaitis 1993; Terrel 1972), joint use of habitats by swamp rabbits and eastern cottontails is less well understood. Toll et al. (1960) documented some sympathy between the 2 species in Missouri, with swamp rabbits preferring more wooded areas and eastern cottontails preferring areas with more herbaceous vegetation. In Texas Taylor and Lay (1949) reported that swamp rabbits replaced eastern cottontails as succession progressed from mostly herbaceous to predominately woody vegetation. In addition, several authors have noted the importance of early-successional upland habitats as refugia for swamp rabbits (Lowe 1958; Terrel 1972; Zollner et al.
If swamp rabbits are driven periodically to these habitats, competition with eastern cottontails could be unavoidable. In areas where both species use early-successional habitats the influence of competition on patch occupancy remains unknown. Probert and Litvaitis (1996) suggested that patch occupancy of eastern and New England cottontails was influenced by scramble competition rather than direct behavioral dominance.

Species co-occurrence models (MacKenzie et al. 2004) available in program PRESENCE allow researchers to estimate detection and occupancy probabilities for multiple species with imperfect detection within a single modeling framework (MacKenzie et al. 2006). Unfortunately, we were unable to implement this method because of the large number of parameters estimated in this model (as compared to single-species, single-season occupancy models) relative to our sample sizes. Although we were unable to explicitly model co-occurrence, our study is the 1st to document joint use of recently afforested wetlands by swamp rabbits and eastern cottontails and to explain habitat characteristics that might determine occupancy. Both species seem to be responding to the increased cover provided by the early-successional nature of these habitats; however, the distance to a semipermanently flooded or intermittently exposed wetland largely dictates occupancy of recently afforested wetlands by swamp rabbits in southern Illinois.

We provide novel information regarding the use of early-successional bottomlands by eastern cottontails and swamp rabbits and the effects of habitat structure and landscape configuration on these sympatric lagomorphs. BLHs benefit numerous mammal and avian species (Wigley and Roberts 1997), yet the majority of historic BLH exists in agriculture and private ownership. As these forests mature, they become less suitable for swamp rabbits because of increased canopy closure and decreased ground vegetation (Allen 1985; Scharine et al. 2009). Management of these forests, such as thinning to create canopy gaps, can be beneficial by providing open areas for understory vegetation. Furthermore, federal farm programs that create large areas of early-successional BLH have been instrumental in successful bottomland restoration (King et al. 2006). In the Cache River Watershed, these lands provided suitable habitat for both eastern cottontails and swamp rabbits. That we detected eastern cottontails a total of 209 times at 21 of 27 sites attests to the suitability of afforested bottomlands or lands otherwise managed for early-successional habitats for eastern cottontails. Regarding the less abundant swamp rabbit, if restoration efforts continue, suitable habitats will be created and existing populations could be linked at the northern fringe of their range.

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